Dynamics of omnivorous crayfish in freshwater ecosystems

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Dynamics of omnivorous crayfish in freshwater ecosystems

"The crayfish is a small, freshwater, lobster-like creature which in nature inhabits ponds, streams and rivers."(Groves, R.E. 1985).

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Abstract

Crayfish are regarded as keystone species in freshwater ecosystems and often dominate the benthic biomass in lakes and streams. Their omnivorous feeding behaviour makes their role in the food web complex and their function in these systems rather unique. In this thesis I examine the dynamics of crayfish in freshwater ecosystems. I have studied the influence of abiotic and biotic factors on abundance, growth, trophic position, niche width and recruitment of juvenile crayfish, by conducting field studies, an outdoor channel experiment and time-series analysis.

My results show that abundance of crayfish is mostly affected by the biomass of predatory fish, but in the absence of predators, or at low densities, substrate size influenced crayfish abundance. Crayfish abundance also fluctuates from year to year and I found that both climatic and density-dependence factors drive these fluctuations. The best model for both native crayfish and introduced crayfish revealed that the temperature during winter explained most of the observed fluctuations in adult crayfish abundance. I also show that growth rate, trophic position, carbon signature and niche width of crayfish are influenced mostly by the biomass of invertebrates. Especially, a high biomass of large, sedentary and less mobile invertebrate groups placed crayfish at a higher trophic position and increased the niche width of crayfish. Crayfish are regarded cannibalistic and it is generally thought that the larger crayfish consume smaller ones, which may influence the recruitment success. In the outdoor channel experiment I show that cannibalism was more pronounced between juvenile crayfish and that the presence of large adults only influenced juvenile activity. However, the most important factor for survival and growth of juveniles were attributed to habitat complexity. A habitat of high complexity (i.e. high amount of cobbles) increases the shelter availability for the juveniles, and thus increases survival and growth rates of juvenile crayfish.

The main conclusion from my results is that crayfish dynamics, such as abundance, growth, trophic position, niche width and recruitment are affected by specific abiotic and biotic factors in a complex way. The knowledge this thesis has revealed may have implications for conservation and management purposes.

Key words: Omnivorous crayfish, population fluctuation, abundance, trophic position, niche width, growth rate, recruitmant, stable isotopes, RNA:DNA, food availability, freshwater ecosystems

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Dynamics of omnivorous crayfish in freshwater ecosystem

Karin Olsson

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I Olsson, K., Stenroth, P., Nyström, P., Holmqvist, N., McIntosh A.R. and Winterbourn, M.J. 2006. Does natural acidity mediate interactions between introduced brown trout, native fish, crayfish and other invertebrates in West Coast New Zealand streams? *Biological Conservation* 130: 255-267.

II Olsson, K., Granéli, W., Ripa, J. and Nyström, P. Fluctuations in harvest of native and introduced crayfish are driven by temperature and population density in previous years. *Manuscript.*

III Olsson, K., Stenroth, P., Nyström, P. and Granéli, W. Prey biomass influenced niche width of native and invasive crayfish in Swedish streams. *Submitted.*

IV Olsson, K., Nyström, P., Stenroth, P., Nilsson, E., Svensson, M. and Granéli, W. 2008. The influence of food quality and availability on trophic position, carbon signature and growth rate of an omnivorous crayfish. *Canadian Journal of Fisheries and Aquatic Sciences*, in press.

V Olsson, K. and Nyström, P. 2008. Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*). *Freshwater Biology,* in press.

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Dynamics of omnivorous crayfish in freshwater ecosystem

Introduction

Background

There are over 500 crayfish species in the world and they are found on all continents except Antarctica (Ackefors, 2000). In Europe crayfish are popular food and has been of interest to mankind at least since the time of Aristotle (Holdich, 2002). In Europe noble crayfish (*Astacus astacus*) are found in at least 28 countries from France in the west to Russia in the east, and from Italy in the south to Scandinavia in the north (Cukezis, 1988; Holdich, 1999). However, native crayfish are declining all over Europe since the outbreak of crayfish plague in 1860, but lately also due to habitat loss, pollution and introductions of exotic species throughout their distribution area (Lowery and Holdich, 1988, Barbaresi and Gherardi, 2000).

Noble crayfish and signal crayfish (*Pacifastacus leniusculus*) are the two crayfish species found in Swedish freshwaters today. Noble crayfish is regarded as the only native species in Scandinavia (Skurdal et al., 1999) and is today found in most parts of Sweden (Fig. 1). Signal crayfish, which originate from North America, was introduced in Sweden in the 1960s to compensate for the drastic decline of noble crayfish populations in southern Sweden caused by the crayfish plague (Skurdal et al., 1999). It has been stocked into large parts of southern Sweden, and can be found up to Dalälven river system, but a few illegal introductions have also been found further up in the north (Fig. 1). The two species are ecologically similar in many ways, but there are also differences that may influence their abundance and interactions with other trophic levels. They are similar in size, morphology (Fig. 2) and life history, and their life cycles are synchronous (Abrahamsson, 1971; Söderbäck, 1995). Both species are omnivorous feeders, are most active during night and seem to prefer the same type of habitat (Abrahamsson, 1983). The signal crayfish is considered to grow faster, be more aggressive and have denser populations than noble crayfish. This may lead to a stronger impact on the ecosystem by the introduced species than from the native one (Nyström, 2002).

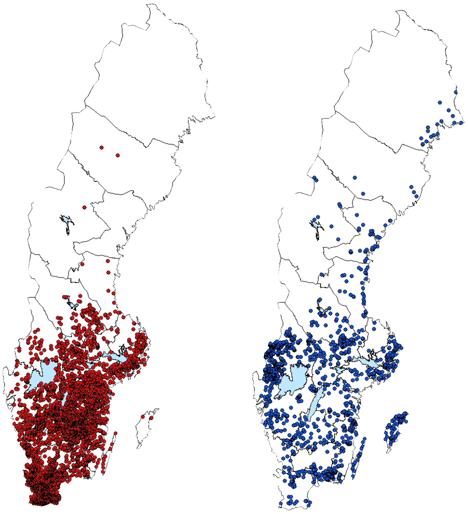

Figure 1. The distribution of signal crayfish (left, red dots) and noble crayfish (rigth, blue dots) in Sweden (data from the Swedish Board of Fisheries Crayfish database, 2004).

Figure 2. Signal crayfish to the left and noble crayfish to the rigth. Illustrations by Linda Nyman.

Crayfish dynamics in freshwater ecosystems

Crayfish are the largest mobile invertebrate in freshwater ecosystems. Crayfish are often regarded as keystone species in these systems where they in many cases dominate the benthic biomass (Abrahamsson, 1966; Mason, 1975; Holdich, 2002). Most crayfish species have a nocturnal activity pattern (i.e. active during night) and they use chemical and mechanical receptors to locate food, predators and conspecifics (Nyström, 2002). Since they are omnivorous feeders they can have an impact on several trophic levels and thus their role in the food web is rather complex and unique in freshwater ecosystems. Due to their omnivorous feeding behaviour crayfish probably also occupy large niches and their niche widths may depend on the habitat they inhabit. Several abiotic and biotic factors influence the dynamics of crayfish populations (Fig. 3). Crayfish have the ability to grow and reproduce in a variety of habitats if certain thresholds are met. For example, a certain amount of calcium is needed for growth and successful reproduction.

Environmental condition of the habitat affects food availability, diet patterns and foraging cost of consumer species (Esteves et al., 2008, and references therein), such as crayfish. According to the Optimal Foraging Theory individuals should choose food with the highest energy content that gives the smallest energetic cost, e.g. in terms of foraging costs, handling time and metabolic costs (MacArthur and Pianka, 1966). It has been suggested that animal food sources (i.e. invertebrates) are the most important food source for crayfish growth (Nyström, 2002). Crayfish have been shown to alter the invertebrate composition in aquatic ecosystems due to selective predation. Large, less mobile benthic invertebrates are often negatively affected by the presence of crayfish (summarised in Nyström, 1999), while small and free swimming invertebrates are less affected by crayfish presence (Abrahamsson, 1966; Parkyn et al., 1997; Perry et al., 1997). Crayfish can also eliminate some species of macrophytes due to intensive grazing or just by their active search for food (Lodge and Hill 1994, Gherardi and Acquistapace 2007). Hence, most crayfish species strongly affect the structure and function of benthic food webs (Nyström, 2002).

Furthermore, competition for food and shelter within and between crayfish species can have a strong influence on the distribution, abundance and production of crayfish populations (Nyström, 2002). High densities of crayfish promote competition which may increase aggressive interactions and also lower the growth of individual crayfish. Intraspecific predation, i.e. cannibalism, can be important for the regulation and structuring of animal populations (Polis, 1981). Crayfish are in general regarded as cannibalistic and are therefore potentially able to influence their own population dynamics. It is commonly assumed that large crayfish consume smaller ones and that especially large males can suppress the recruitment of juveniles by consuming and/or destroying all eggs and juveniles produced by the population (Polis, 1981; Dercole and Rinaldi, 2002). There are, however, few studies from nature supporting this cannibalistic behaviour and it might not be as common as previously thought.

Crayfish are also important as prey for other predatory species, such as fish, wading birds and some mammals (especially mink). The introduction of potential predators on crayfish can have significant effects on the crayfish populations inhabiting streams and lakes. For example, experimental studies have shown that predatory fish can severely reduce the abundance of juvenile crayfish (Dahl, 1998) and it has been shown that juveniles respond to predatory fish by seeking shelter and by reducing their activity level (Mather and Stein, 1993; Garvey et al., 1994; Lodge and Hill, 1994). This in turn may decrease the growth of the juveniles due to lost feeding opportunities (Stein and Magnusson, 1976; Resetarits, 1991; Hill and Lodge, 1999).

Several species of crayfish are today threatened or have already become extinct (Nyström, 2002). Taylor (2002) estimate that around one-third to one-half of the world's crayfish species are vulnerable to severe population declines or extinction. At the same time there has been and still are numerous crayfish introductions throughout the world (Hobbs et al., 1989), most often negatively affecting native species and the invaded community (Holdish, 1999). This has led to a decline of some species while others have increased and become more abundant (Nyström, 2002). These changes may have affected energy flow, species composition and diversity of aquatic food webs (Nyström, 2002). To prevent further extinctions of crayfish and negative effects on native biota it is crucial to build up a detailed knowledge of crayfish ecology and population biology (Nyström, 2002). Further, since crayfish play an important role in freshwater ecosystems, it is important to clarify their ecological role to understand the energy flow in lakes and streams (Whitledge and Rabeni, 1997).

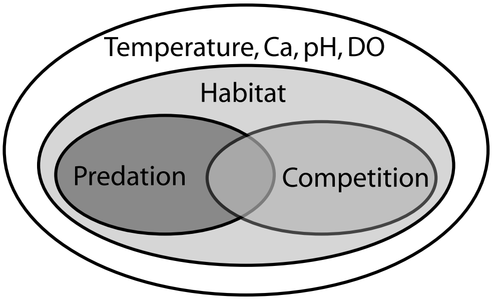

Figure 3. Several abiotic and biotic factors interact to influence crayfish dynamics, such as species composition, population size, and productivity. After Lodge and Hill, 1994. Ca is calcium and DO is dissolved oxygen.

The objectives of the thesis

The aim of this thesis is to investigate which factors that affect the dynamics of crayfish populations. Habitat structure may both directly and indirectly affect crayfish population dynamics in lakes and streams. It can for example provide adequate amounts of food and shelter, which at the same time can minimise the risk of predation and cannibalism. Temperature is important for several stages in the crayfish life-cycle and is known to influence for example growth and reproduction. Crayfish has an omnivorous feeding habit, but what type of food that is most important for growth and determines trophic position and niche use by crayfish is still poorly known. Hence, increased knowledge of factors affecting crayfish abundance, niche width, trophic position and growth rate are important in order to understand crayfish dynamics in freshwater ecosystems. Within this thesis I address the following issues:

- Which factors are most important for determining crayfish abundance and size distribution in freshwater ecosystems? (Paper I and II)

- What factors affect niche width in crayfish and do native and introduced crayfish species differ in trophic position and niche width? (Paper III)

- Does the availability and quality of food affect trophic position and growth rate of crayfish? (Paper IV)

- What factors affect the survival and growth of juvenile crayfish? (Paper V)

Methods

Field studies

In addition to data from two previously conducted field surveys, two extensive field surveys were conducted. The first was conducted on the West Coast, South island, New Zealand (see Fig. 1 in paper I). On the West Coast, 18 streams were surveyed in order to investigate the influence of introduced brown trout (*Salmo trutta*) on abundance and size distribution of the native crayfish Koura (*Paranephrops planifrons)*.

The second field survey was conducted in 13 streams with the native noble crayfish (*Astacus astacus*) in the southern parts of Sweden. By using data from this survey and a previously conducted survey in 10 streams with the introduced signal crayfish (*Pacifastacus leniusculus*) I investigated if there were any differences in abundance, size distribution, trophic position and niche width between the native and the introduced crayfish species (Paper III). From the 13 streams with noble crayfish I also used the data to investigate if availability and quality of food influence trophic position and growth rate of crayfish (Paper IV). At each survey site crayfish abundance and size distribution were estimated with baited traps and predatory fish were caught by electrofishing. In addition, five Surber samples were taken at each site to estimate the invertebrate biomass and species composition, water samples were taken for chemical analyses and in addition other factors such as velocity, substrate size, canopy cover and macrophytic cover were also estimated (for more detailed explanations see Paper I and IV).

In order to investigate why crayfish populations fluctuate from year to year and if there are differences between the native noble crayfish and the introduced signal crayfish I used yearly catch data from a lake in southern Sweden. The lake was inhabited by noble crayfish from 1946 to 1974 and then by signal crayfish from 1985 until today. I also used air temperature data from Swedish meteorological and hydrological institution (SMHI) as parameters to investigate if temperature influences the catches from year to year (time-series analysis) (Paper II).

Outdoor channel experiment

Previous field studies of signal crayfish show that habitat complexity is important for the abundance of crayfish when the abundance of predatory fish is low. In an outdoor channel experiment I therefore investigated the influence of habitat complexity and the presence of adult crayfish males on survival and growth of juvenile signal crayfish. In a flow through system with 16 channels (Fig. 4), juvenile signal crayfish were exposed to high or low habitat complexity and presence or absence of adult crayfish males (four treatments, see figure 1 in paper V). At the end of the experiment, activity during day and night were observed, surviving juveniles counted and checked for moulting stage, cheliped injuries and the length was

Figure 4. The outdoor channel experiment set-up. To the rigth my supervisor Per Nyström and to the left Patrik Stenroth.

measured. This enabled investigation of the importance of habitat complexity and cannibalism for the recruitment of juvenile crayfish.

Stable isotope analysis

Stable isotope ratios give information of assimilated food sources over long time periods. Hence, they are used to identify important food sources for consumers (e.g. crayfish, Nyström, 2002). In food web studies, the most commonly used elements for stable isotope analysis are carbon and nitrogen (Whitledge and Rabeni, 1997). The carbon isotopic ratio ($^{13}C/^{12}C$) reflects assimilated food items and the isotopic enrichment from one trophic level to the next is often insignificant (Post, 2002). The nitrogen isotopic ratio ($^{15}N/^{14}/N$) on the other hand typically increases on average 3.4‰ with each trophic transfer (Post, 2002). For example, if predatory invertebrates are an important energy source for crayfish, their carbon isotopic ratios should be similar. However, crayfish should have a nitrogen isotopic ratio about 3.4‰ above that of predatory invertebrates. Stable isotope analysis was used in Paper III, IV and V. For a more detailed description see Paper IV.

RNA/DNA analysis

Analysis of RNA/DNA ratios in muscle tissues can give information about growth rates and has been successfully used on marine organisms (e.g. lobsters, Parslow-Williams et al., 2001). The RNA content of a cell is positively related to the amount of protein syntheses in the cell and thus to growth rate, while DNA content is constant (Clemmesen, 1994). The RNA/DNA ratio therefore enables comparison of relative growth rates among populations. Buckley (1984) consider RNA/DNA ratio to be a instantaneous measure of growth rate since it responds rather quickly to changes in feeding conditions and growth after 1-3 days. Analyses of RNA/DNA ratios were made according to the protocol for zooplankton of Vrede et al. (2002) with some modifications (for more detailed description see Paper IV). RNA/DNA analysis was used in Paper IV.

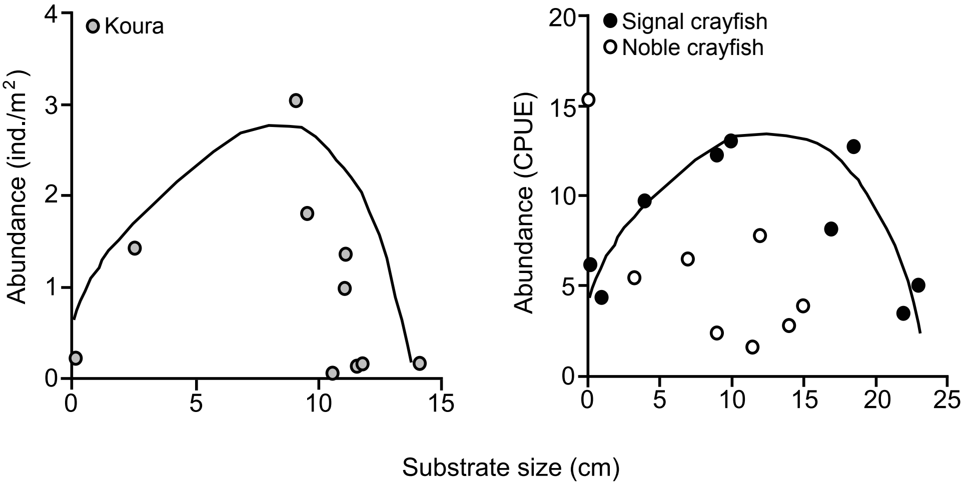

Figure 5. In streams without trout the highest abundance of the native New Zealand crayfish, Koura (left,grey dots and black trend line) was found at a substrate size around 10 cm, which is the same as for introduced signal crayfish (rigth, black dots and black trend line) in Sweden. However, the abundance of native noble crayfish is not affected by substrate size (rigth, white dots).

Summary of papers

Abundance and size distribution

Geographical and environmental factors may affect population density, growth and life history of different species but also different populations within the same species (Momot et al., 1978). Physico-chemical (i.e. abiotic) factors set the limits for crayfish populations based on their physiological adaptations (Lodge and Hill, 1994). Even if there are differences between crayfish species certain requirements have to be met for all crayfish species to grow, survive and reproduce. However, which factors that determines crayfish species abundance, size distribution and recruitment in streams and lakes is still not fully understood.

Abundance
Several abiotic and biotic factors have been found to affect abundance patterns in crayfish populations (Mather and Stein, 1993). Among others, water temperature, water quality, habitat structure, physical disturbance, diseases, competition and predation can influence the abundance of crayfish in freshwater ecosystems (Lodge and Hill, 1994). For example, acidity can affect crayfish abundance and growth and pH has been found to explain more than half of the variation in crayfish abundance in streams (France, 1993; Lodge and Hill, 1994). Seiler and Turner (2004) showed that acidification had a negative impact on the individual growth of crayfish but not at population level where it had a positive effect. In the New Zealand study (Paper I) the native crayfish Koura could live and reproduce in streams with a pH as low as 4.1. These acidic streams acted as a refuge for the threatened crayfish species. The decline of crayfish in more neutral streams in New Zealand is to some extent subjected to the introduction of brown trout. The biomass of predatory fish (predominantly trout) is also regulating the abundance of noble- and signal crayfish

in Swedish streams (Nyström et al., 2006; unpublished data).

Substrate size has also been found to be an important factor determining crayfish abundance (Blake and Hart, 1993; Savolainen et al., 2003). I show that this was the case for both the New Zealand crayfish Koura and the introduced signal crayfish in Sweden when the biomass of predatory fish was low. Both crayfish species had their highest abundance in streams that was dominated by cobbles with a mean size of 9-11 cm (Fig. 5). However, the abundance of native noble crayfish in Swedish streams was not related to substrate size, when the abundance of predatory fish was low. The highest abundance was found in streams that were dominated by very small substrate grain size (Fig. 5). Flinders and Magoulick (2003) argue that some species of crayfish that live in temporary habitats and/or have the ability to burrow into the streambed may not be equally affected by substrate composition as non-burrowing species. Noble crayfish in streams dominated by small substrate grain sizes did burrow into the streambed (Fig. 6), and one could observe crayfish guarding its burrow against intruding crayfish. Habitat complexity (i.e. amount of cobbles) was also very important for the survival and growth of juvenile signal crayfish (Paper V). Hence, substrate grain size and habitat complexity seem to influence some crayfish species more than others. Further it may affect the recruitment of young and, thus, influence the abundance of crayfish.

Abundance fluctuations in crayfish populations

Temperature regulates several behaviours in crayfish, such as moulting, growth, survival of juveniles, reproduction, egg development and overall activity (Mason, 1979; Westin and Gydemo, 1986; Hessen et al., 1987; McMahon, 2002; Parkyn and Collier, 2002; Reynolds, 2002, and references therein). For example, noble crayfish need at least 3 months of temperatures in excess of 15°C during summer for successful reproduction (Abrahamsson, 1966, 1971). Abrahamsson (1966) also observed that a cold summer, below 15°C reduced growth in noble crayfish compared to normal summer temperatures. At normal temperatures the weight increase was about 31% higher

Figure 6. This type of borrows were inhabited by individuals of noble crayfish, guarding it against intruding crayfish.

than in the cold years. High temperatures seem to be important for high growth rates (Kristiansen and Hessen, 1992), but too high temperatures can also be stressful and lead to moulting failures. In temperate regions the growth period is limited to the warmer summer months of the year and the decrease in temperature and light in autumn triggers the start of the mating season (Jonsson and Edsman, 1998).

In paper II, I show that climatic as well as density dependent factors drive the observed fluctuations in abundance (measured as catch per unit effort, CPUE) of large adult crayfish (Fig. 7) in Lake Bunn, a southern Swedish lake. However, the optimum temperature for crayfish species are highly variable and can differ with several degrees between species (Nyström, 2002; Whitledge and Rabeni, 2003; Paglianti and Gherardi 2004). In Lake Bunn the winter temperature explained most of the observed variations in abundance of both the native noble crayfish and the introduced signal crayfish. The winter temperature has increased gradually during the study period and it has also become more common with days above the freezing point. Several years during the last 20 years have had a mean temperature above 0°C (Fig. 8). This will probably affect the duration of ice-cover and ice breakup. Studies have shown that a change in ice-cover and breakup will affect the nutrient status in lakes (Pettersson et al., 2003; Jackson et al., 2007). Further increases in winter temperature might also lead to decreased survival of crayfish due to increased activity and aggressive interactions. However, the winter temperature in Lake Bunn is probably still favourable for crayfish survival and hence has a positive effect on the abundance of large crayfish. To be able to predict how a further climate warming will effect crayfish abundance in freshwater ecosystems more studies are needed. These should explore the influence of winter temperature on the survival of crayfish.

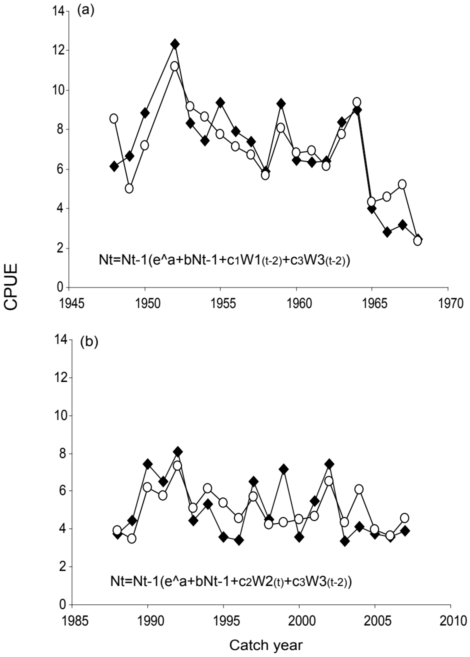

Figure 7. Fit of the observed fluctuations (black diamonds) and the best model (white dots) for a) noble crayfsih and b) signal crayfish during 20 years for each species in Lake Bunn. The form of the best model is shown in the figures, where bNt-1 indicates density dependence since b were smaller than zero for bothe species. W3(t-2) represent the winter temperature with a two year lag, W1(t-2) represent ADD>10°C with a two year lag, and W2(t) represent the temperature during mating season the year before catch.

For noble crayfish annual degree days above 10°C (ADD>10°C), which is the required temperature for crayfish growth, is also an important variable explaining the fluctuations in the abundance of large adults. However, an increase in the number of days exceeding 10°C had a negative effect on the abundance of noble crayfish in Lake Bunn. Verhoef and Austin (1999) observed a decreased survival of crayfish (e.g. *Cherax destructor*) when water temperatures rose above 16°C, due to exceeding thermal capabilities, as well as increased number of

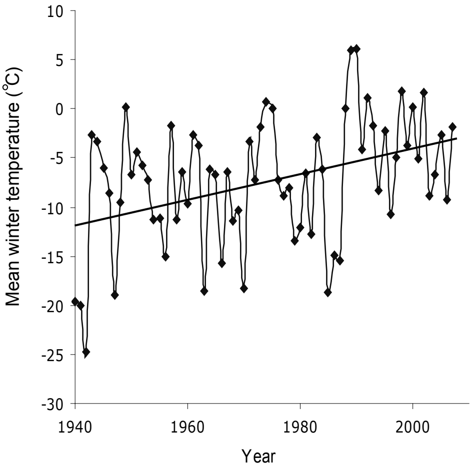

Figure 8. The mean winter temperature from 1946 until today in Lake Bunn and also the freezing point (dotted line) is shown.

aggressive encounters (i.e. cannibalism). Paglianti and Gherardi (2004) also found that growth of crayfish (e.g. *Austropotamobius pallipes* and *Procambarus clarkii*) decreased with increasing temperatures (from 16 to 24ºC). The authors argue that this may be due to increased metabolic consumption exceeding caloric intake, which leave little energy for growth.

For signal crayfish, the temperature during mating season was negatively correlated with abundance of large adult crayfish. A high temperature during early autumn may prolong the growing season and activity period of crayfish and thus influence moulting frequency and mating. This may lead to increased mortality during this period, but also decreased time for building up energy reserves needed to survive through winter (Jonsson and Edsman 1998). These contradicting results, of a positive influence of winter temperature and the negative one for ADD>10ºC for noble crayfish, and the temperature during mating season for signal crayfish, makes it difficult to predict how changes in temperature influence crayfish dynamics in lakes.

The abundance of crayfish one year had an affect on the abundance next year for both species, indicating a density-dependence in the populations. High density in crayfish populations can lead to increased interactions due to higher competition, which will reduce foraging time and lower consumption rates (France, 1985; Guan and Wiles, 1999; Corkum and Cronin, 2004). This in turn may influence the growth rate in crayfish and lead to low inter-moult growth in adults and thus, reduce the abundance of large adult crayfish. Abrahamsson (1966) argues that the slow growth of crayfish in his study pond in southern Sweden was probably due to the population's high density. In my study, a higher percentage of the fluctuation observed for noble crayfish (24.4%) were explained by density dependence than it was for signal crayfish (7.1%). However, these results may not necessarily mean that density dependence is more important in noble crayfish populations. It is likely that the signal crayfish population in Lake Bunn has not yet reached the same abundance as noble crayfish had previously. The higher density of noble crayfish (Fig. 7) can therefore explain the difference in density dependence between the two species found.

There are, however, other factors that might affect the abundance of crayfish that was not included in my model, due to lack of data. The biomass of predatory fish has been shown to affect the abundance of crayfish (Hein et al., 2006; Nyström et al., 2006; Paper I). The crayfish abundance might follow the fluctuations in abundance of predatory fish in lakes. Perch (*Perca fluviatilis*), which is an important predator on crayfish, dominates the fish community in Lake Bunn (Nyström et al., 2006) and 62% of the large perch contained adult crayfish. The perch population could therefore potentially have an influence on the crayfish population abundance. However, Nyström et al. (2006) found a positive correlation between crayfish abundance and the biomass of predatory fish in their study lakes, indicating a minor influence even though crayfish was the most important energy source for large perch. Food availability is also an important factor that was not included in the model. A higher activity of crayfish at higher temperatures, especially during months with low availability of high quality food (i.e. invertebrates) may lead to a decline in crayfish growth and condition. This may be due to the higher energetic costs of feeding on food with low energy content (Whitledge and Rabeni, 2003). Climate change has also been shown to change the macroinvertebrate composition in freshwaters (Daufresne et al., 2007). This might influence the availability of high quality food for crayfish as they have been found to prefer large and less mobile prey (Whitledge and Rabeni, 1997; Nyström et al., 1999; Parkyn et al., 2001).

Winder and Schindler (2004) argue that the effect of warmer temperatures on food web structure and ecosystem functioning might strongly depend on the local adaptation of life-history traits in species. Since, temperature regulates many life-history traits in crayfish, a higher temperature, especially during winter, might have significant effect not only on crayfish abundance but also on the whole freshwater ecosystem. This because of the important role of crayfish, as prey, predator and redistributors of energy, in these systems.

Size distribution

In Paper I, I show that predatory fish did not only influence the abundance of crayfish, they also affected the size distribution of crayfish populations. In New Zealand streams with introduced brown trout present, almost no juvenile crayfish were found and a larger part of the population was above 40 mm in total length (Fig. 9). In streams without brown trout a higher percentage of the crayfish population were 40 mm or smaller compared to streams with brown trout (Fig. 9). This indicates a selective predation on smaller crayfish by brown trout and thus the introduced predator has a size structuring effect on the crayfish population.

Habitat may also influence the size distribution of crayfish populations. A heterogeneous habitat that provides shelter for all size classes will have a broader size distribu-

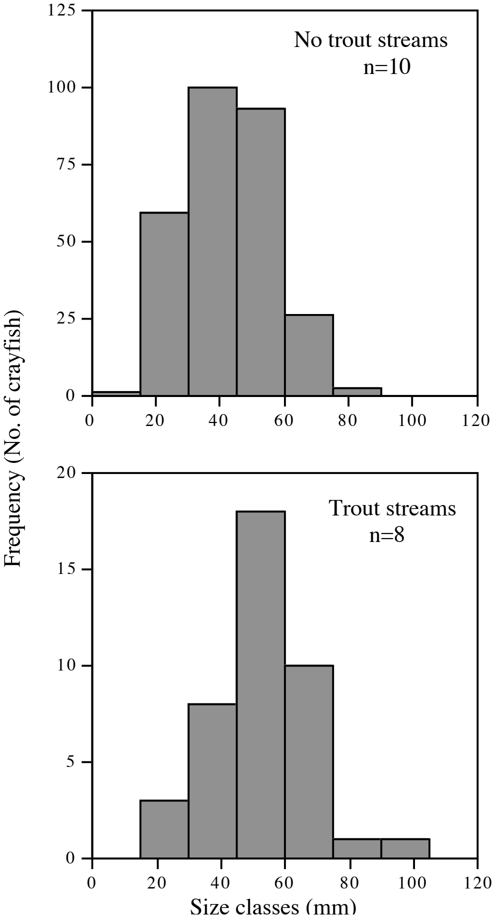

Figure 9. The size distribution of crayfish in streams without (upper) and with (lower) introduced brown trout.

tion within the population than a homogeneous habitat, that only provides shelter for some size classes. Crayfish are very vulnerable to predation and cannibalism during moulting and if there is no available shelter, the risk of being eaten increases. If a habitat can provide large amounts of high quality food this will probably not only effect the trophic position and growth rate in crayfish, but also the size distribution of the population. Large amounts of high quality food will provide enough food for all size classes and decrease the intraspecific competition and will result in crayfish of all sizes in the population. A habitat with less protein rich food available may promote competition between crayfish and smaller individuals will be outcompeted by larger ones. Thus, the size distribution of the population will be more skewed with many large individuals and few small ones. However, the density of crayfish has also been shown to have an influence on the size distribution of crayfish populations. If there is enough food to enhance abundance, competition may in time suppress growth and the population will consist of many similar sized crayfish, so called stunted populations (Svärdson, 1949; Barki and Karplus, 2004). Further, as I showed in the timeseries analysis, both temperature and density affect the abundance of crayfish and the two variables probably act simultaneously to affect also the size distribution of crayfish populations.

