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Dynamics of omnivorous crayfish in freshwater ecosystems

Olsson, Karin

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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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Dynamics of omnivorous crayfish in freshwater ecosystems

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

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or in ms).

Cover illustration, photos and chapter separators: Illustration and photos by Karin Olsson

Contents

The thesis is based on five papers, which are referred to in the text by their roman numerals (I-V):

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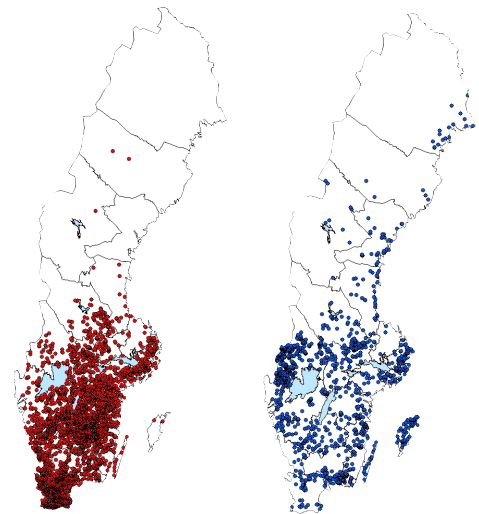
Figure 1. The distribution of signal crayfish (left, red dots) and noble crayfish (rigth, blue dots) in Sweden (data from the Swedish Board of Fisheries Crayfish database, 2004).

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).

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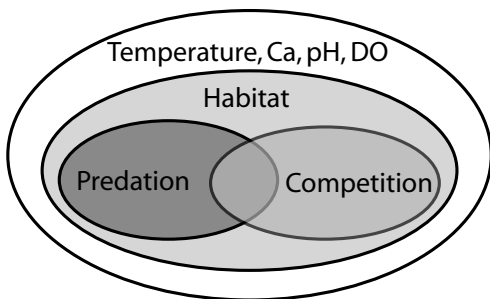
Figure 3. Several abiotic and biotic factors interact to influence crayfish dynamics, such as species composition, population size, and productivity. After Lodge and Hill, 1994. Ca is calcium and DO is dissolved oxygen.

• 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.
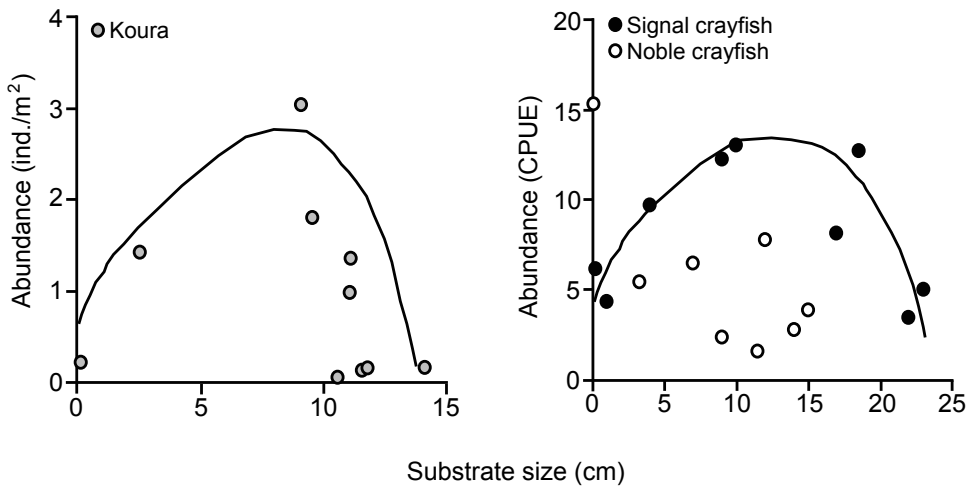
Figure 5. In streams without trout the highest abundance of the native New Zealand crayfish, Koura (left,grey dots and black trend line) was found at a substrate size around 10 cm, which is the same as for introduced signal crayfish (rigth, black dots and black trend line) in Sweden. However, the abundance 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
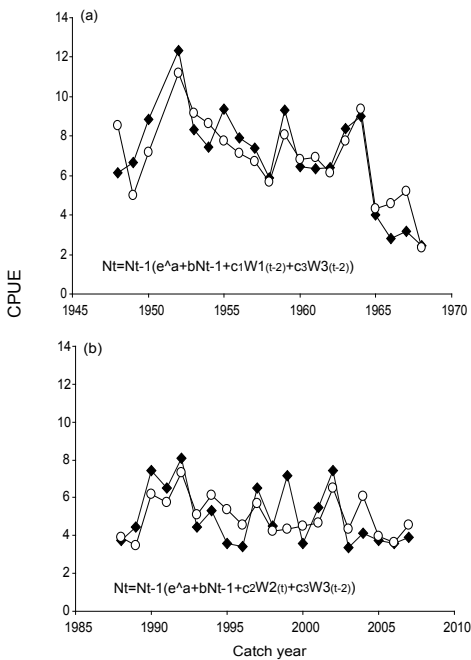