Niche width of crayfish

It is a well known phenomenon in community ecology today that some species have wider niche widths and occurs in more habitats than others (Fridley et al., 2007). Ecological theory states that species all have their unique niche, which is determined by its habitat and its resource use in the presence of competition and predation (Van Valen, 1965; Fox, 1981; Bearhop et al., 2004). Several factors have been shown to affect a species niche width, such as competition, population density, resource density and diversity (Bearhop et al., 2004). Resource competition (due to for example increased population density) within populations may lead to increased diet variation (Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2007) and thus increase the population's niche width. Reduction in niche width has been shown with increased species richness (Werner, 1977; Fox, 1981). However, Winemiller et al. (2001) showed both increased and decreased diet width in different species of lizards according to increased prey species richness. Closely related species may therefore show different responses to factors affecting niche width.

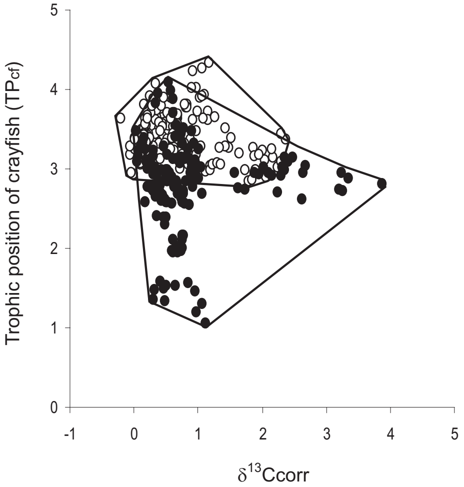

Figure 10. The total niche width (TA) of corrected values represented by convex hull area (inside solid lines) of all crayfish populations examined (each symbol represents one individual) for introduced signal crayfish (black dots) and native noble crayfish (white dots).

Niche width has traditionally been quantified by using gut content analysis across individuals from a population in conjunction with measures of food resource richness and evenness (Bearhop et al., 2004). Gut content analysis do not show what the organism actually assimilate and measures of food resource richness and evenness can be hard to quantify correctly. Due to these limitations stable isotope analysis is an alternative method for the study of trophic niches (Bearhop et al., 2004; Layman et al., 2007). The relative position of individuals of a population in δ^{13}C - δ^{15}N bi-plot space, a two dimensional niche space, can reveal important aspects of trophic structure and may be a powerful tool to test ecological theory and study ecosystems response to anthropogenic impacts (Layman et al., 2007), such as introductions of exotic species.

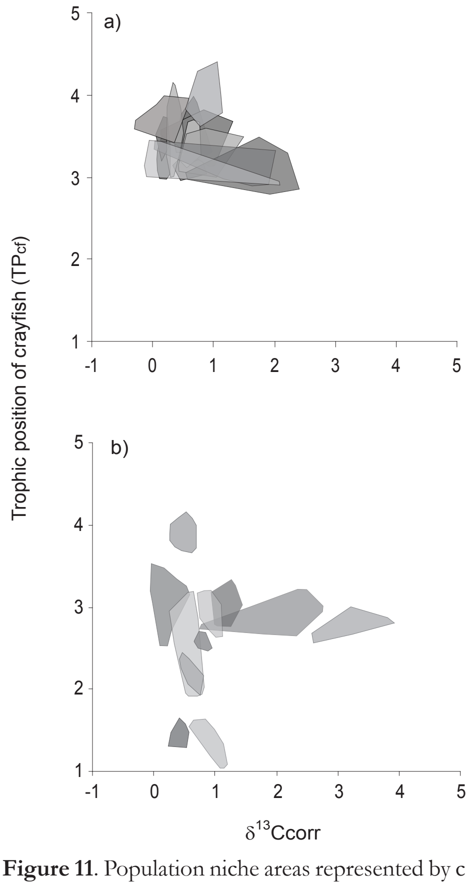

Figure 11. Population niche areas represented by convex hull areas (different grey colors) based on stable isotope analysis (corrected values) of 14-20 individuals per population for a) the 14 native noble crayfish populations and b) the 14 introduced signal crayfish populations.

Invaders are generally thought to have large niche widths and the impacts that invaders have on the community they invade are depending on the invader's niche width (Shea and Chesson, 2002). The ability to change between alternative food resources would make omnivores, such as crayfish, especially successful invaders. My results show (Paper IV) that the introduced signal crayfish has twice as broad niche width as native noble crayfish at the species level in Swedish streams (Fig. 10). This indicates that the introduced species use a wider range of habitats or food items than the native one. In particular from lower trophic levels, since signal crayfish had a much broader nitrogen range (TPcf range) expanding towards lower levels compared to noble crayfish (Fig. 11). However, at the population level there was no significant difference between niche widths of the two species. Some populations had large niche widths, while others had small ones (Fig. 11), indicating that all individuals in a population utilise similar resources regardless of environment or species.

I also show that crayfish niche widths are affected by invertebrate biomass and to some extent, invertebrate diversity, but not by crayfish density (Fig. 12). It has been shown that increased density of predators (i.e. other crayfish) increase selective feeding of crayfish (Nilsson et al., 2000), which may increase the niche width of crayfish. This may be due to individual niche separation within the population. The amount of food sources (invertebrate biomass) may influence the niche width by regulating the level of resource competition. My results indicate that a high biomass of certain invertebrate taxa increases the niche width of crayfish. This was also found by

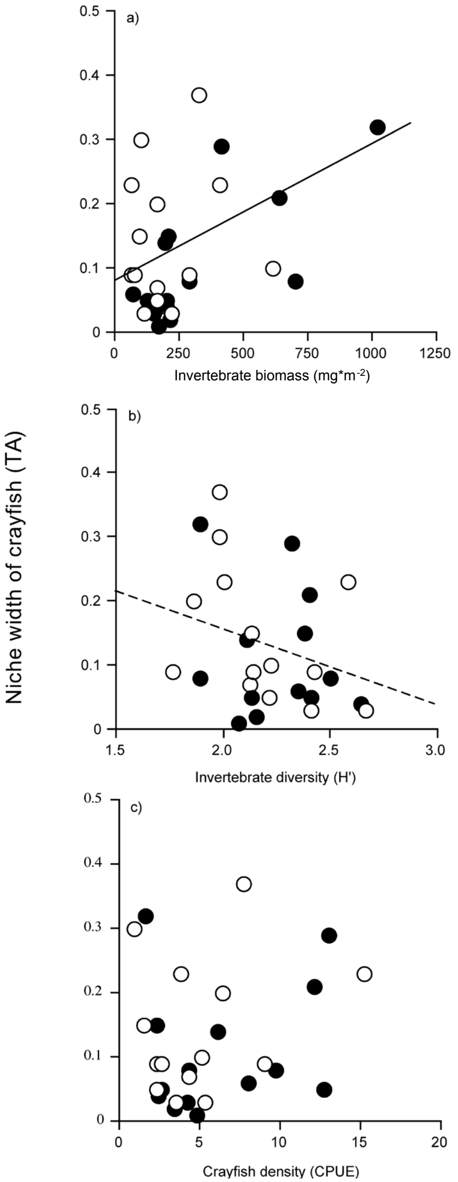

Figure 12. Regressions between the niche width (corrected values) of crayfish and a) invertebrate biomass, b) invertebrate diversity (H'), and c) crayfish density (CPUE). White dots represent noble crayfish populations and black dots represent signal crayfish populations. Significant regressions are indicated by a solid line and trends by a dashed line. Trend lines are calculated by pooling the data for the two crayfish species since there were no significant differences between them. Statistics are shown in Table 2.

Correia (2002) where introduced *Procambarus clarkii* adjusted its trophic niche to the availability of macroinvertebrates in rice fields in Portugal. Correia (2002) further found that *P. clarkii* had a high degree of diet specialization. It has also been found that crayfish play different roles in lakes due to differences in nutrient status (Stenroth et al., 2008), which will influence the availability of food resources for crayfish. In my study the availability (i.e. biomass) of easily consumed food sources of high energetic quality (i.e. large, less mobile and sedentary invertebrates) was positively correlated with the niche width of crayfish. Still, some of the signal crayfish populations in the study streams utilised very different food sources than most other populations. This might be a result of higher ability to use a wider range of habitats or food items of invading crayfish. Hence, this plasticity might explain the larger niche width of signal crayfish than noble crayfish at species level in Swedish streams and might also have contributed to the successful invasion of signal crayfish. Renai and Gherardi (2004) found that the introduced *P. clarkii* in Italy had a more plastic feeding behaviour than the native *A. italicus* and uses a broader range of information to predation risk (Hazlett et al. 2003). Introduced crayfish species may therefore have a greater success in and different impact on natural habitats than native crayfish species in Europe.

In its native area, North America, it has been argued that signal crayfish are mainly herbivores and detrivores (Bondar et al., 2005) and to a lesser extent predatory. In Europe, however, signal crayfish most often occupy the same trophic level as native crayfish species. Have signal crayfish adapted to a different feeding behaviour in Europe than in its native area in North America? Future studies on signal crayfish feeding habits in general in North America can give new insights to its niche use and its great invasive success in Europe and in other parts of the world.

Trophic position and growth rate

There has been a debate about the omnivorous habit of crayfish since Momot (1995) published his article "Redefining the role of crayfish in aquatic ecosystems". The feeding of crayfish in natural habitats is highly variable and affected by several factors. Crayfish seems to be able to find food and maintain their metabolism in most habitats (Nyström, 2002). Since, crayfish can act as herbivores, detrivores and predators, their trophic position in the food web can be hard to estimate.

Trophic position

A number of stable isotope analyses of crayfish have pointed out detritus as an important food source for crayfish (Bunn and Bonn, 1993; France, 1996; Evans-White et al., 2001). Other studies have shown that invertebrates are the most important energy source for crayfish (Nyström et al., 1999; Parkyn et al., 2001; Hollows et al., 2002; Nyström et al., 2006). In paper IV, I show that invertebrates are the most important energy source for noble crayfish in Swedish streams. Noble crayfish were at the same trophic level as predatory fish (Fig. 13), indicating that crayfish acted as predators in these systems. Even though crayfish, according to gut contents, in general are omnivores, stable isotope analyses showed that animal food sources contributed most to the nitrogen and carbon isotope signals in noble crayfish (Fig. 14). The availability of sedentary and slow moving invertebrate taxa had an effect on the trophic position and carbon signature of noble crayfish (Paper IV). Stenroth and Nyström (2003) also found that slow moving organisms declined in stream enclosures with signal crayfish, while more mobile organisms were less affected by crayfish presence. This indicates selective feeding by crayfish and the importance of availability of preferred prey for crayfish in lake and stream habitats. This has been shown for other species of crayfish as well (Lodge and Lorman, 1987; Alcorlo et al., 2004; Gherardi et al., 2004). For example, Alcorlo et al. (2004) found that crayfish (*P. clarkii)* consumed animal prey in accordance to its availability in the environment. They found that when more profitable prey was absent, such as mayflies and water bugs, *P. clarkii* increased their selection for chironomid larvae.

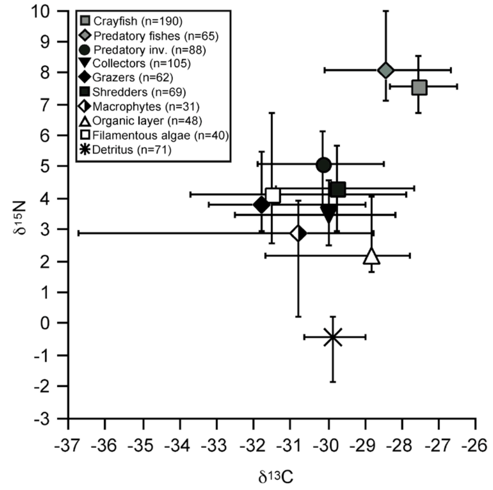

Figure 13. Noble crayfish is at the same trophic position as predatory fish. Invertebrates and macroalgae are one trophic level below, while macrophytes and organic layer (i.e. periphyton) is even further down. Detritus is at the base of the food web. Error bars denote the 25% and 75% quartiles.

Growth rate

Several abiotic factors, such as temperature, productivity, pH, calcium availability and habitat composition, have been proposed to affect crayfish growth and individual size (Holdich, 2002; Nyström, 2002; Reynolds, 2002). Also several biotic factors,

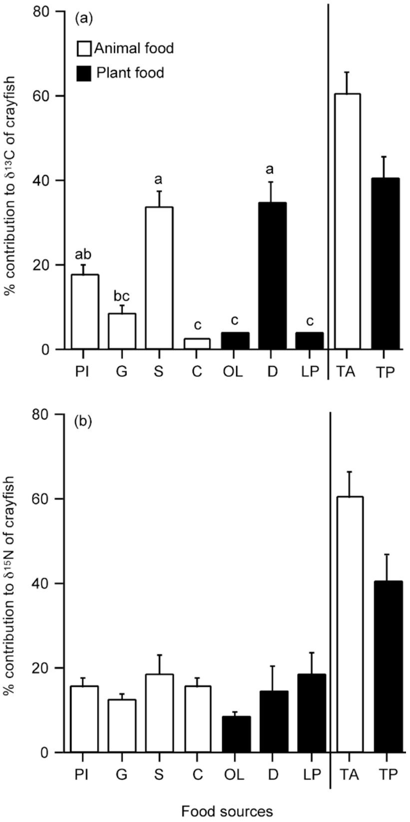

Figure 14. Contributions of different food sources to a) the carbon signal of crayfish and b) the nitrogen signal of crayfish. Different letters (a, b and c) represent a significant difference at the 0.05-level (Tukey's *post hoc* test). PI=predatory invertebrates, G=grazers, S=shredders, C=collectors, OL=organic layer (i.e. periphyton and organic material), D=detritus, LP=live plants, TA=total animal sources and TP=total plant sources. Error bars denote 1SE.

such as food quality and availability, (Momot, 1995), predation risk (Nyström, 2002), intraspecific interactions and population density (Guan and Wiles, 1999) may affect growth rate of crayfish. Crayfish has to moult to grow and the number of moults as well as length increment per moult is influenced by factors such as temperature and food availability (Skurdal and Taugbøl, 2002). The availability and quality of food items had an influence on the growth rate of noble crayfish (Paper IV). Crayfish had a higher growth rate in streams with high biomass of macroinvertebrates compared to crayfish in streams with low biomass of macroinvertebrates. However, invertebrate diversity did not affect the growth rate of crayfish, indicating that consumption of animal food per se increases growth in crayfish. There was a positive correlation between trophic position of crayfish and growth rate indicating a strong relationship between the two variables.

Survival and growth of juvenile crayfish

Recruitment of juvenile crayfish has been suggested to be an important factor for abundance fluctuations in crayfish populations. Dominating age classes of large conspecifics can suppress the recruitment of juveniles for many years, through consumption of nearly all eggs and/or juveniles produced by the population (Polis, 1981; Dercole and Rinaldi, 2002). This indicates that cannibalism may influence crayfish population dynamics. In the outdoor channel experiment (Paper V), I show that habitat complexity is the most important factor affecting survival, moulting stage, cheliped injuries and specific growth rate (SGR) of juvenile signal crayfish (Fig. 15). The presence of adult crayfish did not have any effect on survival and growth of juveniles, but did influence the juvenile's activity during night.

According to Holt and Polis (1997) intraguild predation (whereby potential competitors also eat each other) is similar size driven and may be viewed as an extreme form of interference competition. Newly hatched juvenile crayfish are of similar size and my results show that intraguild predation was important for juvenile survival especially in the low complexity treatments. Competition

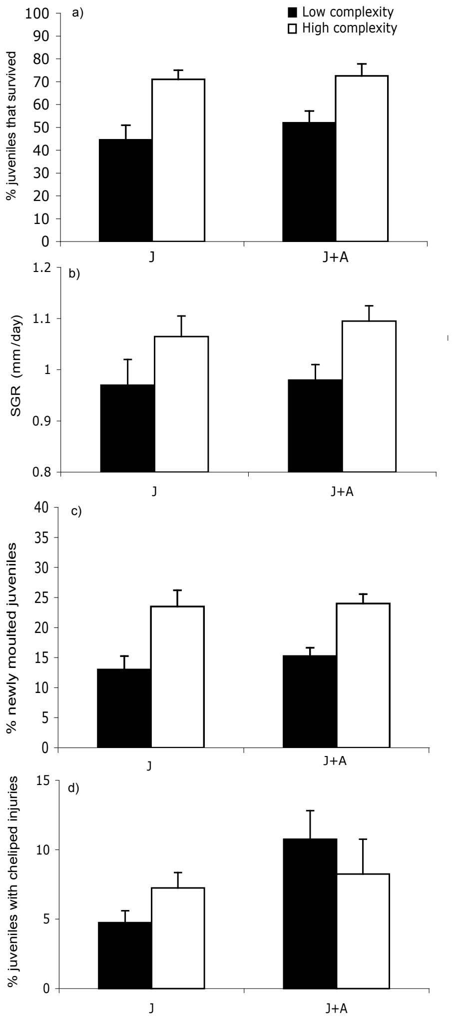

Figure 15. Percent juvenile crayfih that a) survived, b) the specific growth rate (SGR) of juvenile crayfish, c) percent juveniles that were newly moulted, and d) percent juveniles that had cheliped injuries in treatments with only juveniles (J) and in treatments with adults and two adult crayfish males present (J+A). White bars are treatments with high habitat complexity and black bars are treatments with low habitat complexity. Error bars denote 1SE.

and cannibalism between juveniles were also more pronounced than the risk of predation from adult crayfish males.

Prey can minimize the risk of predation by changing their diel activity or shelter and habitat use (Blake et al., 1994) and when predation risk is high most juvenile crayfish choose to hide in shelters (Hill and Lodge, 1999). My results show that the presence of adult males influenced the activity pattern of juveniles during night. In treatments with adult males present the juveniles were less active at night and more active during day when adults are inactive, than in treatments without any adult crayfish present (Fig. 16). However, the complexity of the habitat also influenced juvenile activity during night and day, with more juveniles active in the less complex habitat (Fig. 16). In habitats with low complexity, juvenile crayfish may be forced to forage more in open habitats. They may also choose to be in the open area just to reduce direct interference with juvenile conspecifics.

Altered behaviour may involve costs in terms of lost feeding opportunities and reduced growth rates in response to predation risk (e.g. Pecor and Werner, 2000), a result also shown for juvenile signal crayfish (Nyström, 2005). In channels with adult males present the abundance of chironomids, an important food and energy source for juvenile crayfish, was higher than in channels without adults. This may be a result of an indirect effect of altered feeding behaviour in juvenile crayfish. However, in the treatments with high complexity the growth rate of juveniles was not reduced in channels with adult males present. One explanation can be that in channels with abundant cobbles the juveniles could find enough food sources in the cobble interstices and the change in feeding behaviour did, therefore, not influence growth rate of the juveniles.

The results from my experimental study indicate that survival and growth of juvenile crayfish is mostly affected by availability of cobble habitats and that this effect is independent of the presence of larger and can-

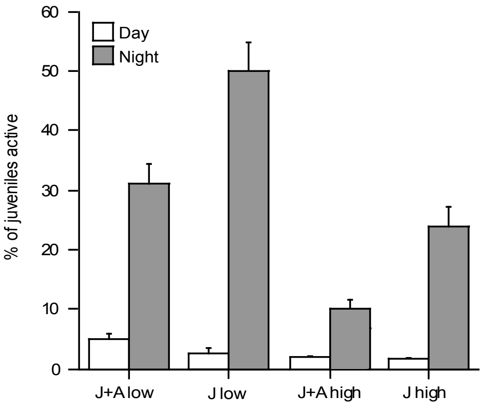

Figure 16. Juvenile activity both during day and night in the different treatments. White bars are day activity and grey bars are night activity. Error bars denote 1SE.

nibalistic adult conspecifics. However, intracohort interactions between newly hatched juveniles can decrease survival, moulting frequency and growth, especially in habitats with low complexity (Fig. 15).

The influence of crayfish on lower trophic levels

Dense crayfish populations can have significant bioturbation effects on the bottom substrate in streams. Especially larger crayfish may stir the bottom layer sufficiently to provide enough oxygenation to release phosphorous and other nutrients, which then become available to other organisms in the system (Momot, 1995). Without crayfish much of the energy in the stream food cycle would be "short-circuited" and large amounts of unprocessed food will leave the system. This may further, lead to decreased energy cycling, community productivity and food availability for other trophic levels in the system (Momot et al., 1978; Huryn and Wallace, 1987). In the outdoor channel experiment (Paper V) the adult crayfish males showed a significant negative effect on the periphyton production on the ceramic tiles. The juveniles, however, were too small to be able to disturb the periphyton growth or sedimentation on the tiles.

In the outdoor channel experiment I also found that juvenile crayfish and adult crayfish males had both negative and positive impact on some of the commonly found invertebrate species. However, habitat complexity and other environmental factors also influence the abundance and composition of invertebrates in natural habitats as shown in Paper I and IV. Invertebrates are an important energy source for crayfish and gut content analyses indicate consumption of invertebrates by crayfish in general (Whitledge and Rabeni, 1997; Parkyn et al., 2001; Stenroth et al., 2006; Paper I and VI). One can therefore assume that crayfish have an impact on benthic invertebrate community in lakes and streams. However, some invertebrate species are unaffected by crayfish, while others are positively or negatively affected by crayfish presence. Juvenile signal crayfish consumed chironomidae larvae in all treatments, but had highest consumption in treatments without adult crayfish present, (Paper V). This indicate a selective predation on chironomids by the juveniles, which is consistent with other studies (i.e. Withledge and Rabeni, 1997; Usio, 2000; Usio and Townsend, 2004). The presence of adult crayfish had, however, a negative effect on the biomass of the larger invertebrates, such as Limoniidae, especially in the low complexity treatment (Paper V, Fig. 17).

Conclusion and future perspectives

In my thesis I have shown that the dynamics of crayfish in freshwater ecosystems are complex and several factors interact to structure crayfish populations. Abundance of crayfish is influenced by the presence of predatory fish, substrate size, temperature and population density. Trophic position,

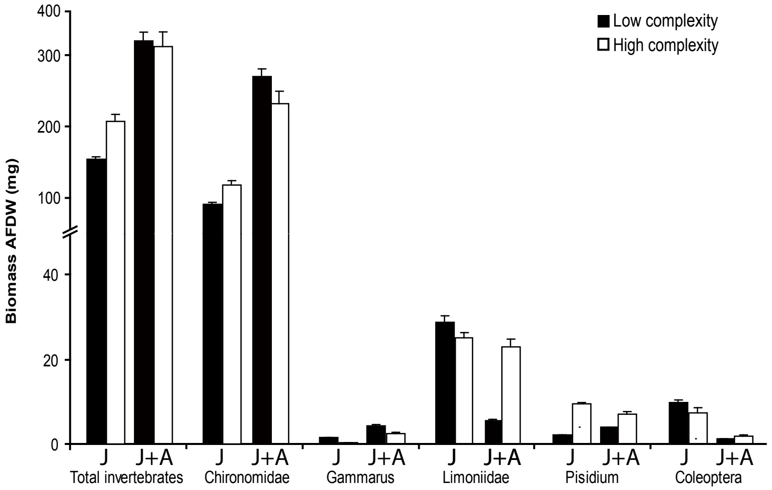

Figure 17. The total invertebrate biomass (AFDW) and the biomasses of dominant invertebrate taxa found in the channels. White bars are treatments with high habitat complexity and black bars are treatments with low habitat complexity. J are treatments with only juveniles and J+A are treatments with juveniles and adult crayfish present. Error bars denote 1SE. **Note the breake on the y-axis.**

growth rate and niche width of crayfish are dependent on the availability of high quality food, i.e. invertebrates. Trophic position and niche width are further influenced by the biomass of large, less mobile and sedentary invertebrates. However, a high biomass of invertebrates per se increases the growth rate of crayfish. Crayfish are omnivorous according to gut content analyses, but with stable isotope analyses I show that animal food is the most important protein source for crayfish. One could thus state that "crayfish are not what they eat, crayfish are what they assimilate". The cannibalistic behaviour of crayfish is supported by my work, but contrary to previous thoughts it was similar sized crayfish that cannibalized on each other. The large adult males influenced the activity of juvenile crayfish but did not affect the survival or growth of juveniles. In the presence of adult crayfish the juveniles foraged near shelter and invertebrates such as chironomids ware released from juvenile predation.

Today, many freshwater ecosystems are altered due to habitat destruction, introductions of invasive species, loss of native species and overexploitation of species for commercial purposes. The methods I have used in this thesis can provide useful tools to predict the possible effects of climate change and habitat alteration on crayfish dynamics, but also on freshwater ecosystems in general. Further, challenges to predict how increased global warming may affect freshwater ecosystems can benefit from more long-time data sets on organism abundances in accordance with related environmental parameters. Today there is a lack of such long timeseries. This makes comparison between species in different areas difficult.

The information gained from my work and from future research can help us predict how crayfish and other animals may respond to changes in their environment. Crayfish are key-species in many freshwater ecosystems and if crayfish densities change, due to for example a warmer climate, this will probably affect the whole ecosystem and several organisms in both positive and negative ways.

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My contribution to the papers

Paper I: I planned the study together with my supervisor Per Nyström. The fieldwork was conducted by me, P. N., Patrik Stenroth (PhD-student, LU) and Niklas Holmqvist (PhD-student, LU) in collaboration with Angus McIntosh at Canterbury University, Christchurch, New Zealand. The identification of invertebrates was done by Mike Winterbourn at Canterbury University, Christchurch, New Zealand. I did all other analyses and wrote the paper with very valuable comments from my co-authors.

Paper II: The data was provided by co-supervisor Wilhelm Granéli. I did all calculations and model selections with the help from Jörgen Ripa (PhD, Theoretical ecology, LU). I did the evaluation of the results. I also wrote the paper with very valuable comments on the manuscript from my co-authors.

Paper III: Data for noble crayfish is from the same study as Paper IV and supplementary data was provided by P. S. I did all calculations and evaluation of the results. Statistical analyses were performed by me together with P. N. I wrote the paper with very valuable comments from my co-authors.

Paper IV: I planned the study together with P. N. The field work was conducted by me, P. N., P. S., and Erika Nilsson (PhD-student, LU). I did all analyses, except RNA/DNA analyses that were performed by me together with Marie Svensson (Technical assistant, LU). I also wrote the paper with very valuable comments from my co-authors. W. G. also provided financial support.

Paper V: I planned and conducted the experiment together with P. N. I performed all analyses and wrote the paper. P. N. helped with the statistical analyses and came with very valuable comments on the manuscript.

Kräftornas komplexa liv och leverne

En sammanfattning på svenska

Det finns över 500 kräftarter i världen och vi hittar dem på alla kontinenter utom Antarktis och Arktis. I Sverige finns två arter, den inhemska flodkräftan och den introducerade signalkräftan. Signalkräftan introducerades till stor del för att ersätta förlusten av flodkräfta i många pestdrabbade vatten i södra Sverige. Att det just blev signalkräftan berodde främst på att den liknar vår inhemska flodkräfta, men också för att den ansågs växa fortare och kunde bilda tätare bestånd. I min avhandling har jag visat att detta inte stämmer i naturliga vattendrag. I en jämförelse mellan de båda arterna fann jag att de blev lika stora och bildade lika täta bestånd och att tätheten styrs framförallt av hur mycket rovfisk som finns. Detta gällde även för kräftor på Nya Zeeland där introducering av öring minskat förekomsten av kräftor i många vattendrag. I vattendrag där det fanns lite rovfisk var det andra faktorer som styrde tätheten. Den nyazeeländska kräftan och signalkräftan hade tätast bestånd i vattendrag med stenar runt 10 cm då det fanns lite rovfisk. Medan flodkräftan inte verkar bry sig om vilken storlek stenarna har.

Andel sten, vilket påverkar ett habitats komplexitet, var också den mest betydande faktorn för överlevnad och tillväxt hos kräftyngel. Mycket stenar ger ett ökat skydd för de små kräftorna som kan undkomma kannibalism från vuxna men även från andra små kräftor. I mitt experiment visade det sig att kannibalismen mellan små kräftor var större än den mellan stora och små, vilket man inte tidigare trott. Detta berodde till stor del på att de små kräftorna minskade sin aktivitet i närvaro av stora kräftor och att de då stannade i gömslen mer än när de var ensamma. I gömslena fanns tillräckligt med föda för att de små kräftorna skulle kunna äta sig mätta utan att riskera kannibalism från vare sig de stora eller de andra små kräftorna. Detta ökade överlevnaden och tillväxten hos de små kräftorna som hade gott om gömslen trots att stora kräftor var närvarande.

Tillväxten hos stora kräftor verkar enligt mina resultat bero på temperatur och tillgång på proteinrik föda som t.ex. mygglarver och andra småkryp som lever i vattendrag och sjöar. Detta stämmer väl med vad som visats i tidigare studier och det är framförallt mängden stora, långsamma och bottenlevande djur som är viktiga som föda för kräftor. Små, snabba och frilevande djur som t.ex. fiskyngel och sötvattensmärla, är svåra för kräftorna att fånga och de bidrar därför inte i någon större utsträckning till kräftornas proteinintag. Sammantaget betyder detta att kräftor försöker äta så mycket smådjur som möjligt eftersom dessa innehåller stor andel protein. Smådjur är dessutom jämförelsevis lättsmälta och innehåller inte några stora mängder kostfiber jämfört med växter. De kräftor som äter mycket småkryp (proteinrik föda) växer snabbare och kan därmed i slutänden få fler yngel. Jag upptäckte att kräftor i vattendrag med en större andel smådjur både växte snabbare och hade en högre position i näringskedjan än de kräftor som levde i vattendrag med lite smådjur. Detta innebär att skillnaderna i kräftors födoval mellan vattendrag, med låg respektive hög andel smådjur, bidrar till att kräftorna antar olika roller i olika vattendrag.

I mina studier har jag även funnit att kräftor kan ta upp kol och kväve från olika sorters föda. Kol är en viktig beståndsdel i t.ex. fett och kväve är en viktig beståndsdel i t.ex. protein. Många djur, t.ex. rovfisk, äter bara en typ av föda och får därmed både kol och kväve, eller både fett och protein, från samma födokälla. De är därmed specialisterna som bara äter andra djur och det finns andra specialister, t.ex. sniglar som bara äter alger. I denna avhandling visar jag att detta inte passar in på allätare som kräftor. De äter i stort sett allt och tidigare studier har visat att kräftor verkar må bäst ifall de får en föda bestående av både djur och växter. Detta innebär att allätare som till exempel kräftor kan vara rovdjur om man tittar på proteinkällorna samtidigt som de är vegetarianer om man ser till fettkällorna. Det att kräftor kan vara vegetarianer i vattendrag med liten andel småkryp och rovdjur i vattendrag med stor andel småkryp påverkar de andra organismerna som lever i samma system. Sammantaget kan man säga att denna skillnad gör att det inte går att säga att kräftor har samma roll och påverkan på andra organismer i alla vattendrag. Vidare visar jag också att andel smådjur påverkar kräftornas nischbredd, d.v.s. den typ av miljö och den roll i födokedjan som kräftorna ockuperar i ett vattendrag. I vattendrag med mycket smådjur innehar kräftorna en större nisch än i vattendrag med låg andel småkryp. Även här är det främst andelen stora, långsamma och bottenlevande smådjur som är viktigast. Så man kan säga att om det finns många olika sorters smådjur och ett stort antal av stora, långsamma och bottenlevande smådjur kommer kräftor att växa bra, ha rollen som rovdjur och uppta en bredare nisch i vattendraget. Detta mönster gäller säkert även för sjöar då det tidigare har visat sig att kräftor i näringsrika sjöar växer bättre än i näringsfattiga sjöar och detta främst för att det finns en större mängd smådjur i näringsrika sjöar.

I sjön Bunn undersöktes varför antalet kräftor varierar så mycket från år till år med hjälp av fångstdata och temperaturdata från 1946 fram till idag. Med hjälp av en matematisk modell kunde olika faktorer testas för att se om de påverkade skillnaden i fångst från år till år. Det var också möjligt att jämföra den inhemska flodkräftan och den introducerade signalkräftan, då flodkräftan fanns i sjön fram till 1974 och signalkräftan planterades in 1985 och finns där än idag. Det var samma faktorer som var viktigast för de två arterna och det var framförallt vintertemperaturen som var viktig. En varm vinter ökar troligen överlevnaden hos kräftor, vilket gör att fångsten ökar följande sommar. Då alla stora kräftor över 10 cm som fångas tas bort för mänsklig konsumtion varje år hade tätheten också en betydelse för hur många stora kräftor man fick följande år. Detta beror främst på att om man minskar antalet stora kräftor så gynnas tillväxten och överlevnaden hos de mindre kräftorna, eftersom konkurrensen från de stora försvinner. Detta frigör föda och gömslen, vilka jag visat i mina studier är de viktigaste faktorerna för tillväxt och överlevnad hos kräftor.

Så, genom att studera kräftor i vattendrag och sjöar kan vi få en bättre förståelse för vad som påverkar kräftor. Detta kan vara av stor betydelse när vi planerar restaureringsåtgärder och gör upp bevarandeplaner inför framtiden. Speciellt om man betänker att under tiden 1946 till 2007 har vintertemperaturen ökat gradvis och fler år har en medeltemperatur över fryspunkten. Detta har säkert redan påverkat kräftorna i sjön Bunn och antagligen ser vi samma mönster på många andra håll i Sverige och i världen. Till en viss gräns kommer kräftorna troligtvis att gynnas av denna temperaturökning, men en vidare ökning kan komma att få negativa konsekvenser. Det är något vi behöver titta närmare på i vår fortsatta forskning om kräftornas liv och leverne.

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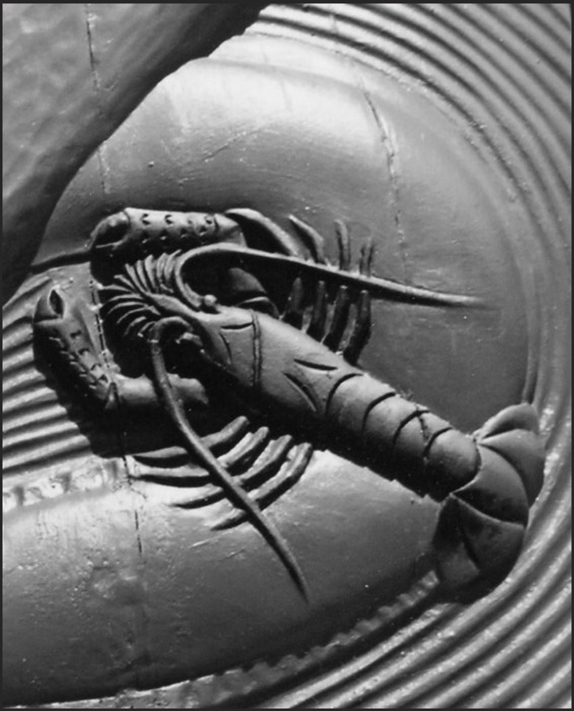

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Does natural acidity mediate interactions between introduced brown trout, native fish, crayfish and other invertebrates in West Coast New Zealand streams?

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ABSTRACT

The presence of introduced brown trout (*Salmo trutta*) on the distribution of native crayfish (*Paranephrops planifrons*), native galaxiid fishes (*Galaxias* spp.) and invertebrate fauna was investigated in 18 West Coast New Zealand streams (8 with trout and 10 without trout) differing in chemical characteristics. Gut contents of trout, crayfish and eels were also examined to evaluate whether competition or predation could be linked to the patterns found. Abundances of crayfish and galaxiids were significantly lower in streams with trout, but in streams without trout, substrate size was one of the most important factors determining crayfish abundance. In contrast to crayfish, other macroinvertebrates were more abundant in trout streams than streams without trout and significantly more taxa were found in streams with trout. Macroinvertebrate abundance was related to environmental factors, such as pH, substrate, depth and total nitrogen. Gut content analysis showed an overlap in diet (mostly invertebrates) between trout and eels. Crayfish, however, had a more omnivorous diet where detritus was the most frequently occurring food material. Differences in chemical characteristics marked the streams with and without trout. Thus, trout were not present in streams with pH < 6.0. Crayfish and galaxiids were present in streams with pH ranging from 4.1 to 7.9, and those with pH < 6.0 may function as trout-free refuges where larger populations of these species may persist. However, other macroinvertebrate taxa may be more negatively affected by acidification than by trout. By protecting naturally acidic, brown water streams, New Zealand crayfish and galaxiid fish populations can be conserved within geographic areas where trout are present.

1. Introduction

Management of non-indigenous (exotic) species is an important factor in maintaining native species and ecosystem functioning (Byers et al., 2002). Understanding the impact of exotic species on native ecosystem functioning and structure is therefore one of the most important challenges in conservation biology today (Parker et al., 1999; Mack et al., 2000; Kolar and Lodge, 2001; Gido et al., 2004). The introduction of exotic species by humans (accidentally or deliberately) into an ecosystem often has effects at several trophic levels (Coblentz, 1990; Lodge, 1993; Allan, 1995; Nyström et al., 2001; Townsend,

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2003). The level of impact of introduced species on interactions within native communities may be influenced by abiotic factors, and they may determine also whether key organisms in the food web are affected or not (Nyström and McIntosh, 2003). It is therefore important to study food webs under a range of environmental conditions. If appropriate conservation measures are to be taken in order to maintain native ecosystem functioning and diversity, it is necessary not only to identify the key interactions in complex food webs, but also the habitats and environmental conditions that influence the impact of the invader.

Trout are some of the most widely distributed exotic species in aquatic ecosystems (Allan, 1995), and their presence in simple food chains often results in cascading, “top-down” effects (Bechara et al., 1992; McIntosh and Townsend, 1996; Nyström et al., 2003). Brown trout (*Salmo trutta*) were introduced to New Zealand in 1867 to benefit recreational fishing and from the time of their first introduction until 1921 more than 60 million brown trout had been raised and released into New Zealand streams (Townsend, 1996). Today they are found throughout much of the country (Townsend, 1996). The introduction of brown trout into New Zealand streams has affected other stream fauna, notably native galaxiid fish, through predation and competition for food and space, and has led to the fragmented distribution of many galaxiid populations (Townsend and Crowl, 1991; McIntosh et al., 1992; McIntosh, 2000a). The presence of trout has also affected invertebrate grazer behaviour, indirectly leading to higher standing stocks of periphyton in some trout streams (Townsend and Crowl, 1991; McIntosh et al., 1992; McIntosh and Townsend, 1995; Townsend, 1996; Nyström et al., 2003). Trout may also influence the species composition and size distribution of invertebrates in streams, and some large invertebrates with long life cycles, and no protective cases or shells (e.g. many predatory species), may be particularly vulnerable to trout predation (Huryn, 1998; Townsend, 2003; Nyström et al., 2003). Consequently, the abundance of less vulnerable invertebrate species (e.g. small grazing caddisflies and snails with cases or shells) may be higher in streams with trout than in streams without fish, or with native galaxiid fish only (Nyström et al., 2003).

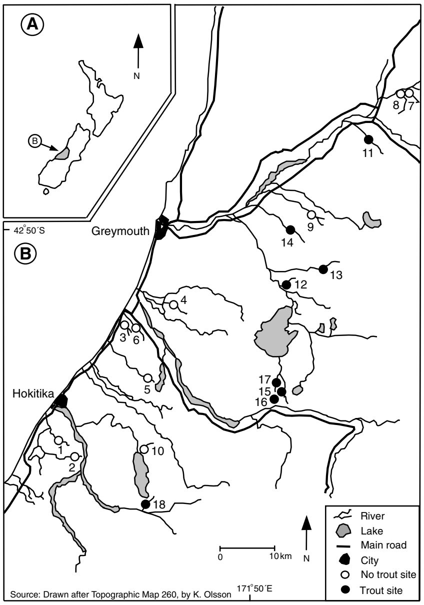
Most studies on the impact of exotic trout in New Zealand have focussed on simple food chains that include native fish species and invertebrate grazers, however, many ecosystems including streams on the West Coast of New Zealand also contain large bodied omnivorous freshwater crayfish, whose distribution may have been affected negatively by the introduction of brown trout (Townsend, 1996, 2003). The two endemic crayfish species (*Paranephrops planifrons* and *Paranephrops zealandicus*) can be regarded as keystone species in New Zealand freshwater communities, as they can play important roles as both predators and detritivores (Usio, 2000). In particular, they may be major processors of leaves in streams (Usio, 2000; Usio and Townsend, 2002), because large, shredding insects are often lacking. Hence, any negative impact on crayfish by trout will likely affect the functioning of an invaded community (Townsend, 2003).

In addition to predation and competitive interactions, abiotic factors can have strong effects on the species composition and abundance of invertebrates and fish in New Zealand streams. For example, physical disturbance, acidification and associated water chemistry, have all been shown to influence stream biota (Winterbourn and Collier, 1987; Collier et al., 1990; Winterbourn and McDiffett, 1996; McIntosh, 2000a). On the West Coast of the South Island many brown water streams with naturally low pH support populations of galaxiid fish and crayfish, but brown trout have not been recorded in waters with pH below 5.0 (Collier et al., 1990). It is therefore possible that brown water streams act as refuges for native species that are tolerant of moderately low pH.

In the present study multiple streams with and without trout and with varying chemical characteristics, including pH were investigated. In each stream the relative importance of abiotic factors (e.g. pH) and trout in determining the composition of food webs was assessed. Additionally, gut contents of trout, eels and crayfish were used to evaluate whether competition for food or predation could be linked to the community patterns found.

2. Materials and methods

Fieldwork was conducted between 22 and 30 January 2003 in 18 streams on the West Coast, South Island, New Zealand (Fig. 1). Eight of the sites were on open streams surrounded by pasture, tussock grassland or shrub/forest, whereas ten sites were in native or exotic forest. Based on data from New Zealand freshwater fish database (http://fwdb.niwa.cri.nz) and observations, it was known that all streams contained a native crayfish species (*P. planifrons*) and that eight were expected to contain the introduced brown trout (*S. trutta*). No physical barriers (e.g. waterfalls) to colonisation by



Source: Drawn after Topographic Map 260, by K. Olsson

Fig. 1 – Map of New Zealand (A) and Westland showing the study sites (B). Site numbers as in Table 1.

trout, crayfish or most other fishes were present in any of the study streams.

2.1. *Physical factors and water chemistry*

At each site a study reach 9.5–28.5 m long, depending on width and availability, (area 17–128 m^2) was established. Water temperature, current velocity, average depth, stream width, substrate size and bed stability (Pfankuch bottom score; a subjective index of streambed stability, as described by McIntosh, 2000b) were measured at each site. Current velocity was estimated by measuring the time taken for fluorescein dye to travel through the study reach. Average depth was estimated from nine measurements (three on each of three cross-stream transects) and average width from three measurements at each site. Average substrate size was estimated by measuring the longest axis of 30 randomly chosen substrate particles within the study reach. Canopy cover (% streambed covered), macrophyte cover (% streambed covered) and undercut banks (% of stream bank length undercut) were estimated visually for each study reach. A water sample, kept frozen until analysis was performed, was used to determine pH, conductivity (at 25 °C), total nitrogen, total phosphorus, calcium and dissolved organic carbon. Except for pH and conductivity, which were measured at the University of Canterbury, all samples were analysed in the Environment Canterbury laboratory (Christchurch, New Zealand), using the APHA 3111 B (20th Ed) acid soluble method for calcium, NI APHA 5310 C (20th Ed) uv-persulphate method for dissolved organic carbon, APHA 4500-N C (20 Ed) – modified method for total nitrogen and APHA 4500-P B5 (20 Ed) – autoanalyser method for total phosphorus.

2.2. *Particulate organic matter*

Coarse particulate organic matter was collected with a Surber sampler (0.0625 m^2, 250 μm mesh). Five randomly located samples were taken at each site, and preserved in 80% ethanol. Invertebrates, macrophytes, twigs and pieces of wood were removed and the remaining organic matter (>1 mm) was dried for 24 h at 65 °C. Coarse particulate organic matter was weighed to the nearest milligram and a subsample ($\sim$1 g) was taken to estimate ash-free dry weight. The subsample was ashed in a muffle furnace at 450 °C for one hour and reweighed.

2.3. *Epilithic algae*

Five stones were selected randomly at each site for the determination of epilithic algal biomass. An 18.7 cm^2 or 8.55 cm^2 circle of epilithon was removed from the upper surface of each stone with a wire brush, filtered on to a glass fibre filter and frozen for later analysis. Chlorophyll *a* was extracted with 95% ethanol (12 h in the dark at 20 °C) and estimated spectrophotometrically according to Jespersen and Christoffersen (1987).

2.4. *Fish, crayfish and invertebrates*

Fish and crayfish were sampled at all sites by electrofishing (Kainga EFM 300 backpack machine). Three downstream runs were made at all sites (9.5–28.5 m), which were delineated by stop nets (5 mm mesh). Captured crayfish were measured to the nearest millimetre (total length, TL) and weighed to the nearest milligram. Fish were anaesthetized, and identified to species level following McDowall (2000), measured and weighed as above. The abundance (per m^2) of crayfish, galaxiids, eels and trout was estimated from the absolute number captured. Thirty-eight trout, 59 crayfish and 24 longfin eels (*Anguilla dieffenbachii*) from various sites were sacrificed for analyses of gut contents. Sixteen eels and four of the larger trout were examined in the field, whereas smaller trout, eight eels and all crayfish were frozen for later identification. Organic matter was separated into fine detritus and plant fragments, and invertebrates were identified to generic level in most cases following Winterbourn et al. (2000). Frequency of food items in trout, eel and crayfish guts was calculated from the data. Only eels larger than 17.3 cm (the smallest eel containing crayfish in this study) were included as earlier studies indicate that smaller eels are not able to eat crayfish (Jellyman, 1989; Schulze et al., 2004). Invertebrates present in the Surber samples (see above) were preserved in 80% ethanol and identified and counted at up to 10× magnification.

2.5. *Statistical analysis*

All statistical analyses were conducted using the software SPSS 11.0 for Windows, except for the canonical correspondence analysis that was conducted in CANOCO 4.5 for Windows. To test whether there were physico-chemical differences between trout and no-trout streams a principal component analysis was performed. It included the following variables: water temperature, depth, width, conductivity, velocity, substrate size, pH, disturbance score (bed stability), total nitrogen, total phosphorus, coarse particulate organic matter, chlorophyll *a*, calcium, dissolved organic carbon, canopy cover, macrophyte cover and bank undercutting. A correlation matrix with varimax rotation was used (Aronsson, 1999). All axes with eigenvalues > 1 were retained, and variables with an absolute loading of 0.606 (1% significance level, $n = 17$) were considered to be important (Watt, 1993; Aronsson, 1999; McGarigal et al., 2000). Principal component analysis scores were compared between trout and no-trout streams with independent sample *t*-tests.

To compare the abundance of crayfish, galaxiids, eels and invertebrates in streams with and without trout, independent sample *t*-tests were used. A two-sample Kolmogorov–Smirnov test (Aronsson, 1999) was used to compare the size frequency distribution of crayfish between streams with and without trout. Previous experimental and field studies in New Zealand streams have shown that multiple factors including the presence of crayfish (Usio, 2000), periphyton biomass (Biggs et al., 2000), canopy cover (Nyström et al., 2003), coarse particulate organic matter (Nyström et al., 2003), pH (Harding et al., 2000) and physical disturbance (Death and Winterbourn, 1995) may affect the abundance of invertebrates. Consequently, it was tested whether the abundances of the 72 identified macroinvertebrate taxa (excluding all *Paranephrops*) were related to any of the measured environmental factors in a canonical correspondence analysis by multivariate constrained ordination and a Monte Carlo permutation test (McGarigal et al., 2000; Leps and Smilauer, 2003). Invertebrate taxa with an absolute loading of 0.302 (1% significance level, $n = 72$) and environmental variables with an absolute loading of 0.606 (1% significance level, $n = 17$) were considered to be important. To test whether the presence of crayfish influenced invertebrate abundance linear regressions were performed on abundances in streams with and without trout, respectively.

To ensure variables were normally distributed, environmental- and abundance data were transformed prior to analysis. For percentage data (canopy cover, macrophytic cover and undercut banks) arc-sin $\sqrt{x}$ was used and for all other variables $\ln(x + 1)$. Temperature, pH, substrate (median) and disturbance (index score) values were not transformed.

3. Results

Streams with and without trout varied considerably in chemical factors, including pH, conductivity, calcium and dissolved organic carbon, but not in physical factors, such as substratum size, depth and disturbance index (Table 1).

Five principal component axes with eigenvalues greater than one, collectively explained 77% of the variation in physico-chemical factors in the streams (Table 2). Scores on the first axis differed between streams with and without trout ($t = 4.195$, df = 3.864, $p = 0.001$). Trout streams had high pH (6.4–7.9), whereas streams without trout had lower pH (4.1–6.6). Other measured physico-chemical variables varied among sites and overlapped considerably between the two kinds of streams (Table 1). Crayfish, galaxiids and eels were found across the whole pH spectrum (4.1–7.9). A total of 258 trout was caught with an average abundance in the trout streams of 0.54 trout/m^2 (range 0.01–2.10 per m^2). The largest trout captured was 50 cm long and weighed 1.2 kg, but most were small (median length 5.1 cm, median weight 1.4 g). Crayfish were found in 17 of the streams, 281 at sites without trout and 41 at trout sites. The largest crayfish was 10.4 cm long and weighed 30.7 g (median length 4.3 cm, median weight 2.0 g). The size distribution of crayfish (Fig. 2) differed between streams with trout (median length 54 mm) and without trout (median length 41 mm) (two-sample Kolmogorov–Smirnov test, Z = 2.2, $p < 0.0001$). In streams with trout no juvenile crayfish (<20 mm) were caught, while some juveniles were caught in streams without trout (Fig. 2). Crayfish abundance was also significantly lower at sites with trout ($t = 2.845$, df = 9.593, $p = 0.018$), but was highly variable at sites without trout. At the latter, crayfish abundance was highest where median substrate size was about 9 cm and lower on both coarser and finer substrates (Fig. 3).

Two species of eel, longfin eel (*Anguilla dieffenbachii*) and shortfin eel (*Anguilla australis*), were caught in 16 of the streams, and 233 galaxiids (belonging to four species, *Galaxias fasciatus*, *Galaxias postvectis*, *Galaxias brevipinnis* and *Galaxias divergens*) were captured at sites without trout and 19 at sites with trout. Four other native fish species were also caught. Galaxiid abundance was lower at sites with trout ($t = 2.406$, df = 9.472, $p = 0.038$), but the abundance of eels did not differ ($t = -0.284$, df = 15.214, $p = 0.780$) between sites with and without trout. Numbers of fish and crayfish caught at each site are given in Appendix 1.

Gut content analysis showed that trout had consumed a wide variety of food items. Nymphs of *Deleatidium* (Leptophlebiidae) and other mayflies were the most frequently found prey, and the largest trout caught contained a crayfish of about 5 cm total length (Fig. 4). However, none of the smaller trout had consumed crayfish. Of the 12 longfin eels from streams with trout, 25% contained crayfish in addition to other macroinvertebrates (Fig. 4). Of the 12 longfin eels from streams without trout, 50% contained crayfish in addition to other macroinvertebrates (Fig. 4). Crayfish had consumed a variety of food items (Fig. 4), of which detritus was found most frequently. However, fresh plant fragments, and several invertebrate taxa, including trichopteran larvae, nymphs of the mayfly *Deleatidium* and other crayfish, were also found in guts.

In all, 72 macroinvertebrate taxa (excluding *P. planifrons*) were identified in samples from the 18 streams. Collector/grazers dominated numerically in all streams and only three shredder taxa were found. Nineteen of the 72 taxa were present only in trout streams and 14 were present only in streams without trout (Appendix 2). The mean number of taxa differed between streams with and without trout ($t = 2.735$, $p = 0.015$), with more being present in trout streams. Furthermore, the mean abundance of invertebrates was more than three times higher in trout streams than streams without trout ($t = 2.944$, $p = 0.019$). The abundance of shredders did not differ between streams with and without trout, but there were more predatory invertebrates in streams with trout (t-tests, shredders, $p = 0.670$, predators, $p = 0.056$). However, significantly more collector/grazers and filterfeeders were found in streams with trout (*t*-tests, collector/grazers $p = 0.022$, filterfeeders $p = 0.045$). Invertebrate taxa with cases or shells (16 taxa, see Appendices 1 and 2) were also more abundant in streams with trout (*t*-test $t = -2.783$, df = 7.013, $p = 0.027$). The two most common invertebrate taxa in the “cased” category were the snail *Potamopyrgus* (mean abundance of 510 individuals/m^2 in trout streams and 0.64 individuals/m^2 in streams without trout) and the caddisfly *Pycnocentrodes* (mean abundance of 564.6 individuals/m^2 in trout streams and 0.64 individuals/m^2 in streams without trout). *Deleatidium* was the only invertebrate present at high densities in all streams (trout vs. no-trout streams $t = -1.406$, df = 15.937, $p = 0.179$).

Canonical correspondence analysis showed that invertebrate abundance patterns were related to environmental variables (Fig. 5). The first axis explained 31.8% of the variation in abundance and was correlated with pH, conductivity (−) and canopy cover (+). The second axis explained 23.5% and was correlated with disturbance score, substrate (−), macrophytic cover and depth (+). A Monte Carlo permutation test with 999 permutations showed that pH ($F = 2.56$, $p = 0.002$), substrate ($F = 1.80$, $p = 0.006$), depth ($F = 1.51$, $p = 0.022$) and total nitrogen ($F = 1.49$, $p = 0.04$) had a significant affect on invertebrate abundance patterns. *Deleatidium* and Chironomidae, the two most common invertebrate taxa, were positively correlated with canopy cover and dissolved organic carbon, respectively (Fig. 5). Of the more common predatory invertebrates, *Stenoperla* was associated with large substrates. However, the abundance of *Neppia*, which was present only in trout streams, was correlated with conductivity and epilithon

Table 1 – Physico-chemical and other environmental factors of the 18 study sites on the West Coast, South Island

Sites	River name	Map coordinates East/North	Site area (m^2)	Width (m)	pH	Cond. (µS/cm)	Ca (mg/l)	DOC (mg/l)	Total nitrogen (mg/l)	Total phosphorus (mg/l)	Substrate (cm)	Depth (cm)	Temp. (°C)	Disturb. score	Velocity (m/s)	Macrophyte cover (%)	Canopy cover (%)	Undercut banks (%)	CPOM (g/m^2)	Chl.*a* ($\mu g/cm^2$)
1	Duskes Creek	23440/58231	63.9	3.0	4.5	41	25.0	41	0.33	<0.008	17.3	27.3	14.4	22	1.0	5	75	5	3.3	0.5
2	Frosty Creek	23462/58205	29.6	2.9	4.4	36	0.5	4.	0.23	<0.008	5.5	45.2	13.2	15	0.4	70	65	0	11.1	0.4
3	Kapitea Creek trib.	25348/58438	40.8	2.3	4.7	58	1.3	46	0.33	0.014	12.5	17.1	13.3	25	0.8	5	10	5	21.1	0.1
4	Nemona Creek	23639/58472	62.3	3.7	6.6	50	2.7	36	0.15	0.011	12.3	11.0	12.8	20	0.4	0	95	20	12.7	0.8
5	Kapitea Creek swamp	23598/58340	42.2	2.3	5.3	27	0.6	45	0.18	<0.008	9.8	23.0	12.2	25	0.3	10	50	80	27.1	0.4
6	Serpentine Creek trib.	23578/58430	29.3	3.1	4.4	46	0.6	46	0.27	0.011	10.3	15.6	14.5	16	0.4	15	70	80	6.5	0.1
7	Red Jack Creek trib.	24064/58840	19.7	1.2	5.1	43	13.0	54	0.38	0.023	8.9	8.6	11.4	26	0.6	5	70	40	51.4	0.3
8	Red Jack Creek trib.	24062/58839	52.1	2.2	5.2	40	24.0	51	0.37	0.020	11.4	13.7	12.2	23	0.5	5	5	50	32.2	0.2
9	Graham Creek	23891/58623	48.8	2.4	4.4	41	0.9	52	0.43	0.020	11.0	21.8	11.6	26	0.3	30	75	30	33.3	0.9
10	Lake Kaniere trib.	23585/58213	16.9	0.9	4.1	40	0.3	44	0.27	<0.008	3.4	14.7	12.5	17	0.2	40	90	40	31.7	0.2
11	Duffers Creek	23993/58754	76.7	4.6	6.8	36	17.0	32	0.18	0.021	8.8	17.2	12.7	24	0.8	5	5	10	6.0	0.7
12	Molly Creek trib.	23846/58502	46.2	4.9	7.9	129	7.0	0.9	0.11	<0.008	13.8	21.6	11.7	24	0.7	5	30	5	25.2	6.9
13	Deep Creek	23914/58522	66.7	8.8	6.6	31	1.4	34	0.21	0.010	16.0	19.6	12.8	25	0.7	5	5	5	7.1	0.9
14	Red Jacks Creek	23854/58598	127.9	6.7	6.5	48	12.2	35	0.29	0.023	12.1	19.2	12.8	31	0.7	5	40	15	1.3	0.8
15	Orangipuku River trib.	23836/58302	76.2	2.7	7.4	71	8.6	<0.2	0.30	<0.008	9.3	16.3	12.7	21	0.3	10	5	70	11.5	0.3
16	Orangipuku River	23832/58298	36.8	3.0	7.4	72	8.9	0.4	0.16	0.025	6.3	18.3	13.7	21	0.2	30	60	50	30.3	1.4
17	Bruce Creek trib.	23836/58352	47.6	3.1	6.4	89	11.0	38	0.46	0.013	4.1	33.8	13.7	21	0.3	70	5	70	2.7	0.5
18	Styx River trib.	23596/58123	45.9	3.2	6.9	91	9.9	1	0.17	0.016	9.7	14.6	10.8	29	0.6	50	95	5	7.4	1.0

Map coordinates are for New Zealand Map Series 260. Site numbers are those used in Fig. 1 (sites 1–10 are streams without trout and 11–18 are streams with trout). Cond. is conductivity at 25 °C, Ca is the calcium concentration, DOC is dissolved organic carbon, Substrate is median substrate size, Disturb. Score is the Pfankuch bottom score index (see methods), CPOM is coarse particulate organic matter and Chl. *a* is chlorophyll *a* concentration.

Table 2 – Component loadings of abiotic factors for the 18 streams and percentage of variance explained by the five retained principal component axes

Source	PC1	PC2	PC3	PC4	PC5
Variance explained (%)	25.05	17.92	14.78	11.02	8.0
Eigenvalues	4.26	3.05	2.51	1.87	1.36
pH	**0.882**	0.199	0.227	0.241	−0.030
Dissolved organic carbon (mg/l)	−**0.848**	0.276	0.051	0.057	0.013
Chlorophyll *a* (μg/cm^2)	**0.796**	0.089	−0.094	0.021	0.333
Conductivity (μS/cm)	**0.750**	−0.225	0.052	0.234	−0.078
Total nitrogen (mg/l)	−**0.647**	−0.275	0.175	0.445	−0.234
Macrophytic cover (%)	0.030	−**0.961**	−0.026	−0.064	−0.014
Substrate median size (cm)	−0.069	**0.858**	0.094	0.093	0.249
Depth (cm)	0.060	−0.587	0.487	−0.309	0.323
Coarse particulate organic matter (g/m^2)	0.073	0.096	−**0.782**	−0.037	−0.331
Temperature (°C)	−0.252	−0.080	**0.698**	−0.394	−0.192
Canopy cover (%)	−0.081	−0.177	−**0.624**	−0.258	0.173
Width (m)	0.386	0.314	0.575	−0.018	0.468
Total phosphorus (mg/l)	−0.041	0.023	−0.133	**0.790**	−0.061
Calcium (mg/l)	0.240	0.121	0.320	**0.723**	0.013
Disturbance (Pfankuch bottom score index)	0.109	0.346	−0.090	**0.701**	0.388
Undercut banks (%)	−0.115	0.067	0.035	0.028	−**0.908**
Velocity (m/s)	−0.081	0.475	0.291	0.253	**0.656**
t-test (*p* value)	**0.001**	0.833	0.086	0.188	0.765

Important loadings are shown in bold face. *p*-values refer to Independent Sample *t*-tests, testing the differences in scores between streams with and without trout.

biomass (Fig. 5). The cased or shelled collector–grazers, *Potamopyrgus*, *Pycnocentria*, *Pycnocentrodes* and *Olinga*, were present only in trout streams and were negatively correlated with axis 1 and positively correlated with axis 2 (Fig. 5). In contrast, *Polyplectropus*, *Psilochorema*, Tanypodinae, Oligochaeta and *Zephlebia* (the first three are predators and the last two are collector–grazers), were found only in streams without trout and were positively correlated with both axes (Fig. 5). Overall, the canonical correspondence analysis showed that a majority of invertebrate taxa were negatively correlated with axis 1, indicating they were most common in the more circumneutral streams. Several taxa, such as *Aoteapsyche*, Elmidae, Chironomidae and *Hydrobiosis*, were also negatively correlated with axis 2, suggesting they are adapted to living in streams with a high level of physical disturbance. The linear regressions showed that crayfish abundance was not related to invertebrate abundance in either stream type (trout streams: $r^2 = 0.044$, $F = 0.277$, $p = 0.618$; no-trout streams: $r^2 = 0.001$, $F = 0.006$, $p = 0.943$).