Figure 6. This type of borrows were inhabited by individuals of noble crayfish, guarding it against intruding crayfish.

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).
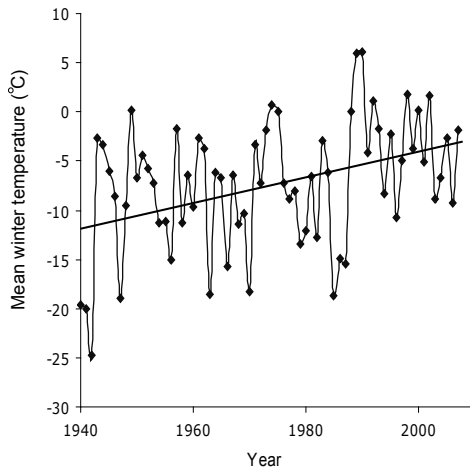
In paper II, I show that climatic as well as density dependent factors drive the observed fluctuations in abundance (measured as catch per unit effort, CPUE) of large adult crayfish (Fig. 7) in Lake Bunn, a south-

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 bN_{t-1} indicates density dependence since b were smaller than zero for bothe species. $W_3(t-2)$ represent the winter temperature with a two year lag, $W_1(t-2)$ represent ADD>10°C with a two year lag, and $W_2(t)$ represent the temperature during mating season the year before catch.

ern 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.

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 24°C). 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>10°C 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-
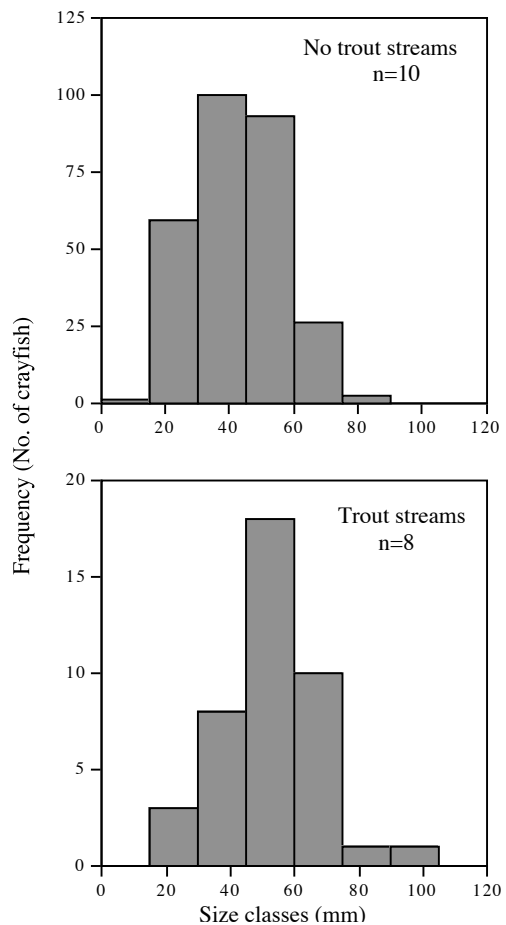

Figure 9. The size distribution of crayfish in streams without (upper) and with (lower) introduced brown trout.

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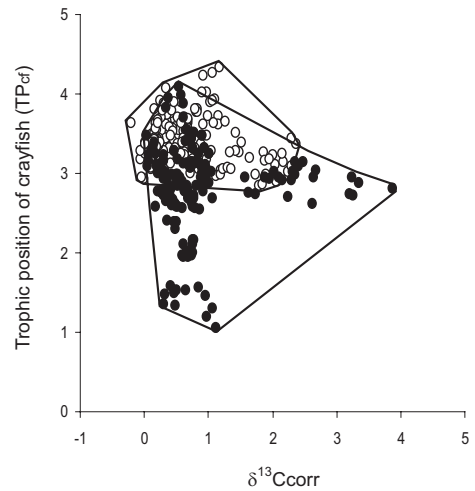
Figure 10. The total niche width (TA) of corrected values represented by convex hull area (inside solid lines) of all crayfish populations examined (each symbol represents one individual) for introduced signal crayfish (black dots) and native noble crayfish (white dots).

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.

Niche width has traditionally been quantified by using gut content analysis across individuals from a population in conjunction with measures of food resource rich-

ness 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 $\delta^{13}C$ - $\delta^{15}N$ 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.

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
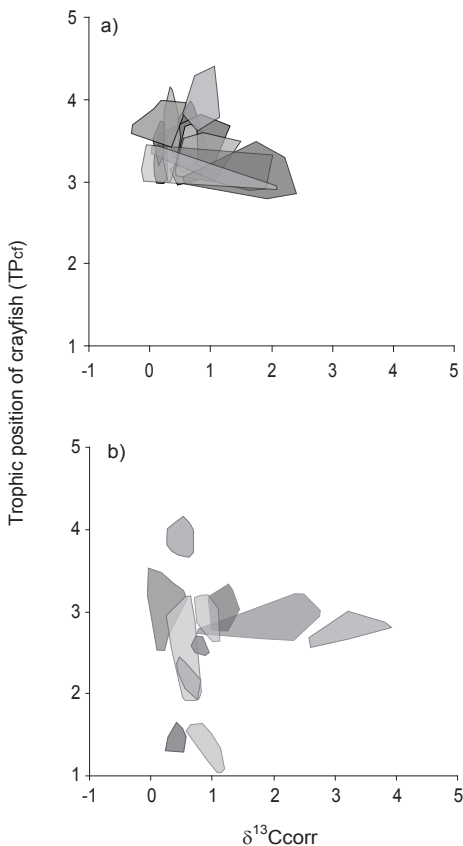
Figure 11. Population niche areas represented by convex hull areas (different grey colors) based on stable isotope analysis (corrected values) of 14-20 individuals per population for a) the 14 native noble crayfish populations and b) the 14 introduced signal crayfish populations.
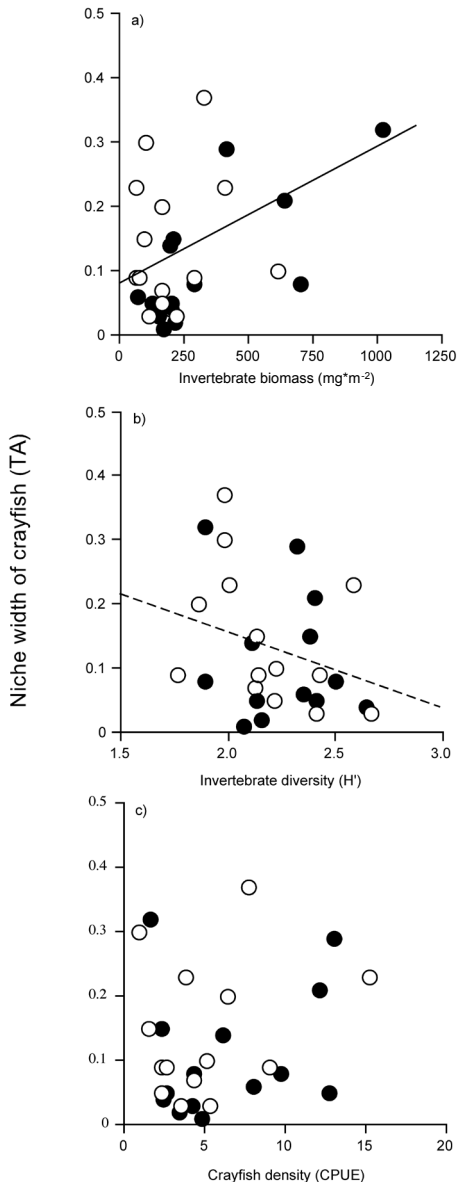
Figure 12. Regressions between the niche width (corrected values) of crayfish and a) invertebrate biomass, b) invertebrate diversity (H'), and c) crayfish density (CPUE). White dots represent noble crayfish populations and black dots represent signal crayfish populations. Significant regressions are 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 in-