4. Discussion

Previous experimental and field studies in New Zealand have shown that exotic brown trout affect the functioning of New Zealand stream ecosystems at the population, community and ecosystem levels, by modifying the behaviour of organisms (summarized in Townsend, 2003). For example, the presence of trout can lead to strong top-down control of community structure and ecosystem functioning by fragmenting the distribution and reducing the abundance of galaxiid fish species, probably through predation and competition (Crowl et al., 1992; McIntosh, 2000a, 2003). Moreover, trout have been shown to affect the structure of the macroinvertebrate community and the abundance of periphytic algae through effects on grazer biomass and behaviour (Flecker and Townsend, 1994; McIntosh and Townsend, 1995, 1996; Nyström et al., 2003; Zhang et al., 2004). The impact of trout on food webs dominated by large omnivores, such as crayfish, is less well known. However, the results of the present study indicate that the abundance of native galaxiid fish, endemic crayfish and other macroinvertebrates differs between streams with and without trout and that naturally acidic, brown water streams on the West Coast of New Zealand can act as refuge areas for native crayfish and galaxiid species. Although numerous New Zealand stream invertebrate species tolerate low pH and moderately elevated concentrations of metals (Winterbourn and McDiffett, 1996), others do not, and overall brown water streams have less species-rich benthic faunas than circumneutral pH streams. The negative effects of acidity seem to have a stronger effect on macroinvertebrate community structure than any indirect effects associated with a reduction in crayfish density in circumneutral streams due to the presence of trout.

The results of the present study indicate that the native crayfish (*P. planifrons*) could be affected negatively by introduced brown trout in West Coast streams. Usio and Townsend (2000) came to a similar conclusion with respect to the second native crayfish (*P. zealandicus*) in a study on the east of the South Island. They showed that crayfish abundance was negatively associated with trout abundance and positively with wood cover, which provided habitat and refuge from predators. The vulnerability of crayfish to predation by trout may in part reflect their inability to respond to chemical cues released by trout (Shave et al., 1994). Because trout have replaced native fishes in many New Zea-

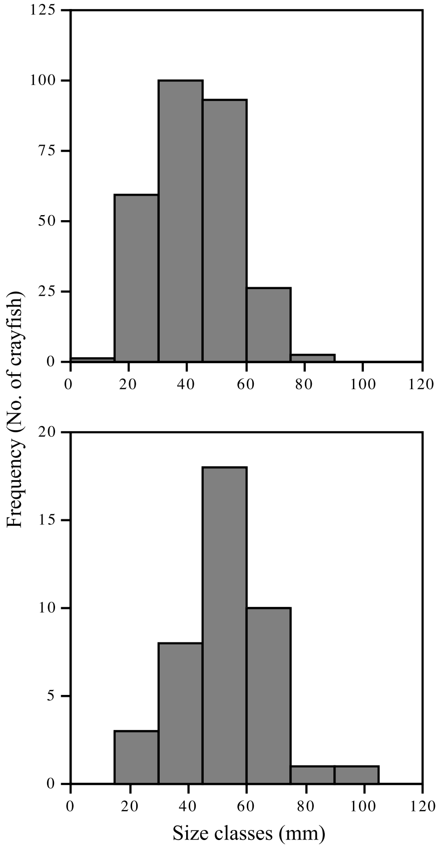


Fig. 2 – Size frequency of crayfish from streams with trout (lower, *n* = 41) and without trout (upper, *n* = 281). Note the different scales on the *y*-axes.

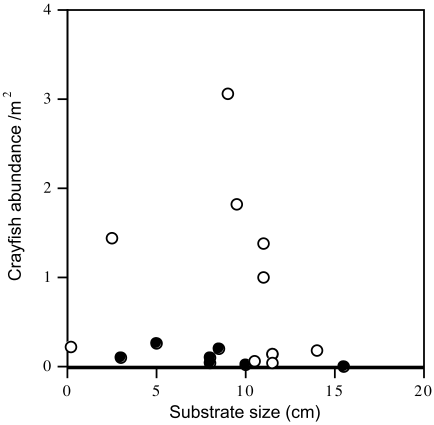


Fig. 3 – Mean crayfish abundance in relation to median substrate size for streams with trout (*n* = 8, black circles) and without trout (*n* = 10, open circles).

land streams (McIntosh et al., 1992; McIntosh and Townsend, 1995), predation pressure on crayfish has probably increased since their introduction. Even though only one trout, the largest one, had consumed crayfish in the present study, it is likely that predation by large trout affects crayfish abundance. Small trout may compete with crayfish for shelter and may exclude juveniles that become more exposed to the risk of predation by larger trout. Most native fishes in New Zealand are small and not major predators of crayfish, although eels eat crayfish (Jellyman, 1989; Schulze et al., 2004; present study) despite crayfish exhibiting antipredatory behaviour towards them (Shave et al., 1994). Although eels were present in most of the West Coast study streams, their abundance, unlike that of trout did not explain the variation in crayfish abundance. This is consistent with a study by Hicks and McCaughan (1997) on the North Island where the abundance and biomass of eels did not affect the abundance and biomass of *P. planifrons*. Instead, both the abundance and biomass of eels and crayfish seemed to be related to environmental conditions in that study. In the present study the gut content analysis also showed that eels and trout had some overlap in diet but little overlap with crayfish diet. This suggests that crayfish are not affected by competition for food from eels or trout.

In addition to trout affecting their abundance, the size distribution of crayfish differed between sites with and without trout, with fewer small individuals being caught in trout streams. Englund and Krupa (2000) also found that fish had a negative effect on small (25–30 mm body length) crayfish (*Cambarus bartonii* and *Orconectes putnami*), but that large crayfish were not eaten even by the largest fishes (120–190 mm body length). Similarly, Usio and Townsend (2000) found a lower percentage of small (15–25 mm) crayfish (*P. zealandicus*) and a higher percentage of large (>35 mm) crayfish in trout pools than no-trout pools in a New Zealand stream. These findings suggest that trout prey selectively on small crayfish. Whitmore and Huryn (1999) showed that *P. zealandicus* was amongst the most long-lived and slowest-growing crayfish species known, therefore small, slow-growing, juvenile crayfish are likely to be particularly vulnerable to trout predation for a relatively long time. In the absence of trout, crayfish abundance seemed to be related to substrate size with more crayfish associating with sites dominated by cobbles (about 9 cm) than with sites dominated by sand or large boulders. In the West Coast streams, which lack trout and primarily terrestrial predators that might feed on crayfish, cobbles provided refuges for crayfish, perhaps mainly from each other during moulting, since *P. planifrons* is cannibalistic like many other crayfish species (Nyström, 2002).

Trout also appeared to have a negative effect on galaxiid species consistent with the results of previous studies (McIntosh, 2000a; Townsend, 2003), but whether crayfish also influence galaxiid distributions is unknown. Some crayfish species potentially have negative effects on the distribution of small benthic fishes through predation, competition for food and shelter (Guan and Wiles, 1997; Dorn and

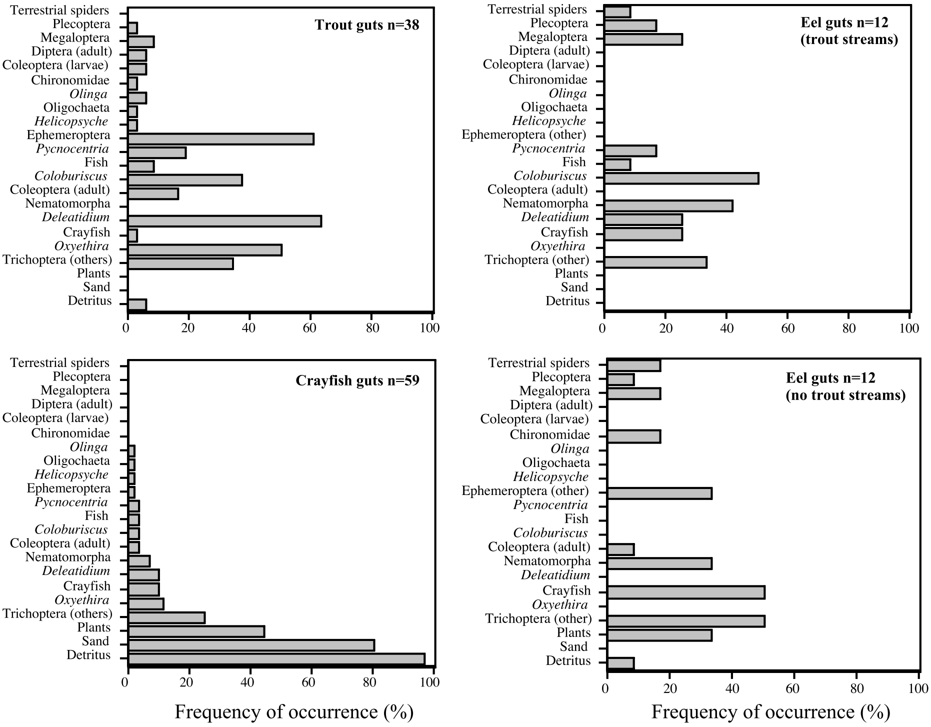


Fig. 4 – Frequency of occurrence (%) of food items in trout, crayfish and eel guts. The crayfish analysed were taken from streams both with and without trout. The eels are divided into eel guts from streams with trout (upper right) and streams without trout (lower right).

Mittelbach, 1999), but in the West Coast streams *P. planifrons* appeared to have few if any negative effects on the abundance of galaxiids.

Tolerance to low pH varies a great deal among crayfish species within the Cambaridae (France, 1993; Seiler and Turner, 2004), whereas species of Astacidae are usually

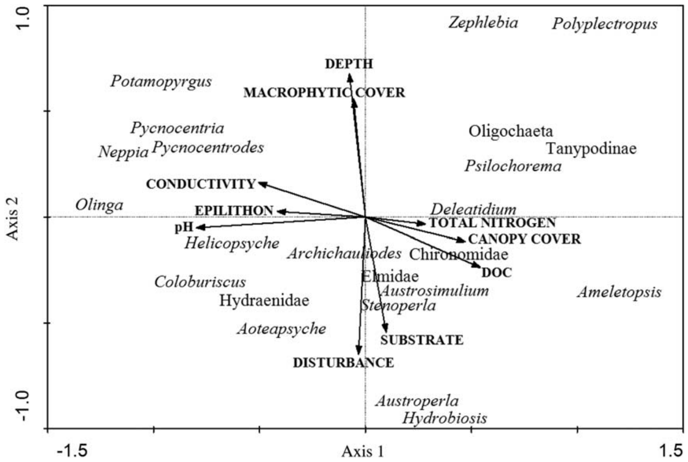


Fig. 5 – Simple correlation plot of the most common invertebrate taxa to axes 1 and 2 from the Canonical correspondence analysis with the environmental factors that explained most of the variation, also shown.

considered to be intolerant of acid water with pH < 5.5 (Nyström, 2002) and low calcium concentrations <2.0 mg/l (Naura and Robinson, 1998). However, in Tasmania *Parastacoides tasmanicus* and other species of Parastacidae live in highly acidic water (Williams, 1974; Newcombe, 1975). *P. planifrons* was found in streams with pH down to 4.1 in the present study and at sites where calcium concentration was as low as 0.9 mg/l. Most brown water streams in New Zealand have a naturally low pH because of high concentrations of organic acids in the water, and also have high concentrations of dissolved aluminium, which is rendered non-toxic through complexation with dissolved organic matter (Collier et al., 1990). Both native crayfish and some native fish species in New Zealand are well adapted to life in this stream environment (Collier et al., 1990) and also occur in circumneutral waters. Seiler and Turner (2004) found that the cambarid crayfish (*C. bartonii*) grew more slowly in acid water (pH around 4) than at more circumneutral sites, but crayfish were less abundant at the circumneutral sites where fish biomass (brook trout, creek shub and mottled sculpin) was significantly higher. It is unlikely that pH, in itself, accounts for the low abundance of *P. planifrons* in the less acidic West Coast streams; instead trout are implicated by the result of the present study. McIntosh (2000a) argued that trout do not affect native New Zealand fishes in some streams, because the physical conditions prevailing do not suit them. Similarly, brown water streams with low pH and low calcium concentrations can act as "safe" havens for native crayfish as well.

The macroinvertebrate fauna of many New Zealand streams is dominated numerically by species that can be categorized as collector–grazers (Death, 1995) and of these a higher proportion had cases (caddis) or shells (molluscs) in trout streams than no-trout streams on the eastern slopes of the South Island mountains (Nyström et al., 2003). Results of the present study are consistent with these patterns as collector–grazers predominated in all streams and species with cases or shells were more common in trout streams. The higher abundance of invertebrates in streams with trout (including consumers with cases or shells) could potentially be an indirect effect brought about by reduced predation by crayfish. However, the variation in invertebrate abundance observed was not related to crayfish abundance. Furthermore, the gut content analyses suggested that few crayfish had consumed invertebrates, although even in low numbers they can make a disproportionately large contribution to the energy required for tissue growth in *P. planifrons* (Parkyn et al., 2001). Instead, variation in invertebrate abundance appeared to be related most strongly to differences in abiotic factors such as pH, conductivity, depth, substrate and disturbance. *Potamopyrgus* requires calcium for shell formation and may be absent from naturally acidic brown water streams for that reason (Winterbourn and Collier, 1987), whereas other physiological constraints and/or low food quantity or quality may limit the distribution and abundance of other taxa (Collier et al., 1990). An increase in the production and/or biomass of algae can have positive effects on the local abundance of grazers, through a bottom-up effect (Forrester et al., 1999) and might help explain why the abundance of many invertebrates (insects and snails) was higher in West Coast streams with trout. In contrast, crayfish and galaxiid abundances were greater where trout were absent, suggesting that interactions with trout have brought about their retreat to trout-free refuges.

Acknowledgement

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Appendix 1

Number of crayfish and fish caught by electrofishing at the different sites

Species	Site no.																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Paranephrops planifrons	11	6	5	2	2	53	60	71	48	24	2	6	0	1	15	9	4	4
Salmo trutta	0	0	0	0	0	0	0	0	0	0	1	8	7	11	160	62	6	3
Anguilla dieffenbachii	8	3	10	4	5	1	1	0	3	0	2	7	8	2	5	3	1	11
Anguilla australis	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Galaxias fasciatus	22	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Galaxias postvectis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Galaxias brevipinnis	0	0	26	1	8	0	12	94	20[a]	1	0	0	0	0	0	0	0	1
Galaxias divergens	0	0	0	0	0	0	0	0	0	0	1[a]	0	0	9[a]	0	0	8	0
Cheimarrichthys fosteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Gobiomorphus huttoni	0	0	0	0	5	0	0	0	0	0	19	0	3	6	0	0	0	6
Gobiomorphus cotidianus	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	17	0
Gobiomorphus hubbsi	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0

a Identification uncertain.

Appendix 2

All invertebrate taxa found in the Surber samples. Total number of individuals caught at each site is presented as absolute numbers. Sites 1–10 are the streams without trout and 11–18 are the ones with trout

Species	Functional group	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15	Site 16	Site 17	Site 18
Ephemeroptera																			
Deleatidium	G	77	5	288	73	224	18	226	79	75	14	165	38	312	104	376	113	238	37
Zephlebia	G	1	8	2	0	8	8	0	0	1	0	0	5	0	0	0	36	0	1
Neozephlebia	G	0	3	0	9	1	0	0	0	1	0	0	0	0	0	0	98	9	0
Austroclima	G	0	0	0	0	0	0	8	0	0	0	0	0	0	0	4	39	0	4
Mauiulus	G	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coloburiscus	F	0	0	0	1	0	2	2	9	0	0	14	51	38	5	114	194	0	2
Nesameletus	G	0	3	0	0	0	0	0	0	0	0	8	0	21	16	0	0	0	0
Ameletopsis	P	7	0	1	1	2	1	2	0	12	0	0	0	0	0	0	0	0	0
Ichthybotus	G	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	0	0
Plecoptera																			
Stenoperla	P	0	0	2	3	2	0	6	7	4	0	0	8	2	5	5	6	0	7
Austroperla	S	0	0	0	1	0	0	10	3	6	0	1	0	3	1	0	2	0	6
Spaniocerca	G	0	0	1	3	0	0	3	7	0	0	1	0	0	0	0	0	0	1
Cristaperla	G	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Zelandobius	G	3	0	3	0	0	3	3	0	34	0	0	0	0	1	0	0	0	1
Acroperla	G	10	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraperla	G	1	0	1	1	18	0	0	0	0	1	0	0	0	1	0	0	0	0
Spaniocercoides	G	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Megaleptoperla	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	11	0	0
Trichoptera																			
Aoteapsyche	F	0	0	13	3	0	0	1	0	0	0	1	2	8	3	13	2	0	1
Hydrobiosella	F	0	0	26	0	0	0	2	3	1	0	0	0	0	3	0	2	0	1
Hydrobiosis	P	0	0	9	2	8	0	4	7	4	0	23	0	23	29	15	5	15	1
Psilochorema	P	10	2	9	2	15	1	3	5	15	1	1	0	4	0	18	15	14	2
Costachorema	P	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Neurochorema	P	0	0	0	0	0	0	0	0	0	0	3	0	1	1	0	0	0	0
Hydrochorema	P	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Polyplectropus	P	2	2	1	0	2	0	0	3	1	3	0	0	0	0	0	0	1	0
Zelolessica[a]	G	3	0	0	1	3	2	0	0	8	0	0	0	0	1	0	0	0	1
Zelandoptila	G	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triplectides[a]	S	0	0	2	5	3	0	2	2	0	2	0	0	0	0	0	18	0	0
Hudsonema[a]	G	0	0	2	0	0	0	0	0	0	0	0	0	3	0	0	1	4	0
Oxyethira[a]	G	0	0	2	0	0	0	0	1	0	0	1	0	0	0	0	0	6	0
Pycnocentrodes[a]	G	0	0	0	0	0	2	0	0	0	0	34	3	26	0	322	56	553	6
Pycnocentria[a]	G	0	0	0	0	1	0	0	0	0	0	0	7	23	0	3	64	24	1
Olinga[a]	G	0	0	0	0	0	0	0	0	0	0	0	72	24	4	15	41	2	0
Beraeoptera[a]	G	0	0	0	0	0	0	0	0	0	0	0	0	61	0	0	0	0	0
Pycnocentrella[a]	G	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oeconesus[a]	S	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	6	6	0
Helicopsyche[a]	G	0	0	42	3	1	0	0	0	1	0	0	4	29	3	60	217	3	1
Rakiura[a]	G	0	12	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Philorheithrus	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20	5	0
Megaloptera																			
Archichauliodes	P	3	0	2	1	1	1	3	8	14	0	6	39	25	11	18	40	3	0
Coleoptera																			
Elmidae	G	21	0	13	42	72	2	163	28	60	2	245	66	320	141	167	46	175	8
Hydraenidae	G	1	0	0	11	0	0	1	1	0	0	1	1	21	1	3	2	3	0
Ptilodactylidae	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	11	0	0

Appendix 2 – *continued*

Species	Functional group	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15	Site 16	Site 17	Site 18
Hydrophilidae	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Liodessus	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
Scirtidae	G	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Diptera																			
Chironomidae	G	2	0	14	16	131	16	22	9	29	14	36	41	9	31	19	25	33	4
Tanypodinae	P	11	9	4	40	28	0	28	2	1	7	2	0	4	0	0	4	3	0
Paradixa	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Aphrophila	G	2	0	0	0	3	1	0	0	0	0	0	9	3	1	3	2	0	0
Hexatomini	G	0	0	5	1	0	0	0	0	0	0	1	0	0	0	3	0	6	0
Austrosimulium	F	0	0	8	1	2	1	18	11	12	0	64	0	6	11	12	7	3	1
Eriopterini	G	0	0	0	0	0	1	0	2	0	0	1	0	1	2	0	0	2	2
Mischoderus	G	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Empididae	G	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0
Ephydridae	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Muscidae	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0
Tabanidae	P	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ceratopogonidae	P	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Crustacea																			
Paraleptamphopus	G	0	3	0	1	0	0	0	0	0	50	0	0	0	0	0	0	0	0
"*P. caeruleus*"	G	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0
Paranephrops	O	0	2	0	1	0	5	0	1	0	0	0	0	0	0	0	0	0	0
Ostracoda	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Arachnida																			
Acari	P	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1
Mollusca																			
Potamopyrgus[a]	G	0	1	1	0	0	0	0	0	0	0	20	96	1	0	234	576	348	0
Sphaerium[a]	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Austropeplea[a]	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Physella[a]	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Annelida																			
Oligochaeta	G	7	10	3	4	38	7	3	20	16	40	30	9	1	0	20	6	250	8
Alboglossiphonia	P	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tricladida																			
Neppia	P	0	0	0	0	0	0	0	0	0	0	11	11	4	0	8	16	4	0
Porifera	F	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Functional groups: G = collector/grazer, F = filterfeeder, S = shredder, P = predator and O = omnivore.

[a] Invertebrates with cases or shells.

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II

FLUCTUATIONS IN HARVEST OF NATIVE AND INTRODUCED CRAYFISH ARE DRIVEN BY TEMPERATURE AND POPULATION DENSITY IN PREVIOUS YEARS

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Abstract

The effects of temperature and density on annual fluctuations in catches (CPUE) of large (>9 cm TL) adult crayfish are evaluated using time-series analysis. We tested if temperature during different stages of the crayfish life-cycle, growth season (ADD>10ºC), mating season, winter, spring hatch season, summer (when the catches of crayfish occur) and also population density (Nt-1) influenced the observed catch (Nt) from 1946 until today in a Southern Swedish lake. From 1946 until 1974 native noble crayfish (*Astacus astacus*) inhabited the lake, but then the crayfish plague wiped out the whole population. In 1982 the exotic signal crayfish (*Pacifastacus leniusculus*) was introduced and is still present in the lake today. This made it possible to model the two species separately and compare how temperature and density influence the abundance of large adult crayfish. We found that both climatic and density dependent factors influenced the observed fluctuations of crayfish abundance in Lake Bunn and there was a time lag for most of the factors included in the model. Winter temperature was positively correlated with abundance of large crayfih and explained most of the fluctuations for both species. Also density dependence was included in the best model for the two species. For noble crayfish the growth season (ADD>10 ºC) was negatively correlated with abundance of large crayfish, while for signal crayfish the temperature during mating season was negatively correlated with the abundance of large crayfish. Based on these contradicting results, of a positive influence of winter temperature and the negative one for ADD>10ºC for noble crayfish, and the temperature during hatching season for signal crayfish, it is difficult to predict how a further climate warming will affect crayfish populations dynamics in freshwaters.

Introduction

Climate fluctuation has become one of the most recognised factors causing inter-annual variability in organism abundance in aquatic and terrestrial ecosystems (Eaton and Scheller 1996, Winder and Schindler 2004, Adrian et al. 2006, Saether et al. 2007, Williams and Middleton 2008). Climate affects species abundance and distribution, and the ongoing climate change poses a significant risk to many species (Crozier and Zabel 2006). In the temperate zone, with strong seasonality, growth and reproduction of many species is restricted to the warmer months of the year (Whitely et al. 1997, Jonsson and Edsman 1998). Ecosystems in the temperate zone, such as temperate lakes, are often characterized by distinct seasonal patterns in physical and biological processes (Winder and Schin-

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dler 2004). Due to the high heat capacity of water, aquatic systems may be especially sensitive to climatic changes and large-scale fluctuations in temperature (Winder and Schindler 2004). For aquatic poikilothermic animals, temperature is in general the major limiting factor, influencing distribution, growth, metabolism, reproduction and life history (Nakata et al. 2002).

Crayfish are poikilotermic and the importance of temperature to the overall life cycle of crayfish is well studied (see Reynolds 2002 and references therein). It has, for example, been reported that a year with higher temperatures and longer growing season increased growth in crayfish with 12% compared to a colder year (France 1985) and that a cold summer reduced the growth of crayfish in an isolated Swedish pond (Abrahamsson 1966). It has also been noted that a decline in crayfish (*Cherax destructor*) survival when water temperatures exceed 16ºC is not only due to the temperature reaching the thermal limits of crayfish (Verhoef and Austin 1999), but also to increased cannibalism and poorer water quality (Hammond et al. 2006). At higher temperatures crayfish will moult more frequently and thereby be more vulnerable to predation and cannibalism. Since temperature influences several stages in the crayfish life cycle it will probably have a strong impact on the population size from year to year. Still, few studies exist today that address the importance of temperature for crayfish abundance, frequently observed to fluctuate, in lakes and streams. This is mainly because long-term data on crayfish abundance are lacking, data that are needed to able to understand population fluctuations.

Native noble crayfish (*Astacus astacus*) and introduced signal crayfish (*Pacifastacus leniusculus*) are the two crayfish species found in Swedish freshwaters today. In many southern Swedish lakes the former noble crayfish population has gone extinct due to the crayfish plague, and many of these lakes have been restocked with signal crayfish. The two species are similar in size, morphology and life history, and their life cycles are synchronous (Abrahamsson 1971, Söderbäck 1995). The signal crayfish has a higher fecundity than the noble crayfish (Abrahamsson 1971), and seems, to grow faster and be more aggressive. The temperature optimum for best growth in signal crayfish is around 22 ºC (Firkins and Holdich, 1993), while for noble crayfish it has been shown to be in the interval 16-24 ºC (Söderbäck et al. 1988). The upper thermal tolerance limit is higher for signal crayfish, which has been shown to tolerate temperatures up to 33 ºC (Becker et al. 1975), compared to up to 28 ºC for noble crayfish (Rognerud et al. 1989). Temperatures above the thermal optima, or variable temperatures during important stages in the life cycle, may increase mortalities following the moult (Jussila and Evans, 1996). Moreover, the signal crayfish is a carrier of the crayfish plague, but can die from it under stressful conditions (Persson and Söderhäll 1983, Persson et al. 1987). Noble crayfish, on the other hand, is vulnerable to the plague and whole populations can be wiped out from lakes rather quickly (weeks) when infested with the plague (Persson et al. 1987, Gydemo 1996).

Due to the above-mentioned factors it is likely that temperature in previous years should influence potential harvest of large crayfish in the following years. Climate change (i.e. changes in temperature) may thus affect the growth and survival in noble and signal crayfish species, possibly in different ways. A high temperature may favour growth in signal crayfish more than in noble crayfish, since the signal crayfish can tolerate higher temperatures. At the same time, a high temperature increases the activity of crayfish and may lead to higher stress, which

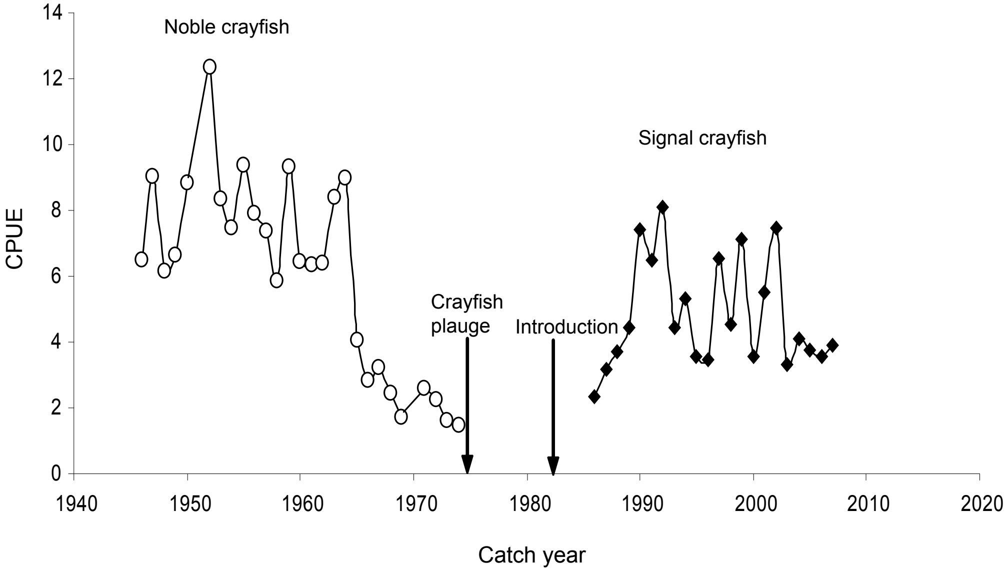

Figure 1. The observed catches of large native noble crayfish (white dots) and introduced signal crayfish (black dimonds) fluctuates annually in Lake Bunn. Noble crayfish inhabited the lake until 1974, when the crayfish plague struck the lake and wiped out the whole population. In 1982 signal crayfish was introduced to the lake and has inhabited the lake since then.

may decrease survival in signal crayfish due to stress from the crayfish plague.

In this study we explored if catches (i.e. abundance) during a twenty-year period for the native noble crayfish followed by a similar period of the introduced signal crayfish in a lake were correlated with temperature. The aim was also to identify the seasonal temperatures that are most important in explaining the harvest of crayfish in the following years.

Methods

Catch and temperature data

The catch (CPUE) data used in this study spans from 1946 until 2007 (Fig. 1) and is from the southern basin of lake Bunn, which is situated in the southern part of Sweden (Longitude: 87°08', Latitude: 14°53'). Lake Bunn has an area of 10 km^2, with a maximum depth of 20 m, and with a volume of 65 Mm^3. From 1946 until 1974 the native noble crayfish inhabited the lake (Fig. 1). Then the crayfish plague struck the lake and wiped out the whole noble crayfish population. In 1982 an introduction of signal crayfish was made and from then until today signal crayfish inhabits the lake (Fig. 1). Since crayfish are caught in August in Sweden, we could not use calendar year; instead we defined a year between September to August. For this study we used timeseries of 20 years for both species even though there are more years available, especially for noble crayfish. However, the last years before the noble crayfish population crashed in the lake, the population may have already been affected by the plague and therefore some years have been excluded. Also, only the proportion of crayfish in the catches that was equal to or longer than 9 cm in TL for noble crayfish and 10 cm in TL for signal crayfish were used. This because there were several missing values of total catches, especially for the earlier years of noble crayfish. Crayfish density (CPUE) was estimated using traps baited with dead cyprinids. The traps are cylindrical with funnel entrances at both ends and were set out in the late afternoon and crayfish are removed the following morning. This methodology provided a rough estimate of the density of larger crayfish (≥ 60 mm, total length) (Abrahamsson & Goldman, 1970). Different traps were used for catching noble (Swedish standard trap) and signal crayfish (Trappy), but since we do not compare the catches of the two species, the use of different traps do not confound our results. Approximately 30 traps were used at each fishing occasion for both species. The measurement of the abundance of large crayfish is therefore calculated as catch per unit effort (CPUE), where differences in the number of traps and fishing nights are included. Further, we used daily air temperature data, from 1946 until today, from a weather station located near the lake. Air temperature has been shown to correlate well with water temperatures in other temperate lakes (Gerten and Adrian 2000, 2002; Winder and Schindler, 2004; Wilhelm et al., 2006) and we are therefore confident in using air temperature as a proxy for water temperature.

Ecologically relevant variables

Since different stages of the crayfish life cycle are affected by temperature we transformed daily temperature data into more ecologically relevant parameters. Crayfish growth only occurs above a certain temperature (Reynolds 2002). It has been shown that growth in most Astacid crayfish species, which both noble- and signal crayfish belongs to, requires a temperature around or above 10 ºC for growth (Abrahamsson 1972, Firkins and Holdich 1993). We therefore used annual degree days above 10 ºC as an estimate for adult crayfish growing season (W1). As mating season occurs in autumn in Sweden we used the mean temperature during September throughout November as mating season temperature (W2). The coldest months in Sweden are January and February and the mean temperature during these two months was used as winter temperature (W3). Several studies have argued that the temperature affects the catches of crayfish when the fishing takes place. A cold night has been suggested to gives less crayfish than a warmer one, since crayfish are more active at warmer temperatures (Somers and Stechey 1986). Therefore, the mean temperature during August, when the catches used for this study was conducted, has been used as a measure of crayfish catchability (W4). Temperature has also been shown to be important for hatching time and the hatching takes place in early summer. Therefore, we used the mean temperature during March to May as the spring hatching season temperature (W5). All ecologically relevant variables were standardised and normalised before used in the time series analysis.

Model selection

To find the model that best explained the observed crayfish population fluctuations, we used a modified Rickert model:

$$Nt=Nt\text{-}1(e^{a+bNti+cWti})$$

where “Nt” is the catch for the year in question and “Nt-1” is the catch the previous year, “a”, “b” and “c” are constants and “W” is one of the ecologically relevant parameters mentioned above. Since the crayfish in this study were caught with baited traps that only catches crayfish equal to or larger than 6 cm in total length, some of the above mentioned parameters may have a lag phase of one to three years. Therefore, the parameters were included for the year in question (t), the previous year (t-1), two years earlier (t-2) or three years earlier (t-3). With this model we could simultaneously test if density dependence and any of the external ecologically relevant factors explained the observed population fluctuations in Lake Bunn. Density dependence is confirmed if any "b_{ti}" are incorporated in the model with a value below zero (Kölzsch et al 2007).

Since we have several parameters and to test all possible combinations would be unrealistic and also incorrect, we allowed for the exclusion/inclusion of all parameters independently (stepwise forward selection procedure) except for the constant "a" that was always kept in the model. This procedure includes models with lagged but not direct density dependence as well as density dependent models (Månsson et al. 2007). First we tested each parameter (density dependence and external ecologically relevant parameters) one by one and selected the parameter with the lowest AICc value (Akaike information criterion corrected for small sample size), to determine which parameters to first include in the model (Burnham and Anderson 1998). Then we did a new run with the first parameter kept in the model and tested all other parameters again one by one. If an inclusion of another parameter gained a lower AICc value than in the first run that parameter was also included in the model and a new run conducted. This was done until no further inclusion of parameters gained a lower AICc value. The final model represents the model that best explains the observed abundance fluctuations of large adult crayfish in Lake Bunn. This was done for the two crayfish species separately, which still enabled us to compare how temperature influences the catches of harvestable sized crayfish in the two species.

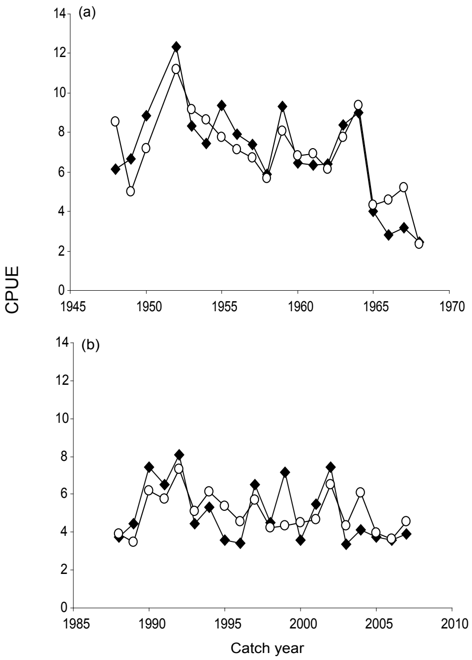

Figure 2. Model fit of the observed catches (black dimonds) and the predicted values from the best model (white dots) for a) native noble crayfish from 1948 until 1968, and b) introduced signal crayfish from 1987 until 2007.

Further, the variables included in the best models of the two species were then correlated to predicted CPUE values to explore how much each variable explained. The variable with the strongest correlation was run in a linear regression with predicted CPUE for the best model and standardized residuals saved for the next run. Then the variable that was next best correlated with predicted CPUE was run in a linear regression against the standardized residuals from the first run and new standard residuals saved. This to be able to explain the remaining variation after the previous variable had been accounted for. This was done for all variables included in the model. All calculations were conducted in Microsoft Excel for Windows, except linear regressions that were conducted in SPSS 11.0 for Mac OS.

Results

Density dependence was included in the best model and of the external ecologically relevant parameters the winter temperature (W3) was included in the best model for both the native noble crayfish and introduced signal crayfish. For noble crayfish also the number of day's exceeding 10°C (ADD>10°C, W1) was included in the best model. While for signal crayfish the temperature during mating season (W2) was also included in the best model. No other parameters were included in the best model that explained the catches of harvestable sized crayfish in either noble- or signal crayfish. There was a time lag of two years (t-2) for the two ecologically relevant parameters included in the best model for noble crayfish. For signal crayfish there was a two-year lag for winter temperature, but no time lag (t) for the temperature during mating season.

Our best model explaining fluctuations in the time series of large adult noble crayfish is of the form:

$$Nt=Nt\text{-}1(e^{a+bNt-1+c1W1(t-2)+c3W3(t-2)})$$

where "bNt-1" indicates density dependence since "b" was smaller than zero (-0.032), W1(t-2) represents ADD>10°C and W3(t-2) represents winter temperature, both with a time lag of two years. The model that best explains abundance fluctuations in the time series of large adult signal crayfish was similar but with some differences, as follows:

$$Nt=Nt\text{-}1(e^{a+bNt-1+c2W2(t)+c3W3(t-2)})$$

where "bNt-1" indicates a density dependence since "b" was smaller than zero (-0,107), W2(t) represents the temperature during mating season the year before the catch and W3(t-2) represents the winter temperature

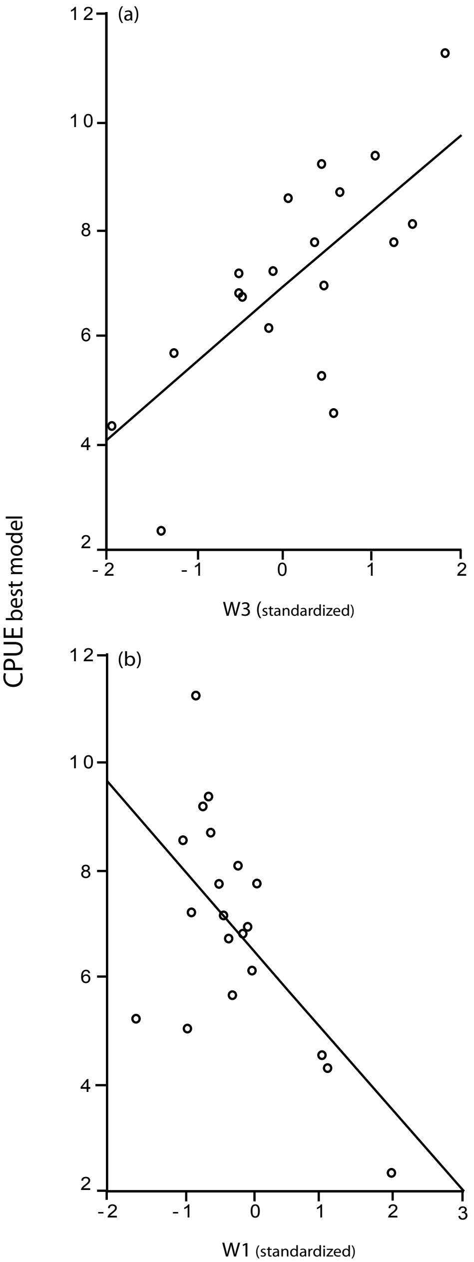

Figure 3. The predicted values of catches of large adult crayfish from the best model (CPUEbest model) for native noble crayfish were a) positively correlated with winter temperature (W3t-2) and b) negatively correlated with the number of days exceeding 10ºC annually (W1t-2, ADD>10ºC). Note the different scales on the x-axes.

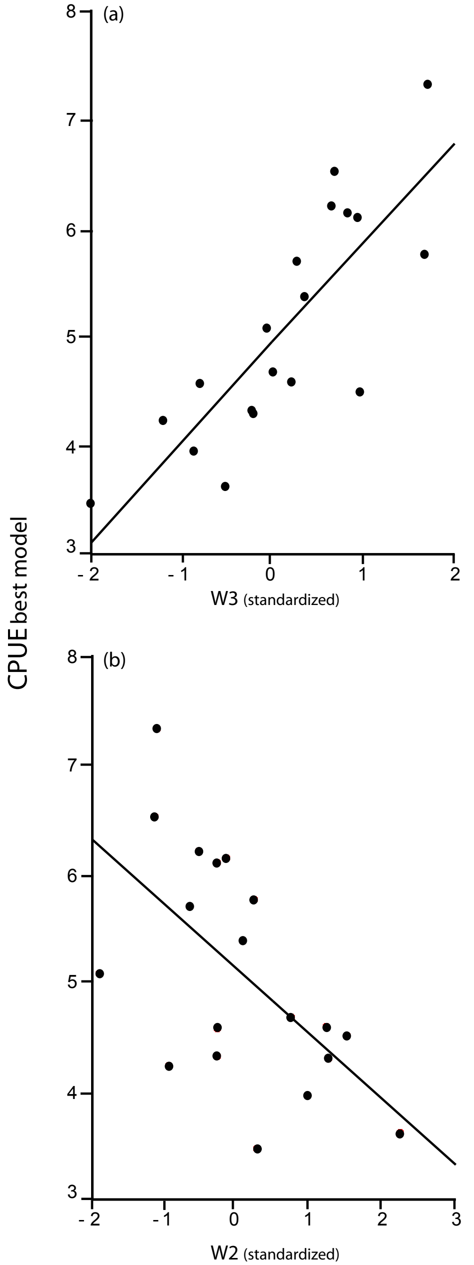

Figure 4. The predicted values of catches of large adult crayfish from the best model (CPUEbest model) for introduced signal crayfish were a) positively correlated with winter temperature (W3t-2) and b) negatively correlated with the temperature during mating season (W2t). Note the different scales on the x-axes.

with a two-year lag. Model trajectories of the final model of noble crayfish and signal crayfish revealed a good fit with the observational data (Figure 2a and b).

For the best model of noble crayfish, winter temperature (W3, t-2) explained 53.6% (linear regression, R^2), ADD>10°C (W1, t-2) 12.9% and population density (Nt-1) explained 24.4% of the variance in CPUE (Nt) of adult crayfish, so the deterministic part of the model explains 91.9% of the variation. For signal crayfish, winter temperature (W3, t-2) explained 66.7%, temperature during mating season (W2, t) 20.8% and population density (Nt-1) 7.1% of the variance in CPUE (Nt) of adult crayfish in the best model. The remaining % of the variation may be accounted for by demographic and some remaining, unknown environmental factor.

A warm winter temperature two years previous to the catches in August increases the "Nt" of large adult noble crayfish (Figure 3a), while a large number of "ADD>10°C" two years previous to the catch decreases the "Nt" (Figure 3b). For signal crayfish a higher winter temperature two years earlier also increased the catches of large adult crayfish (Figure 4a), while a warm temperature during mating season decreases the "Nt" following August (Figure 4b).

Since winter temperature was the most important factor in the best model of both species we further analysed how winter temperature has changed during the study period. The mean winter temperature has increased gradually from 1940 until today and more winters have had a mean temperature above freezing point in the last 20 years (Fig. 5).

Discussion

The crayfish population in Lake Bunn fluctuates in abundance from year to year and

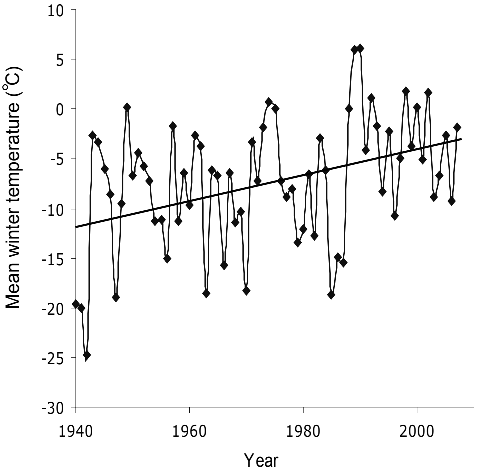

Figure 5. The mean winter temperature from 1946 until today in Lake Bunn (data from SMHI). The dotted line shows the freezing point.

these fluctuations are driven by climatic- as well as density-dependent factors. Crayfish are poikilothermic and many stages in their life cycle are temperature driven. Therefore, temperature is an important factor for crayfish population dynamics and we found that the temperature during winter (i.e. January and February) was the most important factor for the observed fluctuations of large adult crayfish in Lake Bunn. It is not possible to determine the mechanisms behind the observed fluctuations of crayfish abundance in Lake Bunn. We will however shortly discuss implications of the results and point out the additional factors that need to be determined to be able to predict future fluctuations in population size of crayfish. This may be particularly relevant in an era with ongoing changes in temperature, the commercial interest in harvesting crayfish for human consumption and recently unexplained declines of several populations of signal crayfish in Swedish lakes (L. Edsman personal communication).

Temperature has been shown to regulate crayfish survival and growth rates (Mason 1979, McMahon 2002), moulting frequency (Lowery 1988), feed consumption and assimilation (Nyström and Strand 1986; Parkyn and Collier 2002), and reproduction (Hessen et al. 1987, Reynolds 2002). All these factors have the potential to affect the abundance of crayfish. However, our model, which initially included crayfish growth (ADD>10°C), temperature during mating season, winter survival, activity (i.e. catchability), and temperature during spring hatch season, based on temperature data during periods of importance for these factors, indicates that the temperature during winter is most important for the growth and survival of adult crayfish and will determine the abundance of large (>9 cm TL for noble crayfish and >10 cm TL for signal crayfish) adults in the population from year to year in lake Bunn. The winter temperature in Lake Bunn has increased gradually during the study period and it has also become more common with days above the freezing point during winter. Cold-water species may be especially sensitive to increased temperatures. Eaton and Scheller (1996) found that the climate warming effect caused a nearly 50% reduction in thermal habitat for cold and cool water fish species in North American streams. It has also been shown that the duration of ice-cover in shallow lakes can have strong influence on heat storage, light penetration, oxygen concentrations, and thus, nutrient status in lakes (Pettersson et al. 2003, Jackson et al. 2007). How changes in thermal habitats and ice-cover will affect survival, nutrient status, and thus food availability for crayfish, in lakes is not known. The winter temperature in Lake Bunn is probably still favourable for crayfish survival, but a further increase in warmer winters might lead to a decrease in survival of crayfish. However, more studies on the influence of winter temperature on the survival of crayfish under more natural conditions are needed.

It has been shown for several fish species that temperature conditions strongly influence the annual growth increments (Hesthagen et al. 2004) and our results indicate that this might be the case for crayfish as well. The growth season, annual degree-days above 10ºC (ADD>10ºC), was included in the best model for noble crayfish. A year with many days of temperatures over 10ºC might increase the growth in the adult crayfish due to increased moult frequency (Westin and Gydemo 1986). However, we found a negative correlation between abundance of large adult crayfish and annual degree days above 10ºC. Verhoef and Austin (1999) observed a decline in survival rates of crayfish when water temperatures rose above 16ºC due to exceeding thermal capabilities, as well as increased number of aggressive encounters (i.e. cannibalism). Paglianti and Gherardi (2004) also found that growth of crayfish (e.g. *Austropotamobius pallipes* and *Procambarus clarkii*) decreased with increasing temperatures (from 16 to 24ºC). The authors argue that this may be due to increased metabolic consumption exceeding caloric intake, which leave little enrgy for growth.

The temperature during mating season was negatively correlated with the abundance of large signal crayfish. A high temperature during early autumn might prolong the growing season and the activity period of crayfish, influencing moulting frequency and mating. Even though growth rate may increase, the result may be increased mortality during this period, but it may also result in increased mortality later on if the crayfish grow instead of building up energy reserves needed to survive through winter (Jonsson and Edsman 1998). Based on these contradicting results, of a positive influence of winter temperature and the negative one for ADD>10ºC for noble crayfish, and the temperature during hatching season for signal crayfish, it is difficult to predict how a further climate warming will affect crayfish populations dynamics in freshwaters.

Our results suggest that the fluctuation in harvestable sized crayfish in Lake Bunn is density-dependent. That "bNt-1" was included in the best model for both noble- and signal crayfish with a negative "b" value indicates that the density of crayfish in previous years affects the abundance of large crayfish in following years. An increase in crayfish density can suppress growth due to increased competition, decreased food availability and higher aggressive interactions among adult crayfish (France 1985, Guan and Wiles 1999). Also, the removal of the largest crayfish can promote growth of smaller adults due to competitive release from larger conspecifics (Guan and Wiles 1999). All crayfish larger than 9 cm TL for noble crayfish and 10 cm TL for signal crayfish of the catches were taken for consumption in this study. The harvest of large adults fluctuates from year to year and will probably have an affect on the growth and survival of smaller crayfish in the population. Abrahamsson (1966) argued that the slow growth of crayfish, in the Southern Swedish pond he studied, was probably due to the population's high density. However, a higher percentage of the fluctuation observed for noble crayfish (24.4 %) was explained by density-dependence than for signal crayfish (7.1%). These results may not necessarily mean that density dependence is more important in noble crayfish populations. This is because it is likely that the signal crayfish population in Lake Bunn has not yet reached the same abundance in the lake as noble crayfish had before the plague struck the lake. The higher density of noble crayfish can therefore explain the observed difference in density dependence between the two species.

Earlier studies have found that a warm

temperature during harvest increases the catches of crayfish, while a cold temperature decreased especially the catches of smaller adult crayfish (Somer and Stechey 1986, Mundahl and Benton 1990, Richards et al. 1996). We did, however, not find that the temperature during August, when the crayfish are caught, has any influence on the fluctuations of catches of harvestable sized crayfish in Lake Bunn.

One parameter that we did not include, due to lack of data, is the abundance of predatory fish in Lake Bunn. It has been found that the presence of predatory fishes decreases the catches of crayfish (Hein et al. 2006) and also the abundance of crayfish in general (Nyström et al. 2006, Olsson et al. 2006). It may be that the fluctuation in crayfish abundance in Lake Bunn to some extent follows the fluctuations in the abundance of predatory fish. Perch (*Perca fluviatilis*), is an important predator on crayfish and dominates the fish community in the lake (Nyström et al. 2006). In Lake Bunn it was found that 62 % of the adult perch contained adult signal crayfish in 2003 and it is possible that the abundance of perch might affect crayfish abundance in Lake Bunn. Even though Nyström et al. (2006) found a positive correlation between crayfish abundance and the biomass of predatory fish in their study lakes, signal crayfish was the most important energy source for large perch.

Another important factor that we were unable to include in the model is food availability. A higher temperature during months when the availability of high quality food (i.e. invertebrates) are low may lead to a decline in crayfish growth and viability due to higher energy costs for feeding on food with low energy content (Whitledge and Rabeni 2003). Animal food sources are important for crayfish growth (Olsson et al. 2008) and the abundance of aquatic invertebrates fluctuates on seasonal basis (Hildrew and Townsend 1982). Climate change has also been shown to gradually change the macroinvertebrate composition in freshwaters (Daufresne et al. 2007). Changes in temperature may therefore indirectly influence the availability of high quality food for crayfish and potentially the growth and survival of crayfish.

Since abiotic and biotic factors differ significantly between lakes, climate changes may result in different ecological effects. The climatic influences on individuals and populations may act directly through physiology (metabolism, resistance to diseases, and reproductive success) or indirectly through the ecosystem (prey, predators and competition) making it hard to predict effects due to climate change (Stenseth et al. 2002). Winder and Schindler (2004) argue that the effect of warmer temperatures on food web structure and ecosystem functioning might strongly depend on the local adaptation of life-history traits in species. Since temperature regulates many life-history traits in crayfish, a higher temperature, especially during winter, may have significant effects on crayfish abundance, even though the mechanisms behind our obtained results are not known. Due to the important role of crayfish in lake ecosystems, as prey and consumers (summarized in Nyström 2002), any changes in crayfish abundance could have several indirect effects on the entire lake ecosystem. The lack of long time series on abundance of species and relevant environmental variables is a problem when trying to predict the effect of climate change and global warming on ecosystems. The increasing interest in this matter and collections of data for long-time series will improve our knowledge of how temperature affects species abundance and distribution. This will help us to better predict how further climate warming will affect species in terrestrial and aquatic ecosystems.

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III

PREY BIOMASS INFLUENCED NICHE WIDTH OF NATIVE AND INVASIVE CRAYFISH IN SWEDISH STREAMS

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Summary

Human activities have promoted the spread of species worldwide. Several crayfish species have been introduced into new areas, where invasive crayfish species are a threat to native crayfish species and other biota. Invaders success may depend on their ability to utilize a wide variety of habitats and resources. They are generally thought to have broader niches and be more plastic than non-invasive species. Niche width of crayfish may be affected by food availability, food diversity, and competition. Using stable isotope ratios of carbon and nitrogen we compared the niche width of native noble crayfish (*Astacus astacus*) and introduced signal crayfish (*Pacifastacus leniusculus*), a successful invader, in Swedish streams. Moreover, we assessed if population density, prey biomass and prey diversity had an effect on niche width of crayfish. We found, at species level, signal crayfish to have twice the niche width of noble crayfish. However, individual populations of noble- and signal crayfish in Swedish streams seem to have similar niche widths. This suggests that the signal crayfish may have a larger plasticity with respect to habitat utilisation and feeding than noble crayfish. We also found that niche width of both species was large in streams with high benthic invertebrate biomass and diversity.

Introduction

Some species have wider niche widths (or breadths) and occur in more habitat types than others (e.g. Fridley et al. 2007). Theoretically, species occupy unique niches, depending on several abiotic and biotic factors, such as resource density and diversity, population density, habitat and resource use in the presence of competitors and predators (Van Valen 1965, Fox 1981, Bearhop et al. 2004). Increased resource competition, e.g. via increased population density, may lead to increased diet variation (Werner 1977, Svanbäck and Persson 2004, Svanbäck and Bolnick 2007) and thus increased niche width. Further, low prey species richness has been found to decrease niche width (Winemiller et al. 2001). Hence, species may show different responses to factors affecting niche width.

Invaders are generally thought to have large niche widths and the impact invaders have on the community they invade increases with the invader's niche width (Shea and Chesson 2002). Species with

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a generalised diet should have greater impacts and greater invasive success than specialist species since food availability may not be a limiting factor (Moyle and Ligth 1996). Crayfish are omnivores, feeding on vertebrates, invertebrates, macrophytes, algae and detritus, and are therefore expected to have large niche widths. Several North American crayfish species have been introduced in Europe and are now spread throughout Europe. For example, the signal crayfish (*Pacifastacus leniusculus*) is present in many lakes, streams and ponds in Europe posing a threat to native crayfish species by transfering diseases and by competition (Skurdal et al. 1999, Nyström et al. 2001). In this study we compare the niche width of the native noble crayfish and the introduced signal crayfish in Swedish streams and relate it to factors known to affect niche width in other organisms, such as population density, prey availability and diversity. We tested if the successful invader, signal crayfish, had broader niche widths, compared to native noble crayfish.

Material and methods

Niche width has traditionally been quantified using gut content analysis in combination with measures of food resource richness and evenness (Bearhop et al. 2004). Limitations in these methods have led to an alternative method, using stable isotope analysis (Bearhop et al. 2004, Layman et al. 2007a). The relative position of individuals of a population in $\delta^{13}C$ - $\delta^{15}N$ bi-plot space, a two dimensional niche space, can reveal important aspects of trophic structure and can be a powerful tool to test ecological theory and study ecosystem responses to anthropogenic impacts (Layman et al. 2007a), including introductions of exotic species. Recently published data from two extensive field studies conducted in streams in southern Sweden was used. One was conducted at 14 sites in 13 streams with native noble crayfish populations (Olsson et al. 2008) and the other was conducted at 14 sites in 10 streams with the introduced signal crayfish (Nyström et al. 2006). Crayfish density (CPUE) was estimated using traps baited with dead cyprinids and followed Swedish standard sampling methodology for crayfish (for details see Edsman & Söderbäck, 1999). The traps are cylindrical (mesh size 14 mm) with funnel entrances at both ends and were set out in the late afternoon and crayfish are removed the following morning. This methodology provided a rough estimate of the density of larger crayfish ($\geq$ 60 mm, total length) (Abrahamsson & Goldman, 1970). From each site 10-14 noble- or signal crayfish (83-112 mm TL) were taken for stable isotope analyses. For more detailed information on collection of the data, stable isotope analyses, invertebrate biomass estimation see Nyström et al. (2006) and Olsson et al. (2008). To get an estimate of the invertebrate density and diversity (H') for each site, biomass and Shannon-Weaver diversity index was calculated based on five Surber samples from each site.

To test if there were important differences in abiotic and biotic factors between the two stream categories (noble- or signal crayfish) that could influence the interpretation of our results, independent t-tests were conducted comparing stream mean width, mean depth, median substrate size, current velocity, oxygen saturation, pH, total phosphorus, calcium, and biomass of predatory fish. We also compared crayfish mean size and trophic position using independent t-tests for the two species. Since $\delta^{15}N$ and $\delta^{13}C$ for basal resources can vary considerably between sites (e.g. France 1995) we corrected for this differences before further analyses. We let trophic position (TP) represent nitrogen values in bi-plots and calculations of niche width (TA). Trophic position of crayfish was calculated as recommended by Anderson and Cabana (2007) with the following equation:

$$TP_{cf} = ((\delta^{15}N_{cf} - \delta^{15}N_{baseline})/3.4) + 2$$

where TP_{cf} = trophic position of noble- or signal crayfish, $\delta^{15}N_{cf}$ = isotopic ratio of noble- or signal crayfish, $\delta^{15}N_{baseline}$ = isotopic ratio of primary consumers, 3.4 = one trophic level increment in $\delta^{15}N$ and 2 is the trophic position of the organism used to estimate the baseline (i.e. primary consumer). We used the mean nitrogen signals of several individuals of a net-spinning collector caddisfly larvae (Hydropsychidae) and a mayfly grazer (Baetidae) as the baseline for each site since we could not obtain nitrogen signals of more long-lived primary consumers, such as filter-feeding mussels, that have been recommended as baseline by other authors (e.g. Cabana and Rasmussen 1996; Vander Zanden et al. 1999; Post 2002).

Also the carbon isotope signal of basal resources, e.g. detritus and periphyton, can vary between sites influencing consumer signals without reflecting any real difference in consumer diet. Therefore, we corrected for differences in basal resources for carbon (δ^{13}Ccorr) using the following equation:

$$\delta^{13}Ccorr=(\delta^{13}Ccf - \delta^{13}Cmeaninv)/CRinv$$

where δ^{13}Ccf is the carbon isotope signal of crayfish and δ^{13}Cmeaninv is the mean invertebrate carbon isotope signal and CRinv is the carbon range (δ^{13}Cmax - δ^{13}Cmin) of the same invertebrates used for calculation of trophic position (see above). We use CRinv as a correction factor since the difference between detritus and periphyton can significantly vary between sites. TA was then calculated from the corrected carbon and nitrogen stable isotope data by calculating the total convex hull area encompassed by the smallest polygon containing the individuals in a population in the "corrected" $\delta^{13}C$ and $\delta^{15}N$ niche space (Layman et al. 2007b). Convex hull area was calculated using Matlab 7.4.0, where the Quickhull algorithm is implemented (see function: convhulln) (Cornwell et al. 2006). Also the carbon- and nitrogen range

Table 1. Median values and range for the abiotic and biotic variables measured in the streams and that were tested with t-tests between the two categories of streams/species. Median values are shown since it best reflects the typical stream. Bold numbers indicate a significant difference between stream categories (noble- or signal crayfish) and italic numbers indicates a trend.

Physico-chemical variables	Signal crayfish streams		Noble crayfish streams		T-test
	Median	Range	Median	Range	p
Substrate size (cm)	12.3	0.2 – 23.0	8.0	0.02 – 18.0	0.149
Velocity (m•s^{-1})	0.18	0.02 – 0.62	0.19	0.07 – 0.92	0.717
Total phosphorus (µg•l^{-1})	41.0	10.0 – 130.0	6.0	5.0 – 50.0	**0.005**
Calcium (mg•l^{-1})	7.2	2.3 – 56.0	6.1	3.8 – 10.9	*0.055*
Oxygen saturation (%)	92.5	85.0 – 96.0	95.5	72.0 – 101.0	0.743
pH	6.85	6.16 – 7.62	6.85	6.10 – 7.20	0.351
Predatory fish (g•m^{-2})	0.95	0 – 5.74	2.16	0 – 10.84	0.142
Depth (cm)	21.0	11.6 – 65.0	25.7	13.2 – 85.6	0.706
Width (m)	7.0	1.8 – 13.0	4.7	2.1 – 13.4	0.223

Table 2. Results from ANCOVAs on the dependent variables, niche width (TA), carbon range (CR) and itrogen range (NR), with the covariates and fixed variable (crayfish species). Interactions were omitted from the analyses since none were significant. Boldld letters indicate significant p-values and italic letters indicate a trend.

Covariates and fixed variable	TA		CRcorr		NRcorr	
	$F_{1,12}$	p	$F_{1,12}$	p	$F_{1,12}$	p
Invertebrate biomass (mg/m^2)	6.98	**0.014**	1.88	0.183	4.14	*0.053*
Crayfish species	2.94	0.100	0.25	0.622	1.99	0.170
Invertebrate diversity (H')	3.19	*0.086*	3.76	*0.064*	0.40	0.531
Crayfish species	0.33	0.571	0.07	0.789	0.87	0.360
Crayfish density (CPUE)	1.48	0.236	0.01	0.951	1.75	0.198
Crayfish species	1.24	0.277	0.11	0.916	1.09	0.307
Periphyton biomass (Chl a)	1.99	0.171	2.21	0.150	0.01	0.938
Crayfish species	0.08	0.786	0.25	0.622	0.60	0.446
Canopy cover (%)	1.58	0.220	1.07	0.311	0.02	0.885
Crayfish species	1.19	0.287	0.07	0.800	0.621	0.438

of each population was calculated by taking the distance between the two individuals with the largest and the smallest δ^{13}Ccorr (CRcorr) and at the highest and lowest trophic position (TPcf range).