sights to its niche use and its great invasive success in Europe and in other parts of the world.
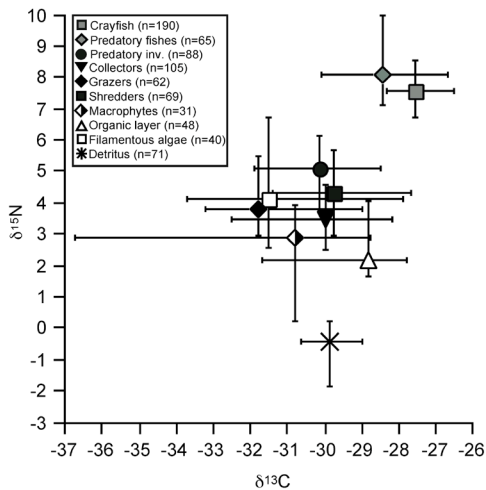
Trophic position and growth rate

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

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.

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.

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,
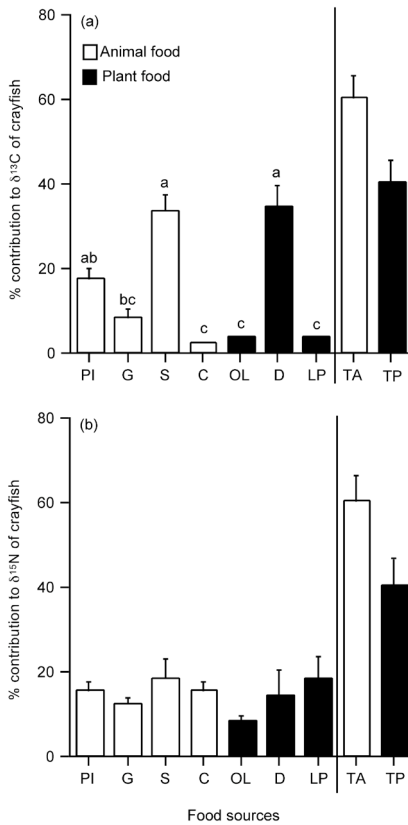
Figure 14. Contributions of different food sources to a) the carbon signal of crayfish and b) the nitrogen signal of crayfish. Different letters (a, b and c) represent a significant difference at the 0.05-level (Tukey's *post hoc* test). PI=predatory invertebrates, G=grazers, S=shredders, C=collectors, 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
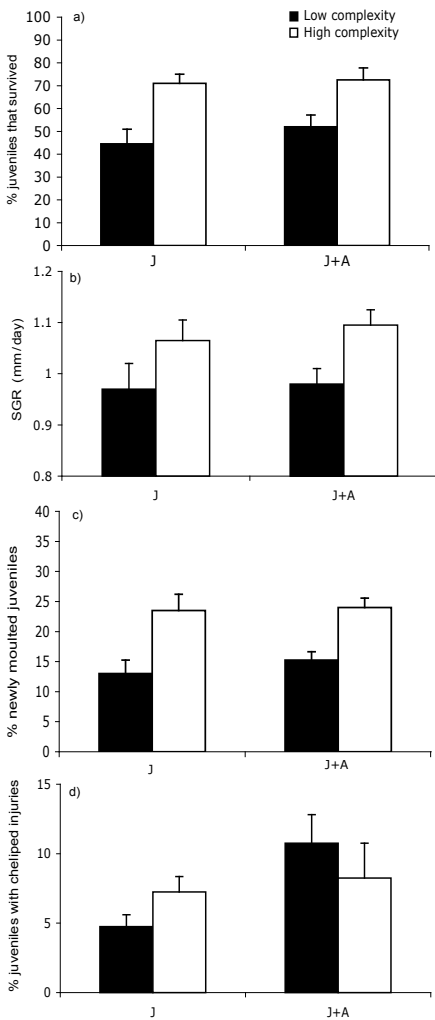
Figure 15. Percent juvenile crayfih that a) survived, b) the specific growth rate (SGR) of juvenile crayfish, c) percent juveniles that were newly moulted, and d) percent juveniles that had