To test if niche width (TA), carbon range (CRcorr) and nitrogen range (TPcf range) of crayfish differed between crayfish species crayfish species and were affected by periphyton biomass (chlorophyll a levels), percent canopy cover, crayfish density, invertebrate biomass or invertebrate diversity (H'), independent ANCOVAs were conducted, with TA, CRcorr or TPcf range as dependent variables, species as fixed factor, and periphyton biomass etc as covariates. To further explore the effects of invertebrate biomass we merged all the individual invertebrate taxon biomasses using principal component analysis (PCA) with varimax rotation. Principal components (PC) (representing biomasses of polyphyletic groups) with eigenvalues greater than one were retained and variables with an absolut loading exceeding 0.5 were considered important (Quinn and Keough 2002). ANCOVAs were then used to test if any of the PC axes were related to the niche width (TA), nitrogen range (TPcf range) or carbon range (CRcorr) of the two crayfish species.

Since all interactions between covariates and "crayfish species" were insignificant, they were omitted and the analyses repeated without the interaction terms. All statistical analyses were conducted in SPSS 11.0 for Mac OS except for the niche width that was calculated in Matlab (as above).

Results

There was an overlap in range between the two stream categories (noble- or signal crayfish) for all abiotic and biotic characteristics measured. Total phosphorus and calcium levels differed between the stream categories (Table 1). None of these variables were significantly correlated with TA, CRcorr or TPcf range of crayfish. There was no difference in mean size of trapped crayfish or trophic position of crayfish (Table 1). According to stable isotopes, both noble- and signal crayfish are predators in most of our studied streams.

The total niche width (TA) of signal crayfish (all individuals from all sites together) was 6.50, more than twice as large as the TA of noble crayfish, where it was 2.67

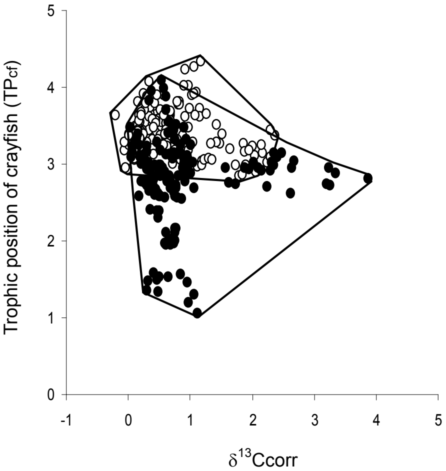

Figure 1. The total niche width (TA) of corrected values represented by convex hull area (inside solid lines) of all crayfish populations examined (each symbol represents one individual) for introduced signal crayfish (black dots) and native noble crayfish (white dots).

(Fig. 1). At species level, signal crayfish had a nitrogen range (TPcf range) of 3.03 and for noble crayfish it was 1.50. The carbon range (CRcorr), at species level, of signal crayfish was 3.85 and for noble crayfish 2.58. However, if a mean of the niche width of all signal crayfish populations (0.11, range 0.01–0.32) was compared to the mean of all noble crayfish populations (0.15, range 0.03–0.37), there was no difference between the two species (Independent t-test: t=0.92, df=26, p= 0.366, Fig. 2a and 2b). The ANCOVAs revealed a positive effect on niche width of crayfish for invertebrate biomass (Table 2, Fig. 3a). However, there was no effect of invertebrate diversity (H'), even though a trend could be seen, or crayfish density (CPUE) on the niche width of crayfish (Table 2, Fig. 3b and c). Periphyton biomass (chlorophyll a) or canopy cover did neither have any influence on the niche width of crayfish (Table 2). There was no difference between the two species for any of the tested variables (Table 2).

There was no difference in carbon range (CRcorr) between the two species (signal crayfish: mean 0.46, range 0.16–1.25; noble crayfish: mean 0.47, range 0.08–1.08, Independent t-test: t=0.120, df=26, p=0.905). Moreover, there were no significant effects of any of the tested variables on the carbon range of crayfish, even though a tendency could be seen for an effect of invertebrate diversity (Table 2). Also, no difference was found in nitrogen range (NRcorr) between the two species (signal crayfish: mean 0.46, range 0.18–1.18, noble crayfish: mean 0.53, range 0.31–1.03, Independent t-test: t=0.830, df=26, p=0.415). However, invertebrate biomass influenced the nitrogen range of crayfish (Table 2).

The PCA revealed five axes with an eigenvalue greater than one (Table 3). First axis (PC 1) represents biomasses of invertebrate groups that are commonly found in crayfish diet; such as Ephemeroptera, Trichoptera and Diptera, and an increased biomass of these groups was positively correlated with the niche width and carbon range of crayfish (Table 3). Axis 3 (PC 3), which represents biomasses of predatory Trichoptera and Mollusca, was positively correlated to the nitrogen range of crayfish (Table 3) and these taxa are also important prey for crayfish. There was no difference between the two species for any of the PC axes (Table 3).

Discussion

The introduced signal crayfish had a broader niche width than the native noble crayfish, at species level, which indicates that the introduced species used a wider range of habitats or food items than the native one. This in particular from lower trophic levels in the food web, since signal crayfish had a much broader nitrogen range (TPcf

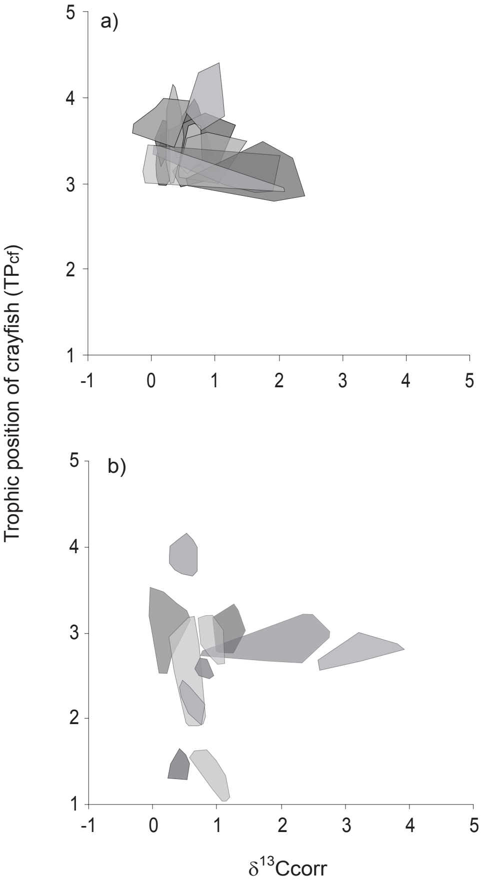

Figure 2. Population niche areas represented by convex hull areas (different grey colors) based on stable isotope analysis (corrected values) of 14-20 individuals per population for a) the 14 native noble crayfish populations and b) the 14 introduced signal crayfish populations.

range) expanding towards lower trophic levels compared to noble crayfish. Signal crayfish also had a broader carbon range (CRcorr) than noble crayfish at species level, but the difference was not as large as for nitrogen range. This suggests that signal crayfish are present in habitats where their trophic position can be lower than where noble crayfish persists. Schmid (1984) argued that the success of colonizing (i.e. invading) species depend on their ability to use wide ranges of habitats and having high ecological plasticity. The idea that invasive species should have broader diets (Lodge 1993, Moyle and Light 1996) and thus larger niche width than non-invasive was supported at species level in our study. However, at population level the two species had similar niche widths and thus it seems as if all individuals within a population utilises similar resources regardless of environment or species. This is consistent with a study by Rehag et al. (2005) where diet preferences and niche width of a population of the invasive fish, Gambusia, did not differ from the non-invasive Gambusia. Living in the same habitat most individuals utilises the same resources and thus the niche width at population level will reflect the resources available for the individuals within a population. The variation in niche width between populations was due to variation in both carbon and nitrogen range. In both species some populations had large carbon or nitrogen ranges, while others had very small.

An increase in niche width could be achieved in two ways, either all individuals shift to use more of the available food sources (this process is not detectable using stable isotope analysis) or they shift to using a narrower range of food sources that their conspecifics do not exploit (Bolnick et al. 2007). It has been shown that the niche width of top predators in lakes, such as perch, increases with increased population density due to increased intraspecific competition causing individual diet specialization (Svanbäck and Persson 2004). In our study the population density of crayfish did not affect the niche width of either the introduced signal crayfish or the native noble crayfish. However, population density may not reflect the strength of intraspecific competition for food in crayfish. It has been shown that productivity

Table 3. Component loadings for biomass of invertebrate groups and precentage of variance explained by the five PC axes with eigenvalues grater than 1. Bold numbers indicate loadings that are considered to be important (absolute loading >0.5). P values refer to ANCOVA of niche width (TA), nitrogen range (NRcorr) and carbon range (CRcorr) of crayfish populations against the scores of the five PC axes and between species effects. Bold letters indicate significant p-values and italic letters indicates a trend.

		PC 1	PC 2	PC 3	PC 4	PC 5
Eigenvalue		3.87	2.80	1.87	1.35	1.26
% variance explained		25.77	18.65	12.47	8.97	8.41
Turbellaria		$-2.6x10^{-02}$	0.906	$8.8x10^{-02}$	0.242	$-6.8x10^{-02}$
Megaloptera		$-8.8x10^{-03}$	$-2.8x10^{-02}$	$-9.0x10^{-02}$	$-7.4x10^{-02}$	0.768
Oligochaeta		$2.3x10^{-02}$	0.729	-0.163	0.263	$7.5x10^{-02}$
Crustacea		0.964	$-6.2x10^{-02}$	$-7.3x10^{-02}$	$-6.4x10^{-02}$	$2.5x10^{-02}$
Odonata		$-2.4x10^{-02}$	0.175	$-6.5x10^{-02}$	0.880	-0.176
Ephemeroptera		0.954	$1.9x10^{-02}$	0.167	$1.5x10^{-02}$	$-3.8x10^{-02}$
Predatory Trichoptera		0.623	0.311	0.603	-0.139	$-3.6x10^{-02}$
Non-predatory Trichoptera		$-4.6x10^{-02}$	$-5.8x10^{-02}$	0.864	$-5.6x10^{-02}$	-0.138
Coleoptera		0.123	0.745	$-9.1x10^{-02}$	-0.203	-0.158
Plecoptera		$-2.3x10^{-02}$	0.813	0.416	$-4.3x10^{-02}$	$7.4x10^{-02}$
Diptera		0.879	0.245	-0.205	-0.119	$-6.7x10^{-03}$
Mollusca		$1.6x10^{-02}$	$3.9x10^{-02}$	0.716	0.145	$-2.9x10^{-02}$
Hirudinea		0.786	-0.171	$9.9x10^{-02}$	0.389	-0.109
Heteroptera		$-4.6x10^{-02}$	$-2.5x10^{-02}$	-0.222	-0.480	-0.355
Lepidoptera		$-6.1x10^{-02}$	$-3.3x10^{-02}$	$-7.9x10^{-02}$	$2.5x10^{-02}$	0.700
TA Species	p=	0.138	0.667	0.267	0.229	0.468
TA PC#	p=	**0.015**	0.110	0.257	0.315	0.726
NRcorr Species	p=	0.345	0.369	0.161	0.707	0.421
NRcorr PC#	p=	0.451	0.651	**0.011**	0.296	0.882
CRcorr Species	p=	0.599	0.764	0.890	0.480	0.943
CRcorr PC#	p=	*0.057*	0.155	0.903	0.115	0.584

of lakes and streams determines the growth in crayfish. (Nyström et al. 2006, Olsson et al. 2008). The amount of preferred food sources (invertebrate biomass), however, may affect the niche width by regulating the level of resource competition. Our results indicate that a high biomass of invertebrates increases the niche width of crayfish. This is contrary to e.g. Svanbäck and Persson (2004) but in agreement with a study by Correia (2002) who found that the introduced crayfish *Procambarus clarkii* adjusted its trophic niche use to the availability of different macroinvertebrates in a rice field. Correia (2002) also found *P. clarkii* to have a high degree of diet specialisation. However, a diversity of potential food sources is a prerequisite for increased competition to influence trophic niche width. Increased invertebrate biomass might just add the necessary diversity of food sources in the studied streams. It has also been suggested that crayfish play different roles in lakes due to differences in nutrient status and prey availability and that crayfish may show higher diet diversity (i.e. degree of omnivory) in lakes with intermediate nutrient status (Stenroth et al. 2008). This is in accordance with our study, where the availability (biomass) of large, slow and sedentary invertebrates had a positive effect on the niche width of crayfish. Species from these groups are commonly found in crayfish guts (Stenroth and Nyström 2003, Nyström et al 2006, Olsson et al. 2008). This influence of certain invertebrate species on trophic position and carbon isotope signals of crayfish has been shown previously (Olsson et al. 2008).

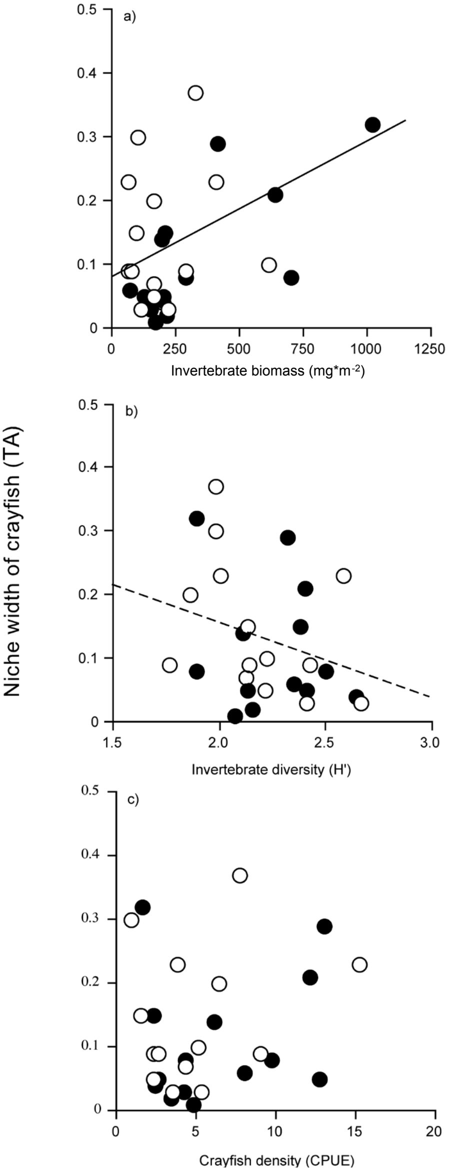

Figure 3. Regressions between the niche width (corrected values) of crayfish and a) invertebrate biomass, b) invertebrate diversity (H'), and c) crayfish density (CPUE). White dots represent noble crayfish populations and black dots represent signal crayfish populations. Significant regressions are indicated by a solid line and trends by a dashed line. Trend lines are calculated by pooling the data for the two crayfish species since there were no significant differences between them. Statistics are shown in Table 2.

Signal crayfish has been introduced to large parts of Europe where it has replaced native species of crayfish in many lakes and streams. In lakes and streams where native- and introduced crayfish species coexist it has been shown that the introduced one often outcompete the native one (Mather and Stein 1993, Hill and Lodge 1999, Westman et al. 2002). This may to some extent be a result of the introduced species having great abilities to use a wide range of habitats or food items. Renai and Gherardi (2004) found in Italy that the introduced *P. clarkii* had a more plastic feeding behaviour than the native *A. italicus*. The findings in this study suggest that introduced signal crayfish form populations where native crayfish are not present. This could explain the larger niche width of signal crayfish than noble crayfish at species level in Swedish streams and might also have contributed to the successful invasion of signal crayfish.

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IV

THE INFLUENCE OF FOOD QUALITY AND AVAILABILITY ON TROPHIC POSITION, CARBON SIGNATURE AND GROWTH RATE OF AN OMNIVOROUS CRAYFISH

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Fourteen sites in thirteen streams were surveyed to address the importance of food quality and quantity on trophic position, carbon signature and growth rate of the noble crayfish (Astacus astacus), by combining the analyses of gut content, stable isotopes and RNA/DNA ratio. The gut content analysis showed an omnivorous feeding habit, but total animal food sources contributed more to the nitrogen and carbon isotope signals of this species. The biomass of invertebrates (i.e. high quality food) influenced the trophic position, carbon signature and growth rate. Our results show that crayfish in streams with a high biomass of invertebrates were at a higher trophic position and had a higher growth rate than crayfish in streams with a low biomass of invertebrates. A high biomass of relatively sedentary invertebrates indicates a habitat with high algae biomass, which is reflected in the more autochthonous carbon signature of crayfish. Further, noble crayfish in temperate streams seems to have dual functional roles by acting as a predator and as a shredder by processing large amounts of detritus.

Introduction

Omnivory, the consumption of resources from more than one trophic level, is common (Polis et al. 1989; Diehl 1993) and omnivores, such as crayfishes, exist in most freshwater ecosystems. The diet of omnivores has been proposed to be influenced by the relative abundance and quality of food types at different trophic levels (Diehl 2003), but also by encounter rates and capture success (Rosenheim and Corbett 2003).

Omnivorous crayfishes can dominate the benthic biomass (Momot et al. 1978; Rabeni et al. 1995) and as omnivores they can affect several trophic levels both directly and indirectly (Nyström et al. 1996). Several studies indicate selective feeding by crayfishes. Alcorlo et al. (2004) showed that the crayfish *Procambarus clarkii* consumed animal prey according to the latter's availability in the environment. Parkyn et al. (2001) showed a similar result, where the percentage of invertebrate groups consumed by the crayfish *Pharanephrops planifrons* largely reflected the invertebrate composition in the environment. However, sedentary taxa such as chironomids and gastropod snails constituted a higher proportion in the diet than available in the environment (Parkyn

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et al. 2001), indicating selective feeding on these groups by crayfishes. Several other studies also show that large sedentary or less mobile species are commonly consumed by crayfishes, while fast swimming invertebrates are less abundant in crayfish guts (Abrahamsson 1966; Whitledge and Rabeni 1997; Nyström et al. 1999).

Most gut content analyses show that crayfish are omnivores, consuming detritus, macrophytes, periphyton, invertebrates, fishes and even other crayfishes (Whitledge and Rabeni 1997; Parkyn et al. 2001; Stenroth and Nyström 2003). Gut content analysis gives information on recent crayfish feeding activity (Gherardi et al. 2004) but has several shortcomings. Different food items are digested at different rates (Momot 1995; Nyström 2002) and in addition gut content analysis may not show long term feeding habits (i.e. trophic position). To circumvent this problem stable isotope analysis has been commonly used. Stable isotope ratios give information on assimilated food sources over long time periods. Hence, they are used to identify important food sources for consumers including crayfish (Nyström 2002). A number of stable isotope analyses of crayfish have pointed out detritus as an important food source (Bunn and Bonn 1993; France 1996; Evans-White et al. 2001). On the other hand, studies have also shown that invertebrates are the most important food source for crayfish (Parkyn et al. 2001; Hollows et al. 2002; Nyström et al. 2006). Lancaster and Waldron (2001) argue that crayfish, as omnivores, would encounter signatures from all food sources consumed and therefore it can be hard to distinguish the contribution of individual food sources to the isotopic signals in crayfish. However, it should be possible to distinguish between the contributions of different food sources to the isotopic signals in crayfish by combining stable isotope analysis and mixing models.

Further, increased primary productivity may increase the trophic position of crayfish by supporting higher densities of invertebrates (Stenroth et al. 2006). In streams not only productivity but also characteristics such as canopy cover, water velocity, substrate, pH, and predation may affect the biomass and species composition of invertebrates (Orth and Maughan 1983; Biggs et al. 2000; Nyström et al. 2003). It is therefore possible that multiple abiotic and biotic factors influence resource supply for crayfish and hence their trophic position.

Crayfish feeding habits may not only influence trophic position, but also the individual growth rates of crayfish. Several abiotic factors have been proposed to affect crayfish growth and individual size, such as temperature, productivity, pH, calcium and habitat composition (Reynolds 2002; Nyström 2002). Also several biotic factors would likely affect crayfish growth, such as food quality and availability (Momot 1995), predation risk (Nyström 2002), intraspecific interactions and population density (Guan and Wiles 1999). D'Abramo and Robinson (1989) found that crayfish has a dietary protein requirement of at least 30-35% for optimal growth. In order to meet their energetic demands crayfish have to ingest animal food and do so by consuming the most profitable prey items available (Alcorlo et al. 2004). There are few studies on growth rates of freshwater species (Tardif et al. 2005) and in natural crayfish populations, mainly because of the lack of feasible methods to estimate growth in situ. Analysis of RNA/DNA ratios in muscle tissues can give information about growth rates and has been used successfully on many marine organisms including lobsters (e.g. Parslow-Williams et al. 2001). Buckley (1984) consider RNA/DNA ratio to be a instantaneous measurement of growth rate since it responds rather quickly to changes in feeding conditions and growth after 1-3 days. Therefore, it should be possible to address the relative growth rate of individual crayfish and compare individuals from different populations in freshwater ecosystems.

By combining gut contents, stable isotopes and RNA/DNA ratios it was possible to determine the feeding habits, trophic position, carbon signature and its consequences for individual growth rates of omnivorous crayfish in different environments with different availability of high quality food (i.e. invertebrates). This study, conducted in multiple temperate streams, tests the following hypotheses:

1) Crayfish are omnivores according to gut content analysis, but animal food sources contribute more than plant material to the carbon and nitrogen isotope signals in crayfish.

2) The availability of high quality food for crayfish is influenced by abiotic and biotic factors and availability of high quality food affects the trophic position and carbon signature of crayfish.

3) The growth rate of crayfish is influenced by the availability of high quality food. Therefore, crayfish occupying a habitat with a low biomass of invertebrates would have a lower growth rate (RNA/DNA ratios) than crayfish in habitats with high invertebrate biomass.

Methods

We surveyed 13 streams in southern Sweden between August and September 2005. At one stream two different sites were surveyed that differed substantially in stream characteristics and were more than one km apart. These sites were therefore considered as independent, which gave a total of 14 sites. Streams with established crayfish populations that differed in characteristics and location (forest or agriculture/pasture) were chosen. At each site, a study reach 8.3 – 55 m long, depending on width and availability, was investigated. The mean stream area investigated was 140 m^2 (range 60.3 - 346.8 m^2). Water temperature, oxygen levels, water velocity, canopy cover and macrophyte cover were determined at each site. Water samples were frozen for later analysis of calcium, total nitrogen, total phosphorus, dissolved organic carbon (DOC) and pH.

To sample epilithon for biomass and stable isotope analysis, five cobbles were haphazardly collected within each study area and a 6.16 cm^2 circle of organic layer (i.e. epilithon, decomposed organic material and microbes) was removed from the upper surface of each cobble with a wire brush, filtered onto a glass fibre filter (GF/C Whatman ®) and frozen. Chlorophyll *a* was then extracted in ethanol (12 h in darkness at 20°C) and estimated spectrophotometrically according to Jespersen and Christoffersen (1987). Samples of the organic layer for stable isotope analysis were prepared with a similar procedure, except for the chlorophyll *a* extraction.

Abundance and size distribution of noble crayfish (*Astacus astacus*) were estimated using traps. At each site 30 Lini traps (crayfish $\geq$ 60 mm TL are caught in this type of trap) were baited with pieces of frozen cyprinid fish, following Swedish standard sampling method for crayfish (Edsman and Söderbäck 1999). The number of crayfish caught per trap and night (CPUE) was used as a relative measure of crayfish abundance. Traps that contained predatory fish or had been re-positioned by the water current in a way that prevented crayfish from entering were excluded (Table 1). One hundred haphazardly chosen crayfish (or all when less was caught) were individually weighed to the nearest 0.1 g and measured to the nearest millimetre (total length, TL). From each population, 14 crayfish were collected (70 – 120 mm TL) and samples of abdominal white-muscle tissue were immediately frozen in liquid nitrogen for RNA/DNA analysis. The remaining parts were frozen (-20°C) for analysis of gut content and stable isotopes (carbon and nitrogen).

The abundance and biomass of fishes were estimated by electrofishing (three depletion passes) a mean area of 140 m^2 (range 60.3 - 346.8 m^2). All fishes were identified to species, weighed to the nearest 0.1 g and measured to the nearest mm (TL) prior to release. At the 12 sites where carnivorous fishes were caught we collected 3-10 fishes considered to be predators on crayfish and other invertebrates (*Salmo trutta*, *Perca fluviatilis*, *Cottus gobio*, *Lota lota*, *Esox lucius* and *Anguilla anguilla*) (Nyström 2002) for stable isotope analysis. In total, 65 individuals were collected and analysed.

To estimate the availability of high quality food (i.e. benthic invertebrate biomass), five surber samples (0.09 m^2, 250 um mesh size) were taken at each site. Invertebrates were preserved in 95% ethanol and identified to the lowest possible taxonomic level (after Nilsson 1996, 1997) and counted at up to 10x magnification. To determine total invertebrate biomass, all individuals belonging to an invertebrate species were dried for 24 h at 60°C and weighed to the nearest 0.1 mg and then combusted in a muffle furnace at 450°C for four hours and reweighed (AFDW). Samples for stable isotope analysis were collected separately with a surber sampler or by searching cobbles and vegetation. Invertebrates were categorized into functional feeding groups (FFG: predatory invertebrates, grazers, shredders and collectors) after Elliott et al. (1988), Nilsson (1996, 1997), Wallace et al. (2003) and Edington and Hildrew (2005). This to decrease the number of food sources in our analyses (*a priori* aggregation of sources that have similar isotopic signatures and that are logically related, e.g. Phillips et al. 2005). All invertebrates were frozen for later stable isotope analysis (3-20 animals from each FFG per stream).

Gut content and stable isotope analysis

A total of 90 crayfish guts, haphazardly chosen from the 14 sites (6 to 10 from each site), were examined under a binocular microscope (10x magnification). Organic matter was separated into detritus, wood, algae and green plant fragments, and invertebrates were identified to generic level when possible, following Nilsson (1996, 1997), or classified as unidentified animal remains. The frequency of occurrence of food items in crayfish guts was calculated from the data.

In food web studies, the most commonly used elements for stable isotope analysis are carbon and nitrogen (Whitledge and Rabeni 1997). The carbon isotopic ratio ($^{13}C/^{12}C$) reflects assimilated food items and the isotopic enrichment from one trophic level to the next is often insignificant (Post 2002). The nitrogen isotopic ratio ($^{15}N/^{14}/N$) on the other hand typically increases on average 3.4‰ during each trophic transfer (Post 2002). For example, if predatory invertebrates are an important energy source for crayfish, their carbon isotopic ratios should be similar, whereas crayfish should have a nitrogen isotopic ratio about 3.4‰ above that of predatory invertebrates.

Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were obtained for crayfish, predatory fishes, shredding invertebrates (Capniidae and Leuctridae), grazing invertebrates (Baetidae and Gastropoda), collector invertebrates (Simuliidae and Hydropsychidae), predatory invertebrates (free-living Trichoptera, Hirudinea, Zygoptera and Anisoptera), organic layer, detritus and live plant material (filamentous algae and macrophytes). Samples for analysis consisted of untreated abdominal tissue of crayfish (as recommended by Stenroth et al. 2006), a tissue sample taken just behind the head of predatory fishes, abdominal tissue or whole body samples of invertebrates and a 0.5x0.5 cm sample of organic layer, detritus and live plant material (approximately 0.2 mg of carbon). Samples were dried at 60°C for at least one hour, and analysed with a PDZ Europa Ltd. (Sandbach, Cheshire, UK) 20-20 stable isotope analyser. The δ notation is the relative difference between samples and known standards:

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

where X is either ^{15}N or ^{13}C and the corresponding ratio (R) is either $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Atmospheric nitrogen is used as the standard ratio for nitrogen, and Vienna Pee Dee Belemnite is used as the standard ratio for carbon. Glycin was used as internal standard and the internal precision for the standards was <0.3‰ for both C and N in each run. All isotope values are given in per mill (‰).

Growth rate

The RNA content of a cell is positively related to the amount of protein synthesis in the cell and thus to growth rate, while DNA content is constant (Clemmesen 1994), so the RNA/DNA ratio enables comparison of relative growth rates among populations. Analyses of RNA/DNA ratios were made according to the protocol for zooplankton of Vrede et al. (2002) with the following modifications: RNA-later was not used, RNA and DNA were extracted from approximately 1 mg of abdominal white-muscle tissue (Moss 1994, Parslow-Williams et al. 2001) in 1 ml of buffer from which 10 ul subsamples were taken and diluted ten-fold before used in the analysis. The samples were then heated at 60°C in a water-bath to inactivate naturally present RNase (Weatherford et al. 1972, Pasloske and Wu 2004) for 10 minutes prior to one hour of shaking. After the first reading (RNA and DNA), RNase was added to eliminate RNA and the samples were incubated in darkness for twenty minutes before the second reading (only DNA). RNA/DNA ratios of duplicate samples of homogenized tissue were determined with a Fluostar spectrometer. Ratios for eight to ten crayfish of the 14 collected (70 to 120 mm, TL) were determined for each site.

Statistical analysis

We tested if the biomasses of different invertebrate groups were related to any of the measured environmental factors in a canonical correspondence analysis (CCA) by multivariate constrained ordination (Leps and Smilauer 2003). Environmental factors with an absolute loading exceeding 0.5 were considered important. To ensure that the data on biomasses of invertebrate groups were normally distributed they were ln (x+1) transformed prior to analysis.

To examine how the different food sources contributed to the isotopic signatures of crayfish, a separate IsoSource mixing model for each element was used (Phillips and Gregg 2003). A mass balance tolerance of 0.05 ‰ and a source increment of 2% were used to avoid impractical amounts of computation when using seven sources (Phillips and Gregg 2003). No solutions could be computed for nitrogen at 2 sites and for carbon at one site. This was probably because there were additional unsampled food sources or differences in turnover rate or fractionation. Nitrogen isotopic ratios of crayfish were adjusted for trophic enrichment by subtracting 3.4‰ from each value prior to analysis (Post 2002). Correction for carbon fractionation (-0.39 as recommended by Post 2002) had no effect on the results, so no correction was used. We used One-way-ANOVA to test if there was a difference in contribution among the different food sources to the carbon or nitrogen isotope signals in crayfish at each site where a solution was generated. Significant differences in contribution among food sources were followed by Tukey's *post hoc* test. Further, the contribution of all animal food sources together against all plant food sources together was tested with Wilcoxon test for both carbon and nitrogen isotope signals in crayfish.

Trophic position of noble crayfish was calculated using the equation:

$$TP_{cf} = ((\delta^{15}N_{cf} - \delta^{15}N_{baseline})/3.4) + 2$$

where TP_{cf} = trophic position of noble crayfish, $\delta^{15}N_{cf}$ = isotopic ratio of crayfish, $\delta^{15}N_{baseline}$ = isotopic ratio of primary consumers, 3.4 = one trophic level increment in $\delta^{15}N$ and 2 is the trophic position of the organism used to estimate the baseline (i.e. primary consumer). We used the nitrogen signals of collector invertebrates as the baseline since we did not have nitrogen signals of more long-lived primary consumers, such as filter-feeding mussels, that have been recommended as baseline by other studies (e.g. Cabana and Rasmussen 1996; Vander Zanden et al. 1999; Post 2002). Collector invertebrates were chosen as baseline because they had the lowest $\delta^{15}N$ signals of the primary consumers and were present at all sites as recommended by

Site no.	Stream name	Invest. Area (m^2)	Water Temp. (°C)	PH	Ca (mg l^{-1})	Chl. *a* (μgcm^2)	Canopy cover (%)	Macroph. cover (%)	Oxygen (mg l^{-1})	Tot. N (μg l^{-1})	Tot. P (μg l^{-1})	DOC (mg l^{-1})	Velocity (m s^{-1})	Substrate (cm)	Total no. of crayfish	No. of traps	CPUE	Pred. fish. (g m^{-2})	Inv. bio. (mg m^{-2})
1	Hånälven	75.4	17.7	6.9	6.6	1.27	75	2	9.1	330	5	8.45	0.08	12	231	30	7.7	0	722
2	Rommenäs	110.8	15.1	6.4	4.1	0.99	20	10	10.1	510	6	7.98	0.68	15	105	28	3.8	0.68	910
3	Hämnäs	123.2	15.9	6.4	4.0	2.17	2	30	9.5	400	15	10.1	0.16	0.2	261	29	9.0	2.85	145
4	Bärhus	143.5	18.6	7.2	6.4	0.20	85	0	8.9	330	5	8.41	0.35	9	69	30	2.3	1.16	641
5	Lillälven	346.8	17.4	6.9	3.8	0.92	3	45	9.4	290	5	5.94	0.92	3.25	155	29	5.3	0.15	482
6	Stömne I	177.6	17.4	7.0	5.8	1.35	90	0	9.2	300	5	5.59	0.09	1.5	102	29	3.5	4.13	176
7	Steneby	147.1	17.1	6.8	4.8	1.37	85	1	9.3	280	6	8.38	0.18	14	79	30	2.6	0.09	134
8	Stömne II	60.3	16.6	6.9	5.5	4.01	50	20	9.2	310	7	6.07	0.21	1	65	28	2.3	8.84	360
9	Töftedal	139.9	15.5	6.7	8.9	1.67	2	10	9.6	670	14	17.7	0.17	14	27	29	0.9	10.84	233
10	Sågån	220.0	17.6	6.7	8.8	1.97	90	0	8.2	-	50	8.71	0.40	18	147	29	5.1	3.26	1353
11	Bodane	183.1	16.4	6.1	5.1	1.59	40	50	7.7	670	26	21.9	0.07	0.02	457	30	15.2	1.47	139
12	Ö. Derome	92.2	18.5	7.0	9.6	1.47	85	10	6.6	350	5	5.4	0.13	0.2	107	25	4.3	10.48	389
13	Hämnäs trib.	92.1	16.7	6.3	6.6	3.42	40	5	7.3	490	27	25.7	0.20	7	128	20	6.4	0	366
14	Faxeröd	48.4	16.7	6.9	10.9	0.20	98	2	8.8	610	5	15.5	0.22	11.5	44	30	1.5	7.33	640

Anderson and Cabana (2007).

To test if total invertebrate biomass influenced the trophic position (Tp_{cf}), carbon signature ($\delta^{13}C$) and/or the growth rate (RNA/DNA ratio) of crayfish, linear regressions were performed. To examine whether any specific invertebrate group could explain these relations, we reduced the number of invertebrate groups using principal component analysis (PCA) with varimax rotation. Invertebrate biomasses were ln (x+1) transformed prior to analysis to ensure that they were normally distributed. Principal components (PC) with eigenvalues greater than one were retained and variables with an absolute loading exceeding 0.5 were considered important (Quinn and Keough 2002). Stepwise linear regression was then used to test if any of the PC axes were related to the trophic position (TP_{cf}), carbon signature ($\delta^{13}C$) or growth rate (RNA/DNA ratios) of crayfish.

All statistical analyses were conducted in SPSS version 11.0 for Windows, except for the isotope-mixing model, which was conducted in IsoSource (www.epa.gov/web/pages/models.htm), and the canonical correspondence analysis (CCA) which was conducted in Canoco 4.0 for Windows.

Results

A total of 1977 noble crayfish was caught at the 14 sites with the number per site ranging between 27 and 457. Crayfish density (CPUE) ranged from 0.9 to 15.2 individuals caught per trap and night. Predatory fish biomass ranged from 0 to 10.84 g•m^{-2} and invertebrate biomass ranged from 0.134 to 1.353 g•m^{-2}. Abiotic factors such as canopy cover (range from 2% to 98%) and macrophyte cover (range from 0% to 50%) also differed greatly among sites. The concentration of total nitrogen had a mean of 0.426 mg•L^{-1} and the concentration of total phosphorus had a mean of 0.013 mg•L^{-1} (Table 1). Water temperature was above 15°C, oxygen concentration above 6 mg•L^{-1} and pH above 6 at all sites (Table 1), which indicates good conditions for noble crayfish.

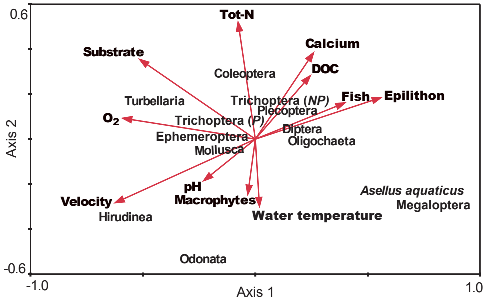

Figure 1. Correlation plot of invertebrate groups to axis 1 and 2 from the Canonical correspondence analysis (CCA), with the environmental factors that explained most of the variation. Trichoptera are divided into predatory (P) and non-predatory (NP) taxa.

The CCA (Fig. 1) showed that the biomasses of invertebrate species were influenced by several environmental factors. The first axis explained 33.5 % of the variation in invertebrate biomasses among sites and was correlated with oxygen (-), current velocity (-), substrate size (-), and epilithon biomass (chlorophyll *a*) (+). The second axis explained 20.9 % of the variation and was correlated mostly with total nitrogen (-). The biomasses of the different invertebrate groups were influenced by different environmental factors. For example, Diptera and Oligochaeta were mostly influenced by epilithon biomass (chlorophyll *a*) and the biomass of predatory fish (Fig. 1).

Gut content and stable isotopes

The gut content analysis showed a varied diet in noble crayfish (Fig. 2). At all sites 83% to 100% of the guts examined contained

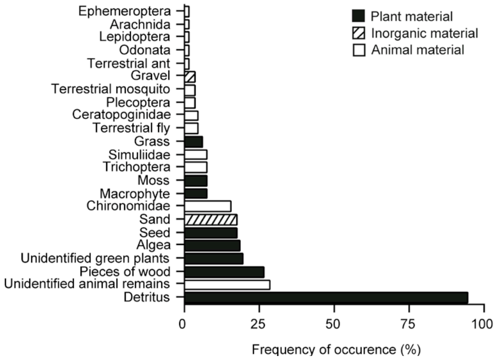

Figure 2. Frequency of occurrence of different food items in 90 crayfish guts. Fish items were excluded since they were likely to originate from the bait.

fish remains from the bait. Remains of plant food items were present in 94 % and animal food items (fish remains excluded) in 52% of the guts examined (empty guts excluded). The IsoSource mixing models indicate that noble crayfish derive their nitrogen mostly from invertebrates and their carbon from detritus, shredders and predatory invertebrates (Fig. 3a and b). For the carbon isotope signals in crayfish the ANOVA showed a significant difference in contribution between the different food sources (F=22.47, df=6, p=*<0.001*). Tukey's *post hoc* test showed that detritus and shredders contributed the most followed by predatory invertebrates, whereas remaining sources did not contribute significantly to the carbon isotope signal of crayfish (Fig. 3a). The ANOVA showed no significant difference in percent contribution to the nitrogen isotope signal (adjusted for trophic transfer: δ^{15}N crayfish - 3.4‰) of crayfish between the different food sources (F=0.796, df=6, p=0.576) (Fig. 3b). However, if all food sources of animal origin were pooled and all plant sources pooled (Fig. 3a and b), a trend could be seen that animal food sources contributed more to both carbon and nitrogen isotope signals in crayfish even though this was not statistically significant (Wilcoxon test, Z=-0.91, p=0.362, for carbon and Z=-1.67, p=0.096, for nitrogen).

The dual isotope plot on median values from all organism groups from the 14 sites show that noble crayfish are at the same trophic level as predatory fishes (Fig. 4). All invertebrate groups and filamentous algae are clustered together approximately one trophic level below crayfish and predatory fish, while the organic layer from cobbles and macrophytes are somewhat below and detritus is at the base of the food chain (Fig. 4). The carbon signal of crayfish in the dual isotope plot looks like it is derived from the organic layer, shredders and collectors, which is not in agreement with the results from the IsoSource mixing model. However, the organic layer consists of more than pure epilithon (i.e. chlorophyll *a*) and there was a significant correlation (linear regression, F=2.99, df=13, p=*0.013*) between the measured chlorophyll *a* levels and the δ^{13}C of crayfish if the δ^{13}C of detritus was subtracted. This indicates that the carbon isotope signal of crayfish comes, directly or indirectly, from consumption of predatory invertebrates, shredders and collectors, from detritus.

Trophic position and carbon signature

The mean δ^{15}N for all crayfish was 7.6 ‰ (range from 5.8 to 9.3) and for δ^{13}C it was -27.5 ‰ (range from -26.1 to –30). The standard deviation within crayfish populations for both nitrogen and carbon isotope values from the 14 sites varied from 0.24 ‰ to 0.94 ‰ with a mean of 0.59 ‰.

The trophic position (TP_{cf}) was positively related to invertebrate biomass (linear regression, F=8.11, df=13, p=*0.015*). Crayfish at sites with a high biomass of invertebrates were at a higher trophic position than crayfish at sites with a low

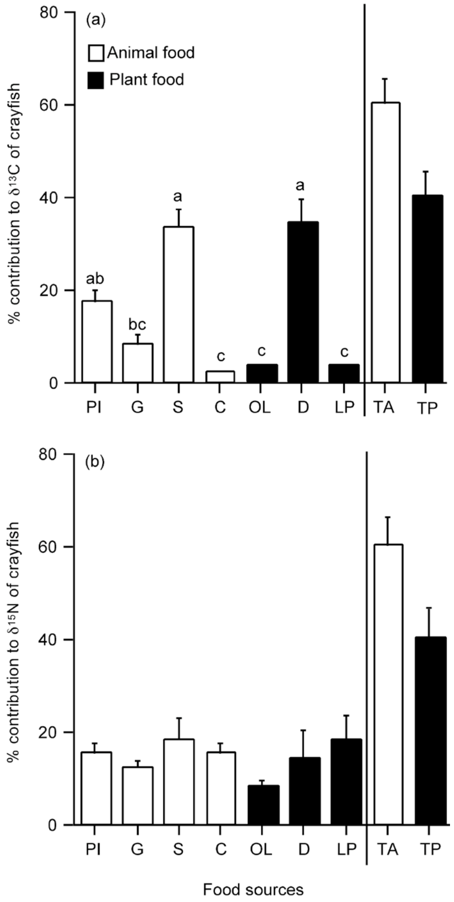

Figure 3. The mean percentage contribution of the different food sources to (a) $\delta^{13}C$ and (b) adjusted $\delta^{15}N$ signals of noble crayfish. Different letters represent a significant difference at the 0.05-level (Tukey's *post hoc* test). Also the contributions of total animal food sources and total plant food sources are shown to the right of the line. Note: PI=predatory invertebrates, G=grazers, S=shredders, C=collectors, OL=organic layer, D=detritus, LP=live plant material, TA=total animal food sources and TP= total plant food sources. Error bars denote +1SE.

invertebrate biomass (Fig. 5a). The carbon signature ($\delta^{13}C$) of crayfish was not related to the biomass of invertebrates (linear regressions, F=0.003, df=13, p=0.96) (Fig. 5b). However, the PCA derived five axes with eigenvalues greater than one (Table 2) and two axes were significantly related to the trophic position and carbon signature of crayfish. The first axis (PC 1) represents biomasses of invertebrate groups that are commonly found in the crayfish diet; such as Ephemeroptera, Trichoptera, Plecoptera and Mollusca, and the second axis (PC 2) represents biomasses of groups that are relatively sedentary such as Turbellaria, Oligochaeta, Coleoptera larvae and Diptera (Table 2). Stepwise linear regressions show that PC 1 (F=5.03, df=13, p=*0.045*) had an influence on the trophic position (TP_{cf}) of crayfish and PC 2 had an influence on the carbon signature ($\delta^{13}C$) of crayfish (F=5.9, df=13, p=*0.032*) (Table 2).

Growth rate

The growth rate (RNA/DNA ratio) of crayfish was positively related to the biomass of invertebrates, although not statistically significant (linear regression, F=3.958, df=13, p=0.07). If, however, the water temperature was controlled for, there was a positive relation between RNA/DNA ratios of crayfish and the total invertebrate biomass (multiple linear regression, F=8.18, df=13, p=*0.014*, Fig. 6a). There was also a positive relation between the trophic position (TP_{cf}) of crayfish and the RNA/DNA ratios of crayfish (multiple linear regression, F= 5.625, df=13, p=*0.035*) when the water temperature was controlled for. Crayfish at a higher trophic position had higher growth rates than crayfish at a lower trophic position (Fig. 6b).

Discussion

Animal food sources together with detritus were the most important contributors to the nitrogen and carbon signals of noble crayfish, even though detritus was found in 94% and animal food sources only in 50%

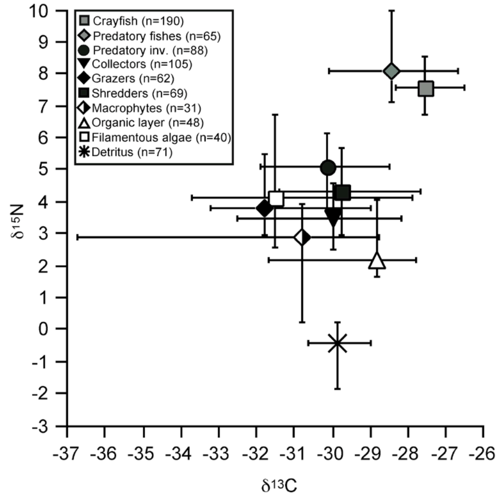

Figure 4. Dual isotope plot on median $\delta^{15}N$ and $\delta^{13}C$ from all sites combined, showing signals in predatory fishes, noble crayfish and potential food sources for crayfish. Live plants are divided into filamentous algae and macrophytes, since they differed substantially in carbon and nitrogen signals. Error bars denote the 25% and 75% quartiles.

of the crayfish guts examined. Crayfish held a position as top-invertebrate predator in our study streams and the availability of high quality food (i.e. biomass of invertebrates) explained both the trophic position and growth rate of noble crayfish. The biomass of the most commonly found invertebrate groups in crayfish guts influenced the trophic position of noble crayfish, while the biomass of relatively sedentary invertebrate groups gave an indication of the carbon origin of the system, which was shown in the carbon signature of noble crayfish. Overall, our results suggest that local variations in abiotic and biotic factors influence the biomass and species composition of invertebrates in temperate streams, which in turn affects the feeding of omnivorous crayfish and their subsequent trophic position and growth rate.

Gut content and stable isotopes

Noble crayfish in our study streams function as omnivores by consuming large amounts of detritus and invertebrates. This is consistent with several other studies of gut contents in crayfish (*Astacus astacus*: Abrahamsson 1966; Hessen and Skurdal 1986; *Pacifastacus leniusculus*: Stenroth and Nyström 2003; *Paranephrops zealandicus*: Hollows et al. 2002; *Paranephrops planifrons*: Parkyn et al. 2001; Olsson et al. 2006) indicating an omnivorous feeding behaviour of crayfish in general. Several studies, including ours, show high amounts of detritus in crayfish guts which might be due to the small energetic costs of consuming detritus and the microbial flora colonizing leaf litter (Momot et al. 1978; Parkyn et al. 2001; Roth et al. 2006). Parkyn et al. (2001) and Roth et al. (2006) further argue that by consuming leaf litter crayfish may gain enough energy for respiration and maintenance. However, more than 50% of the guts examined contained both animal and plant items and the models by Diehl (2003) predict that growth rate in omnivores is higher when feeding on both plant and animal food types compared to when feeding on either plant or animal items alone. It has been suggested that by consuming plant material crayfish get essential minerals and nutrients such as carotenoids that are needed for pigmentation and thus necessary for optimal growth (Goddard 1988; Nyström 2002).

However, despite their omnivorous feeding habit crayfish seem to occupy the trophic position of top-invertebrate predator. The isotope data showed that noble crayfish are at the same trophic level as predatory fish and animal material contributed more to the nitrogen isotope signals of noble crayfish than plant material. This is consistent with the findings by Parkyn et al. (2001), where the dominant food items consumed by

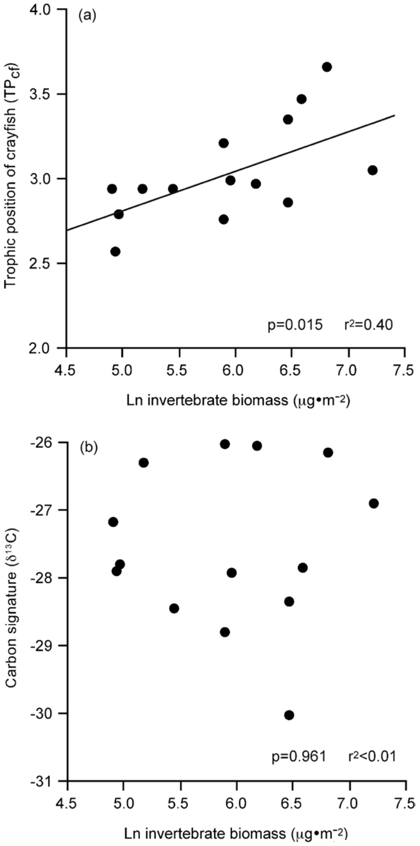

Figure 5. Linear regression between (a) trophic position (TP$_{cf}$) of crayfish and the biomass of invertebrates, and (b) carbon signature of crayfish ($\delta^{13}C$) and the biomass of invertebrates.

crayfish were invertebrates and detritus, but the isotope data showed that crayfish (*Pharaneprops planifrons*) obtained most of their energy from invertebrates. Predatory invertebrates, shredders and detritus contributed more than other food sources to the carbon isotope signal of crayfish according to the IsoSource mixing model, but from the dual isotope plot it looked like noble crayfish derived the carbon isotope signal from organic layer, shredders and collectors. However, there was a positive relationship between the carbon isotope signals of crayfish, when the carbon signals of detritus were subtracted, and the chlorophyll *a* levels at our sites. This might have confounded the position of noble crayfish in the dual isotope plot. The carbon signal of noble crayfish is likely to be derived mostly from detritus, either directly or indirectly by consumption of predatory invertebrates and shredders that were approximately one trophic level below noble crayfish and one trophic level above detritus in the dual isotope plot. Parkyn et al. (2001) showed a similar result from pasture streams, where crayfish had a carbon isotope signal between epilithon and filamentous green algae through the consumption of mayflies and snails.

Trophic position and carbon signature

The biomass of invertebrates, which indicates prey availability, affected the trophic position of crayfish. The biomasses of certain invertebrate groups also correlated with the carbon signature of noble crayfish in our study streams.

A high trophic position of crayfish seemed to be related to high biomasses of Ephemeroptera, Turbellaria, Trichoptera, Plecoptera and Mollusca. Moreover, these were the most commonly found invertebrate groups in the guts of noble crayfish. Many species among these groups are large and/or slow moving, which probably makes them easy for crayfish to catch in comparison with smaller and faster moving invertebrates (Nyström et al. 1999; Stenroth and Nyström 2003). The carbon isotope signals in noble crayfish seemed to be related to the biomass of Turbellaria, Oligochaeta, Coleoptera and Diptera. Crayfish had lighter carbon isotope signals in streams that had a high biomass of these four groups. Most species in these four invertebrate groups are considered to be relatively sedentary (Mellanby 1948) and will

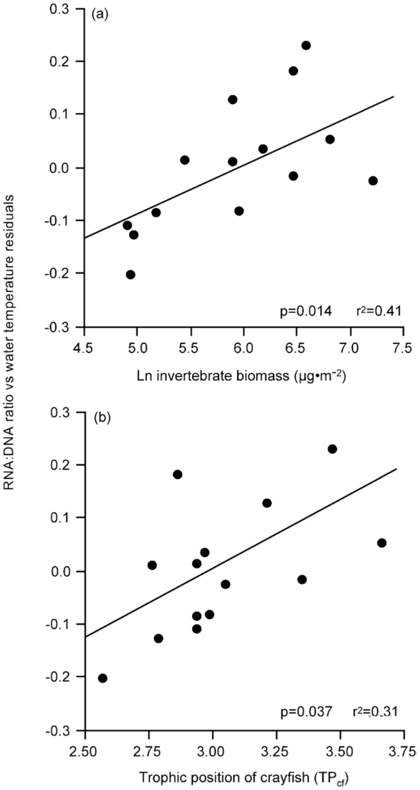

Figure 6. Multiple linear regression between (a) the growth rates (RNA/DNA ratio) of crayfish and the biomass of invertebrates, when the water temperature was controlled for and (b) between the growth rates of crayfish and the trophic position (TP_{cf}) of crayfish when water temperature was controlled for.

reflect the carbon signals of basal resources in streams. If the energy base is from allochthonous or autochthonous sources this will be reflected in the carbon signal of sedentary species and transferred up the food chain. Parkyn et al. (2001) showed that the energy base for crayfish in forested streams originated from allochthonous sources, while the energy base for crayfish in pasture streams originated from both allochthonous and autochthonous sources. This is in agreement with our study, where the streams differed in canopy cover from 2% to 98% and represented both forested and pasture streams. Further, the biomass of these sedentary species is generally higher in more open habitats with higher algal standing crop (Sabater et al. 1998) and epilithon biomass (chlorophyll *a*) was the main environmental variable that influenced the biomass of Oligochaeta and Diptera in our study.

Selectivity for food sources in omnivorous crayfish has been reported in several other experimental studies (e.g. Hanson et al. 1990; Nyström et al. 1999) as well as under natural conditions (Lodge and Lorman 1987). Noble crayfish seem to be selective feeders as well since specific invertebrate groups were responsible for the patterns found and the availability of high quality food determines the rate of selectivity shown by crayfish. In a study by Correia (2002), crayfish (*Procambarus clarkii*) adjusted their trophic behaviour to the availability of invertebrates in the environment. Several other studies have also addressed the importance of animal food sources for crayfish and argued that the availability of specific invertebrates determines the consumption of high quality food (Momot 1995; Nyström 2002; Alcorlo et al. 2004). Our results show that crayfish in natural streams have a trophic position that reflects the availability of high quality food in the environment and that the carbon signature of crayfish reflects the carbon origin at the base of the system.

The use of stable isotopes and mixing models for estimating trophic position requires rather precise estimates of isotopic signatures in the baseline organisms or end members (Syväranta et al. 2006). Several studies have shown high spatial and temporal variability of isotope ratios in primary consumers (Vander Zanden and Rasmussen 1999; Anderson and Cabana 2007). Post (2002) states that obtaining an appropriate baseline is one of the most difficult tasks when using stable isotope techniques in food web analyses. Moreover, several primary consumer taxa are not strictly collectors, shredders, grazers or predators, but have a slightly omnivorous diet (Anderson and Cabana 2007), which increases the problem with choosing a proper baseline. Also, species can be strictly detritus feeders in one stream and be more omnivorous in another, so caution should always be taken when interpreting results from stable isotope data in food web analysis. However, the use of stable isotope analysis and mixing models can give us a better understanding of the different roles of omnivores, such as crayfish, in food webs and their role for the flow of energy in stream ecosystems (Anderson and Cabana 2007).

Growth rate

Water temperature has been recognised as one of the most important factors affecting growth in crayfish (Lodge and Hill 1994; Reynolds 2002), but other variables such as food quality and availability may affect the growth rate if temperature is suitable for growth (Tardif et al. 2005). Our study shows that the biomass of invertebrates had an effect on the growth rates of crayfish when temperature effects were accounted for. Crayfish in streams with a high biomass of invertebrates had higher RNA/DNA ratios than crayfish in streams with low biomass of invertebrates. However, there was no particular invertebrate group that was responsible for this pattern, in contrast to the trophic position and carbon signature of crayfish. It was rather the availability of high quality food *per se* that affected the growth rates of crayfish. Tardif et al. (2005) argue that higher growth in juvenile perch on the south shore of their study lake in summer may have been coupled with a larger quantity of benthos at the south shore compared to the other study areas. Several experimental studies have shown that crayfish growth rate is affected by food availability (Hill et al. 1993; Edsman et al. 1994; Paglianti and Gherardi 2004) including studies of noble crayfish (Nyström and Granéli 1996). Our results show that growth rate in this species is affected by food availability also in natural streams. Furthermore, there was a positive correlation between trophic position and growth rate. Crayfish at a higher trophic position had higher RNA/DNA ratios than crayfish at a lower trophic position. Thus the availability of high quality food had a combined effect on the trophic position and growth rate of noble crayfish in our study streams. Crayfish at a higher trophic position consume more animal material than crayfish at a lower trophic position and therefore will have higher growth rates.

Noble crayfish in this study had low RNA/DNA values compared to lobsters (Parslow-Williams et al. 2001). Several other studies record similar ratios to ours in fish larvae (Clemmesen 1996), barnacles (Desai and Anil 2002), and gastropods (Okumura et al. 2002). We therefore assume that the RNA/DNA ratios in noble crayfish in this study are what can be expected in natural stream populations of adult crayfish. It has been suggested that moult stages and stress when handling the organism could affect the RNA concentration and thus confound the results of RNA/DNA ratios. Moss (1994) showed that different moult stages did not affect the RNA/DNA ratios in juvenile shrimp (*Penaeus vannamei*) and Clemmesen (1996) argued that short time stressors related to catching procedure and handling does not affect RNA/DNA. The RNA/DNA ratio is a quite conservative measurement and will give a good picture of the factors influencing an organism's growth and survival in a period for about a week prior to sampling (Clemmesen 1996). Further, an adult noble crayfish moults once or twice a year and will probably have a low growth rate compared to juveniles and species with a shorter life cycle. Moreover, the variation in growth rate within a population was very low, which indicates similar uptake of nutrients between individual crayfish. This is also consistent with the low variation in trophic position between individual crayfish from the same population, which indicates a similar diet in crayfish living in the same environment.

Overall, in this study we have shown that noble crayfish derive most of their energy from animal food sources and occupy the trophic position of a top-predator. The availability of invertebrates varies between streams due to differences in abiotic and biotic factors and the biomass of invertebrates influences feeding, trophic position and growth rate in noble crayfish. However, the availability of preferred invertebrate groups seems to partly explain some of the observed variation in trophic position of crayfish between streams. This could be because a stream supporting a high biomass of large, slow and/or sedentary invertebrates can enable a higher intake of animal resources for crayfish and thus place them at a higher trophic position. A higher trophic position (i.e. higher consumption of animal material) will also increase the growth rate of crayfish. Furthermore, a high biomass of sedentary invertebrates, such as oligochaeta and diptera, indicates a habitat with high algal biomass, which can be seen in the carbon signature of crayfish. In a habitat with a high biomass of these sedentary taxa the carbon signature of crayfish is a mix of both autochthonous and allochthounos sources compared to less productive habitats where the carbon isotope signals of crayfish are solely from allochthonous sources.

By combining gut contents, stable isotopes and RNA/DNA ratios it is possible to address the importance of different food sources for the trophic position, carbon signature and growth rate of omnivorous crayfish in different ecosystems.

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Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*)

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SUMMARY

1. In a 1-month outdoor stream channel experiment, we investigated the relative importance of habitat complexity (i.e. cobbled area) and the presence of adult signal crayfish (*Pacifastacus leniusculus*) males on the survival and growth of juveniles.
2. In treatments with high habitat complexity, more juveniles survived, more were newly moulted and they had a higher specific growth rate (SGR) at the end of the experiment than juveniles in treatments with low habitat complexity. The presence of adult males did not affect survival, moulting stage or growth of the juveniles.
3. The presence of adult males decreased juvenile activity during night. Juveniles in treatments with low habitat complexity were more active than juveniles in high habitat complexity during both day and night.
4. There was no difference in total invertebrate biomass between treatments. However, some invertebrate taxa, such as Chironomidae larvae, were affected by habitat complexity or the presence of adult crayfish. Juvenile crayfish in all channels had consumed detritus, algae and Chironomidae larvae and there were no differences in gut contents or stable isotope signals (carbon and nitrogen) between treatments, indicating a similar diet among the juveniles across treatments. However, the biomass of chironomids was significantly higher in channels with adult crayfish present, indicating a decreased consumption of chironomids by juveniles in the presence of adults.
5. Our results suggest that the recruitment of juvenile crayfish is mostly affected by habitat complexity. The competition for food and shelter and aggressive interactions between the juveniles were most pronounced in low habitat complexity, indicating that habitats with a good access to shelter will enhance recruitment of juvenile crayfish in streams.

Keywords: cannibalism, growth, habitat complexity, juvenile crayfish, survival

Introduction

Freshwater crayfish are omnivores that play important roles in many temperate food webs. Crayfish population size and individual growth rates may vary substantially due to abiotic and biotic factors. Acidification, diseases, predatory fish, cannibalism, habitat complexity and human harvesting often determine population size in crayfish (summarized in Lodge & Hill, 1994; Nyström, 2002). Several factors affect growth rate in crayfish, including temperature, food availability and predation risk. High individual growth rates affect fitness components in crayfishi for example, larger crayfish are less vulnerable to predation, larger females carry more eggs, and a large size attained during the first summer may increase the probability of surviving during winter (Abrahamsson, 1971). It is possible that crayfish population size is

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regulated both by adult survival and juvenile recruitment, but few studies have addressed this (but see Jones & Coulson, 2006).

Field observations in temperate streams suggest that predatory fish can regulate crayfish abundance, while food availability and temperature may influence individual growth rates. Moreover, when the abundance of predatory fish is low, crayfish abundance seems to be influenced by habitat complexity (i.e. substratum particle size distribution) (Nyström *et al.*, 2006; Olsson *et al.*, 2006), potentially by affecting intraspecific interactions such as cannibalism. Indeed, increased structural complexity has been found to reduce intraspecific competition and cannibalism in cultivated crayfish (Mason, 1979). To our knowledge there have been no studies that address habitat complexity and intraspecific competition simultaneously to explore their effects on crayfish abundance under more natural conditions.

Cannibalism may influence population structure, life history, competition for resources and behaviour in many species (Polis, 1981; Polis, Myers & Holt, 1989; Elgar & Crespi, 1992) and seems to be common in natural environments. Typically, smaller individuals are at high risk of being consumed by larger (older) conspecifics (Polis, 1981; Elgar & Crespi, 1992). Dominant age classes can suppress the recruitment of juveniles (young) due to large individuals eating nearly all the eggs and/or juveniles produced by the population (Polis, 1981; Dercole & Rinaldi, 2002), which indicates that cannibalism can be a very important factor in population dynamics (e.g. Nilsson, Nilsson & Nyström, 2000). Recruitment of juvenile crayfish has been suggested as an important mechanism behind observed fluctuations in crayfish population size, possibly as a result of adult crayfish cannibalizing newly hatched juveniles (Westman, Savolainen & Julkunen, 2002). Even though cannibalism is evident in many experimental studies of crayfish (Taugbøl & Skurdal, 1992; Nyström, 1994), and there is correlative support for strong intraspecific interactions in crayfish in less complex habitats (Nyström *et al.*, 2006; Olsson *et al.*, 2006), few field studies have addressed the interactions between juveniles and adults and whether the strength of these interactions could be modified by habitat complexity. Based on previous work we would, however, expect the frequency of cannibalism in crayfish to be dependent on the availability of food, shelter and the presence of larger conspecifics.