cheliped injuries in treatments with only juveniles (J) and in treatments with adults and two adult crayfish males 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-
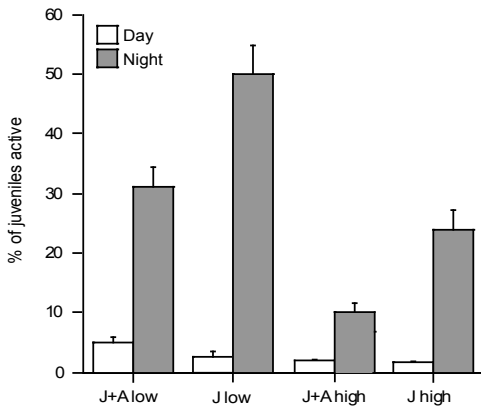
Figure 16. Juvenile activity both during day and night in the different treatments. White bars are day activity and grey bars are night activity. Error bars denote 1SE.

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,
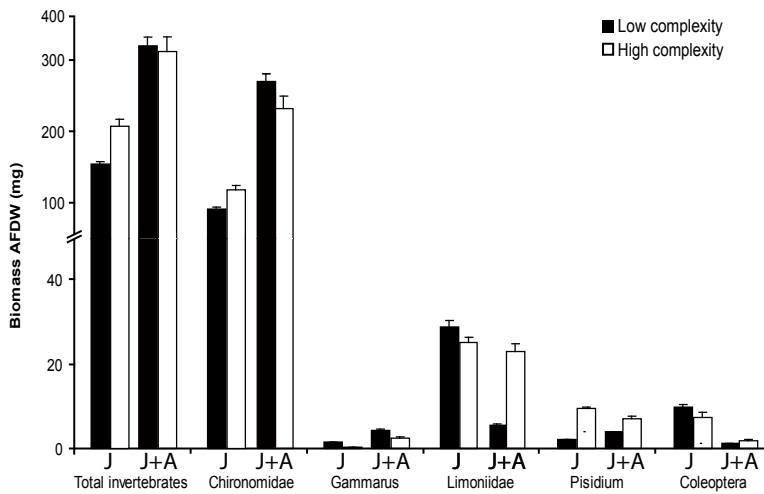
Figure 17. The total invertebrate biomass (AFDW) and the biomasses of dominant invertebrate taxa found in the channels. White bars are treatments with high habitat complexity and black bars are treatments with low habitat complexity. J are treatments with only juveniles and J+A are treatments with juveniles 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, intro-ductions 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 field-work 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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