Larger conspecifics may not only consume juveniles, they may also have non-lethal effects on the juvenile stages by affecting their behaviour and feeding. For example, Blake, Nyström & Hart (1994) showed that juvenile crayfish were less active at night and more active during the day in the presence of adult crayfish. Juvenile crayfish typically reduce predation risk by seeking shelter and changing their activity pattern (e.g. Stein & Magnuson, 1976; Blake *et al.*, 1994; Gelwick, 2000). Such avoidance behaviour may be costly and has been shown to reduce growth by missed feeding opportunities (Stein & Magnuson, 1976; Resetarits, 1991; Hill & Lodge, 1999; Nyström, 2005). However, growth rate may also be density dependent and increased mortality may result in more food for the survivors, indirectly having positive effects on individual growth rates (Nyström & Åbjörnsson, 2000; Turner, 2004).

Crayfish are omnivores but animal food, such as invertebrates, are the most important energy source for crayfish growth (Whitledge & Rabeni, 1997; Parkyn & Collier, 2002). Moreover, the abundance of stream invertebrates may vary locally due to food supply and habitat heterogeneity (Death, 1995; Bis, Zdanowicz & Zalewski, 2000; Taniguchi & Tokeshi, 2004). Chironomids are a particularly important food and energy source for juvenile crayfish (Nyström, 2005), but are also eaten by adult crayfish (Guan & Wiles, 1998; Stenroth & Nyström, 2003). Therefore, both habitat complexity and adult crayfish may affect juvenile survival and growth in complex ways by influencing survival, behaviour, feeding and food availability. To understand fully the dynamics of crayfish populations, the mechanisms affecting survival during the juvenile stage must be understood.

In an experiment in outdoor stream-channels we tested how habitat complexity and the presence of adult male signal crayfish (*Pacifastacus leniusculus* Dana) affected the survival and growth of juvenile signals. Moreover, we also investigated the behaviour and feeding of juvenile and adult crayfish. We tested the hypothesis that adult crayfish have negative effects on juvenile survival and growth through cannibalism and by affecting feeding through changes in juvenile behaviour and resource competition for food (i.e. reducing benthic invertebrates). Furthermore, we also tested if juvenile survival and growth was greater in complex habitats by reducing intraspecific interactions among juveniles and between adults and juveniles.

Methods

General methods and experimental design

The experiment was performed during June and July 2006, in outdoor artificial stream channels, with a flow-through system where invertebrates except crayfish could emigrate and immigrate freely. The experimental channels were placed next to a stream, near Lund, in a pasture area. Water was gravity fed from the nearby Stampen Creek (longitude: 55°35′; latitude: 13°33′), using a siphon, into two large channels. From these two channels water was then distributed to 16 experimental channels (Fig. 1). At the end of each of the 16 channels there was an outlet, that had a 4 mm mesh to prevent juvenile crayfish from escaping but allowed invertebrates to exit, leading the water back to the stream. The mean flow in the channels was 0.06 L s^{-1} (measured once at the start of the experiment) and resembled a typical slow flowing reach of Swedish streams with signal crayfish (Nyström *et al.*, 2006). The channels (PVC) were 2.2 m long and 0.4 m wide with an average water depth of 0.15 m. A net (10 mm mesh size) was put on top of each channel to prevent adult crayfish from escaping and birds and mammals from disturbing the experiment.

We estimated periphyton biomass (chlorophyll-*a*) on ceramic tiles that were exposed to adult crayfish bioturbation and feeding. For this purpose, two glazed ceramic tiles (81 cm^2 each) were placed on the sediment in each channel. Since we observed a difference between treatments due to bioturbation by adult crayfish we also estimated periphyton biomass on stones from the cobbled area (Fig. 1) that were not directly exposed to adult crayfish (where water was too shallow). A 6.16 cm^2 circle of epilithon was removed from the upper surface (the light exposed side) of each stone and ceramic tile with a wire brush, filtered onto a glass fibre filter (GF/C Whatman®; Whatman International Ltd., Maidstone, England, U.K.) and frozen. Chlorophyll-*a* then was analysed according to Jespersen & Christoffersen (1987).

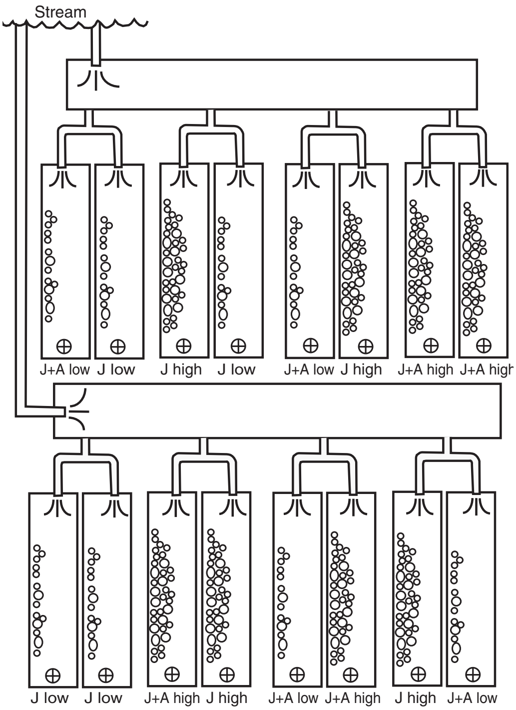

Fig. 1 The experimental set up showing the different treatments. J, juvenile crayfish; A, adult crayfish males. At the start there were 100 juvenile crayfish in all channels and two adult crayfish males in channels with treatment J + A. The channel bottom was covered with a layer of sand and high complexity (high) was achieved by covering approximately 40% of the bottom area with cobbles and low complexity (low) by covering approximately 20% of the bottom area with cobbles.

Treatments

We had four treatments each replicated four times in a fully factorial design (high and low habitat complexity crossed with adult crayfish present or absent; Fig. 1). Two replicates of each treatment were randomly assigned to one of the two test channel rows (Fig. 1). The bottom area of each channel was first covered by a layer of sand (0.06–0.2 cm Ø) and then high complexity was achieved by adding cobbles (4–15 cm Ø) to approximately 40% (average 38%, calculated from digital photos) of the channel bottom area, whereas low complexity was achieved by adding cobbles to approximately 20% (average 21%, calculated from digital photos) of the channel bottom area. The percentage of the bed covered with cobbles in streams with signal crayfish typically varies between 7% and 100% (Nyström *et al.*, 2006). Independent sample t-test showed that there was a significant difference between percent area covered by cobbles in the high and low complexity treatments ($t = -13.55$, d.f. = 14, $P < 0.001$).

Two weeks before the start of the experiment, 30 egg-bearing signal crayfish females, originating from a pond in the Stampen Creek catchment, were placed in a separate channel to provide newly hatched juveniles. Additionally, to promote colonization of invertebrates prior to the addition of crayfish, the water flow in the channels was started and invertebrates were taken with a Surber sampler (0.09 m^2, 250 μm mesh size, $n = 16$) from Stampen creek, then mixed and aliquots of equal volume distributed to the experimental channels. Since the juveniles from the 30 females did not hatch exactly at the same time, newly hatched juveniles (stage III) were distributed to the channels on three occasions during the week preceding the experiment, to a density of 100 juveniles (mean carapace length 5.1 ± 0.2 mm, estimated from 25 randomly chosen juveniles) per channel. On June 15 two adult males (mean total length 91.3 ± 4.6 mm, $n = 16$) were added to channels in the treatments with adult crayfish and the experiment started. These densities of juveniles and adults are within the ranges found in natural streams (Guan & Wiles, 1996). We used adult males since females are less prone to consume newly hatched juveniles when they are carrying or have recently been carrying hatchlings (Levi *et al.*, 1999).

Experimental procedure

The experiment lasted 33 days and channels were checked daily and the outlets were cleaned to prevent clogging. Between 4 and 7 July, we observed exuviae from juveniles in several channels and on 16 July we again observed exuviae and also four dead juveniles that had failed to moult. This indicates that the juveniles generally moulted once or twice and thus had grown during the experiment. Temperature and oxygen were checked once a week in all channels and in one randomly chosen experimental channel in each row of channels we placed a temperature logger (HOBO Water Temp Pro loggers; Onset Computer Corporation, Bourne, MA, U.S.A.) that measured water temperature four times a day throughout the experiment. The water temperature varied between 10.8 (at night) and 18.3 °C (by day) and oxygen saturation was never below 96% in any channel, indicating good conditions for crayfish growth and survival.

During the last 2 days of the experiment, juvenile activity in each experimental channel was estimated three times during the day and twice during the night. Each channel observation lasted 1 min during which the number of active (walking or feeding) juveniles was observed. On 17 July, when ending the experiment, all juveniles were counted, their moulting stage and any loss of chelipedes estimated, and the juveniles were then frozen for later length measurement, gut content and stable isotope analyses (see below). Two tiles and three stones were collected from each channel and frozen for later analysis of chlorophyll-*a* content (as above). In all channels, a macroalgal sample (potential additional food for the juveniles) was scraped off the channel wall and all invertebrates present in the channel were collected and frozen for identification, biomass estimates and stable isotope analyses (see below).

The carapace length (tip of the rostrum to the posteriomedial edge of the cephalothorax) of the 1-month-old juveniles was measured under a microscope with 10× magnification and length lines to the nearest 0.1 mm. Mean specific growth rate (SGR) was calculated for each treatment (on the assumption of exponential growth) according to the following equation:

$$\mathrm{SGR} = 100 \times (\ln \mathrm{CL}_t - \ln \mathrm{CL}_0)/t$$

where CL_t is the mean final carapace length of the 1-month-old juveniles from each treatment, CL_0 is the mean initial carapace length of the 25 newly hatched juveniles taken at the start and t is the time in days.

The contents of all male guts ($n = 14$, since two males escaped when ending the experiment) and five randomly chosen juvenile guts from each channel were examined under a binocular microscope to check if any crayfish had consumed conspecifics and which food items dominated the diet of adults and juveniles. To assess if there were any differences in the diet of the juveniles, stable isotope analyses were performed. Stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) were obtained for juvenile crayfish (8–10 from each channel), Chironomidae larvae (5–10 from each channel) and macroalgae (five samples from each channel). Samples consisted of untreated abdominal tissue from crayfish (as recommended by Stenroth *et al.*, 2006), abdominal tissue or whole body samples of chironomid larvae and a 0.5 × 0.5 cm sample of macroalgae (approximately 0.2 mg of carbon). Samples were dried at 60 °C for at least 1 h, and analysed with a PDZ Europa Ltd (Sandbach, Cheshire, U.K.) 20–20 stable isotope analyser. The δ notation is the relative difference between samples and known standards:

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

where X is either ^{15}N or ^{13}C and the corresponding ratio (R) is either $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Atmospheric nitrogen is used as standard ratio for nitrogen and Vienna Pee Dee Belemnite is used as the standard ratio for carbon. Glycin was used as internal standard and all isotope values are given in per mille (‰).

All invertebrates (except for crayfish) collected from each channel were identified to the lowest possible taxonomic level (Nilsson, 1996, 1997) under a binocular microscope. The invertebrates from each channel were then dried individually for 24 h at 60 °C and weighed to the nearest 0.1 mg and then combusted in a muffle furnace at 450 °C for 4 h and reweighed to enable calculation of ash-free dry weight (AFDW).

Statistical analyses

The overall effects of treatments, 'habitat complexity' and 'adult crayfish', on the 'performance' of juvenile crayfish (juvenile survival, percentage of moulting juveniles, percentage of juveniles with cheliped injuries, individual growth rates, juvenile activity both day and night) and variables that may be affected directly or indirectly by the juveniles 'performance' [invertebrate biomass, periphyton biomass and stable isotopes (nitrogen and carbon) of juvenile crayfish] were analysed in a two-way MANOVA. Individual two-way ANOVAS were then performed to facilitate the interpretation of the MANOVA. To explore further the effects of habitat complexity and adult crayfish presence on the biomass of dominant invertebrate taxa, multiple two-way ANOVAS were performed. Only species that were significantly affected by either habitat complexity or presence/absence of adult males are shown and discussed.

Data were arcsin $\sqrt{x}$ (percentage data) or ln (x or $x + 1$) transformed prior to analyses. All statistical analyses were performed in SPSS 11.0 for Mac OS.

Results

The two-way MANOVA including all dependent variables [juvenile survival, percentage of moulting juveniles, percentage of juveniles with cheliped injuries, individual growth rates, juvenile activity (day and night), invertebrate biomass, periphyton biomass and stable isotopes (nitrogen and carbon) of juvenile crayfish] revealed an overall effect of habitat complexity and of adult crayfish but no interaction between the two treatments (adult crayfish – Wilks' $\lambda = 0.008$, $P = 0.046$; habitat complexity – Wilks' $\lambda = 0.008$; $P = 0.042$; adult crayfish by habitat complexity interaction – Wilks' $\lambda = 0.013$, $P > 0.07$).

Juvenile survival, growth and cheliped injuries

Individual two-way ANOVAS showed that the overall significant effect of habitat complexity on juvenile survival and growth was due to higher juvenile survival in the more complex habitats, but also due to a higher growth rate and a higher percentage of juveniles that recently had been moulting (evident by a soft exoskeleton) (Table 1; Fig. 2). Mean survival in the high complexity treatments was 72% and in the low complexity treatments 48%. The mean SGR of the juveniles in the high and low complexity habitat was 1.1 and 1.0 mm day^{-1} respectively.

The significant effects of habitat complexity on the response variables were not affected by the presence of adult crayfish, since all interactions were non-significant (Table 1). There was, however, a tendency for juveniles to have a higher frequency of lost chelipeds in treatments with adult crayfish (Table 1; Fig. 2d).

Crayfish activity

Juvenile crayfish were mostly active during night, and there were more juveniles active in channels without adult males present and also in channels with low habitat complexity (Table 1; Fig. 3). During the day significantly more juveniles were active in channels

Table 1 Results from two-way ANOVAS on variables related to juvenile survival, percentage of newly moulted juveniles, percentage of juveniles with cheliped injuries, individual growth rates (SRG), juvenile activity (both day and night) and variables that may be affected directly or indirectly by juvenile 'performance' [periphyton biomass, stable isotopes (nitrogen and carbon) of juvenile crayfish, remains of crayfish in juvenile guts and frequency of juvenile guts that contained chironomids]

	Adult crayfish		Habitat complexity		Adult crayfish × habitat complexity	
Dependent variable	$F_{1,12}$	*P*-value	$F_{1,12}$	*P*-value	$F_{1,12}$	*P*-value
% Survivals	0.73	>0.41	**19.87**	**0.001**	0.32	>0.58
% Newly moulted	0.45	>0.51	**21.82**	**0.001**	0.18	>0.67
% Cheliped injuries	*3.95*	*0.070*	0.01	>0.92	2.01	>0.18
SGR	0.60	>0.46	**15.31**	**0.040**	0.12	>0.73
Activity day	2.57	>0.14	**6.23**	**0.028**	1.58	>0.23
Activity night	**20.84**	**0.001**	**41.94**	**>0.001**	0.60	>0.45
Periphyton biomass (tiles)	**20.05**	**0.001**	0.02	>0.88	0.15	>0.69
Periphyton biomass (stones)	0.02	>0.90	0.22	>0.64	1.27	>0.28
δ^{15}N of juveniles	1.90	>0.19	0.27	>0.62	0.01	>0.92
δ^{13}C of juveniles	0.64	>0.44	1.29	>0.28	0.12	>0.74
Remains of crayfish in juvenile guts	0.57	>0.47	0.29	>0.60	0.42	>0.53
Frequency of guts containing chironomids	0.14	>0.71	0.69	>0.42	4.29	0.060

Bold values indicate significant *P*-values.

with low complexity than in those with high complexity habitat (Table 1; Fig. 3).

Gut content and stable isotopes

Gut contents analyses of the juveniles showed that detritus (96%), Chironomidae larvae (56%) and algae (43%) were the food items found most frequently. In 11 of the 16 experimental channels, the remains of crayfish were found in 18% of the juvenile guts examined, but there was no difference between treatments (Table 1). Remains from juvenile crayfish were also found in the guts of two adult males (14% of the guts examined) and one contained a whole juvenile. However, 90% of the adult guts contained plant material and animal items, such as Chironomidae larvae, were also frequently found (80%).

Stable isotope analysis showed that juveniles, regardless of treatment, had similar δ^{13}C and δ^{15}N signals (mean $\delta^{15}N = 9.87 \pm 0.32$ and mean $\delta^{13}C = -26.26 \pm 0.48$), which seemed to originate from a diet of Chironomidae larva, where δ^{15}N was 3.4‰ less than crayfish (6.23 ± 1.02) and had similar carbon signal (−27.45 ± 0.48), rather than macroalgae. The latter had a nitrogen signal more than 3.4‰ below that of crayfish (mean $\delta^{15}N = 5.34 \pm 0.71$) and had a very different carbon signal (mean $\delta^{13}C = -20.0 \pm 2.34$). The frequency of juvenile guts containing chironomids did not differ between treatments (Table 1). Neither was there any difference between treatments in the nitrogen or carbon isotope signals of juveniles (Table 1).

Periphyton and invertebrates

There were no significant differences in periphyton biomass (chlorophyll-*a*) between treatments on the stones (Table 1). However, there was significantly less periphyton on the ceramic tiles exposed to adult crayfish bioturbation, but no effects of habitat complexity (Table 1).

In total, 38 invertebrate taxa were found with a mean of 18 taxa per channel. None of the invertebrate taxa found were potential predators on juvenile crayfish. The most common taxon in all channels was the Chironomidae (larval abundance ranged 998–5251 per channel), and they also dominated the total invertebrate biomass (Fig. 4). Even though there was no significant difference in the total biomass of invertebrates between treatments (Table 2; Fig. 4), there were significant differences for some taxa. The biomass of Chironomidae was significantly higher in treatments with adult crayfish, whereas the biomass of Coleoptera (adults) and *Limoniidae* sp. (larvae) was significantly lower (Table 2; Fig. 4). The biomass of *Pisidium* sp. and *Gammarus pulex* was significantly higher in the more complex habitats and for *Pisidium* sp. there were also an interaction effect (Table 2; Fig. 4).

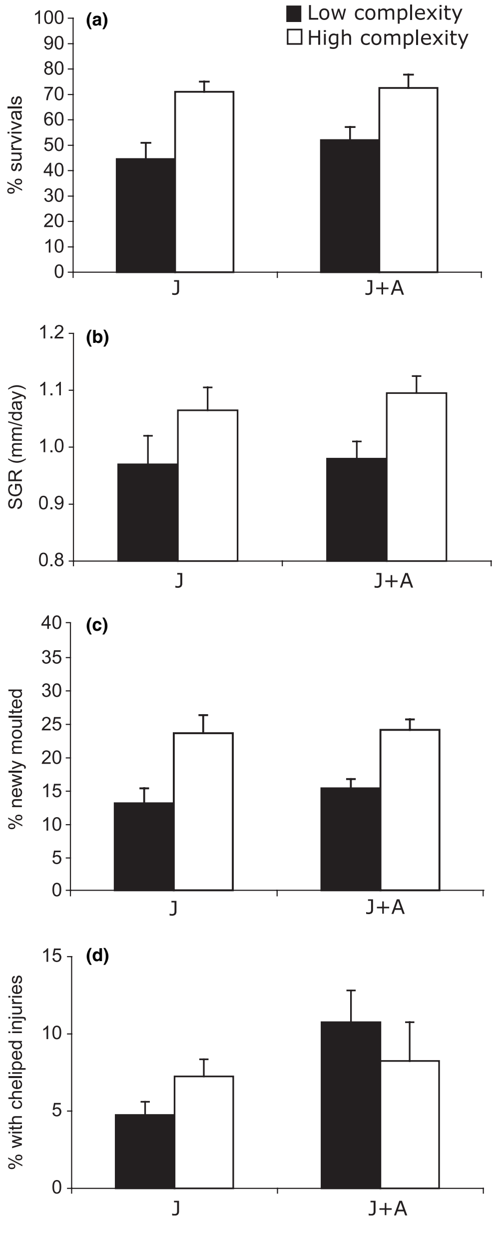

Fig. 2 Per cent juvenile crayfish that (a) survived, (b) the mean specific growth rate (SGR) of juvenile crayfish, (c) per cent juveniles that were newly moulted and (d) per cent juveniles that had cheliped injuries, in treatments with only juveniles (J) and in treatments with juveniles and two adult crayfish males present (J + A). White bars are treatments with high habitat complexity and black bars are treatments with low habitat complexity. Error bars denote 1 SE.

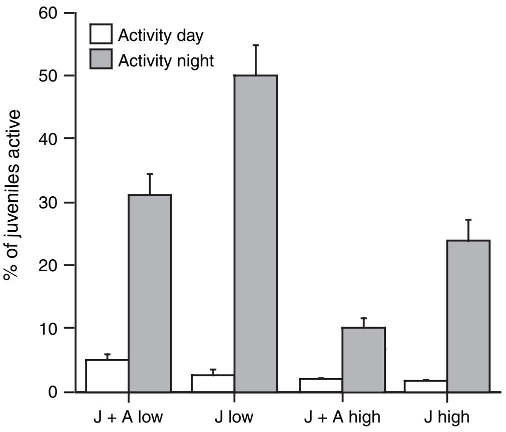

Fig. 3 Juvenile activity both during day and night in the different treatments. White bars are day activity and grey bars are night activity. Error bars denote 1 SE.

Discussion

Our results suggest that the recruitment of juvenile crayfish is affected primarily by habitat complexity and to a lesser extent by the presence of adult conspecifics. Adult crayfish suppressed juvenile activity during the night, but did not affect juvenile survival or growth. Competition for food and shelter and aggressive interactions between juveniles was most pronounced when habitat complexity was low, indicating that habitats with a good access to shelter will enhance the recruitment of juvenile crayfish. Observational studies suggest that crayfish abundance in streams with a low biomass of predatory fish is influenced mainly by availability of cobbles (Nyström *et al.*, 2006; Olsson *et al.*, 2006). Our results indicate that interactions between juveniles, but not between juveniles and adults, could explain these patterns.

Adult crayfish and the survival and growth of juvenile crayfish

Interestingly, the hypothesis that adult crayfish should have negative effects on juvenile survival and growth by cannibalism and competition for food was not supported. Even though we found the remains of juvenile crayfish in the guts of adult crayfish at the end of the experiment, adult crayfish

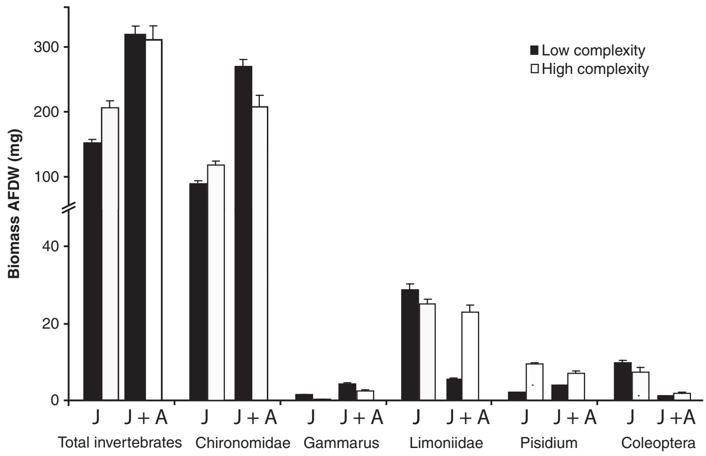

Fig. 4 Total invertebrate biomass and the biomasses (AFDW) of the dominant invertebrate taxa found in the different treatments. White bars are treatments with high habitat complexity and black bars are treatments with low habitat complexity. Error bars denote 1 SE (note the break on the *y*-axis).

Table 2 Results from the two-way ANOVAS on the total biomass of invertebrates and the biomasses of dominant taxa (AFDW in mg)

	Adult crayfish		Habitat complexity		Adult crayfish × habitat complexity	
Invertebrate taxa	$F_{1,12}$	*P*-value	$F_{1,12}$	*P*-value	$F_{1,12}$	*P*-value
Total invertebrate biomass	4.24	>0.06	0.12	>0.74	0.21	>0.65
Chironomidae	**7.46**	**0.018**	0.01	>0.92	0.36	>0.55
Gammarus pulex L.	1.16	>0.30	**9.46**	**0.010**	0.02	>0.90
Limoniidae	**5.70**	**0.034**	1.00	>0.33	2.17	>0.16
Pisidium sp.	0.13	>0.72	**17.40**	**0.001**	**6.85**	**0.022**
Coleoptera adults	**7.80**	**0.016**	0.21	>0.65	0.99	>0.33

Bold values indicate significant *P*-values.

did not affect juvenile survival. It cannot be excluded that the remains found were exuviae, or juveniles that were already dead due to moulting failure, when consumed by adult crayfish. Moksnes *et al.* (1997) and Luppi, Spivak & Anger (2001) observed few cases of intracohort cannibalism in their studies on juvenile crabs. Their studies showed that shelter availability improved the escape rate of juveniles from adult crabs, but was less effective as protection against juvenile predators. This is consistent with our results, where most juvenile crayfish survived in treatments with high complexity and adults present, indicating that the cobbles provided the juveniles with enough shelter to escape predation from the adult crayfish. Further, Blake & Hart (1993) showed in a laboratory study that adult signal crayfish had difficulties in catching juveniles, unless juveniles were immobile during moulting. Lovrich & Sainte-Marie (1997) suggest that the vulnerability to cannibalism of juvenile crayfish depends on the ability of adults to perceive and handle (determined by adult chela gape) the juveniles. This might explain the patterns found in our study, where competition/cannibalism between the juveniles seems to be more important than the risk of predation from the adult males.

Prey can minimize the risk of predation by changing their diel activity or shelter and habitat use (Blake *et al.*, 1994) and when predation risk is high most juvenile crayfish choose to hide in shelters (Hill & Lodge, 1994). We observed that juvenile signal crayfish were less active during night when adult crayfish were active, but increased their activity during day when adults were inactive. There was an overlap in food types consumed by juveniles and adults, but the biomass of the most important food and energy source for the juvenile crayfish (chironomids) was not reduced in channels with adult crayfish. Altered behaviour may involve costs in terms of lost feeding opportunities and reduced growth rates in response to predation risk (e.g. Peacor & Werner, 2000), a result also shown for juvenile signal crayfish (Nyström, 2005). The significantly higher abundance of chironomids in channels with adult crayfish may therefore be an indirect effect of altered feeding behaviour in juvenile crayfish. Crawford, Yeomans & Adams (2006) found that the presence of crayfish had a significantly negative effect on the abundance of chironomids, which is in agreement with our study regarding the presence of juvenile crayfish. Moreover, food supply (e.g. algal biomass) may affect the behaviour and local abundance of invertebrates in streams (Bis *et al.*, 2000) but in our experiment algal food sources was not significantly higher in channels with adult crayfish. On the contrary, algal biomass on ceramic tiles exposed to adult crayfish was significantly lower than on these in channels where adult crayfish were absent. It has been observed in other studies that adult crayfish remove significant amount of sediment and algae when walking and searching for food (Parkyn, Rabeni & Collier, 1997; Statzner *et al.*, 2000; Usio & Townsend, 2004). Adult crayfish did reduce the biomass of some invertebrate taxa, however, but these were too large to be consumed by juvenile crayfish (i.e. Coleoptera and Limoniidae), indicating that competition for food was not strong between adults and juveniles in this study. We speculate that juvenile crayfish in the channels with abundant cobbles in this study could find enough food sources in the cobble interstices. This was supported by the stable isotope analysis and growth rate of juveniles, because adult crayfish did not affect the energy sources utilized by juvenile crayfish, and they did not affect their growth rate.

The lack of an effect of adult crayfish on juvenile survival in this experiment may be due to a low encounter rate. Our experimental channels mimicked the shallow parts of streams, where juvenile crayfish are often found among cobbles, but where adult crayfish may not be able to feed efficiently. In fact, we never observed adult crayfish on the tops of the cobbles in this study. This segregation in habitat use by adult and juvenile crayfish has also been observed in natural streams (Englund & Krupa, 2000), further indicating that interactions between juvenile and adult crayfish in natural streams may also be weak.

Habitat complexity and the survival and growth of juvenile crayfish

In contrast to adult crayfish, habitat complexity had significant effects on the survival and growth of juvenile crayfish by increasing their survival and growth. Interestingly, habitat complexity did not influence the biomass of the most important food source for the juveniles (i.e. chironomids) and growth rate was not density dependent since growth was significantly faster when survival was high (high complexity habitats). The mechanism behind the increased survival and growth in the more complex habitats could be due to reduced physical intracohort interactions in the more complex habitats.

Sokol (1988) argues that shelter may reduce the effects of growth inhibition of subordinates by dominant individuals. Also Barki & Karplus (2004) observed growth inhibition in small juveniles that were paired with larger ones in full physical contact, which is in agreement with our study in which the growth rate of juveniles was higher in the complex habitat treatments, regardless of the presence or absence of adult crayfish. This indicates that the more complex habitat probably decreased interactions between the juveniles, which decreased growth inhibition of the smaller juveniles by the larger ones. According to Holt & Polis (1997), intraguild predation (in which potential competitors also eat each other) is similarly size driven and may be viewed as an extreme form of interference competition. Newly hatched crayfish are of similar size and a lack of shelter and very high densities of juveniles during recruitment season may create favourable conditions for cannibalistic interactions between the juveniles and decrease mean growth (Moksnes *et al.*, 1997; Verhoef & Austin, 1999).

We observed the remains of juvenile crayfish in guts of surviving juveniles at the end of the experiment, probably indicating cannibalism. Moreover, in the less complex habitats juvenile activity increased, and juveniles spent more time outside refuges both during day and night, potentially not just for feeding but also to reduce direct interference with juvenile conspecifics. This altered behaviour may have resulted in lower food intake and higher energy demand leading to reduced growth rate. Size selective mortality may however affect the size distribution of juveniles in this study, and hence our estimated growth rates. Because we observed that more juveniles in the complex habitats were moulting than in the less complex habitats, however, the results indicate that there were actual differences in growth rates between juveniles in the complex and less complex habitats.

Fluctuations in crayfish population size may depend on several interacting factors. The results from this experimental study indicate that the survival and growth of juvenile crayfish is mostly affected by availability of cobble habitats and that this effect is independent of the presence of larger and cannibalistic adult conspecifics. The use of different habitats by adult and juvenile crayfish may reduce the interactions between adults and juveniles. In complex habitats juvenile crayfish may simultaneously be able to feed and to reduce the encounter rate with other juvenile conspecifics. Intracohort interactions between newly hatched juvenile crayfish can decrease survival, moulting frequency and growth. It is possible that the recruitment of juvenile crayfish in streams is reduced in streams lacking shelters (e.g. cobbles), a situation typically found in degraded and human impacted temperate streams.

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