

Björn Söderbäck

## Interactions among juveniles of two freshwater crayfish species and a predatory fish

Received: 27 January 1994 / Accepted: 30 June 1994

**Abstract** Two freshwater crayfish species, *Astacus astacus* L. and *Pacifastacus leniusculus* Dana, co-occur in some Swedish lakes. Observational studies indicate that the introduced, North American species *P. leniusculus* may gradually replace the native *A. astacus*, but the mechanism behind the replacement is not known. This study examined the direct effects of interspecific competition between the crayfish, and indirect effects of competitive interactions and fish (European perch, *Perca fluviatilis* L.) predation. Three different experiments with young-of-the-year (YOY) crayfish were performed. *P. leniusculus* was strongly dominant over similar-sized *A. astacus* in interference competition for shelter in a laboratory experiment. However, in a 35-day experiment in outdoor pools, *A. astacus* growth and survival were about equally affected by interactions with conspecifics and *P. leniusculus*. In contrast, *P. leniusculus* was significantly more affected by intraspecific competition than by competition with *A. astacus*, suggesting asymmetric competition between the two species. The presence of perch in outdoor ponds with mixed-species groups of the two crayfish species resulted in considerably higher predation rates on *A. astacus* than on *P. leniusculus*. Both species showed strong antipredator responses to perch by increasing refuge use. I suggest that higher perch predation rates on *A. astacus* originate from *P. leniusculus* being the superior species in interspecific competition for shelter. Because of displacement from refuges, *A. astacus* individuals become more exposed to the predator. This indirect effect of interactions among the two crayfish species and the predator may be important in the observed in situ replacement of *A. astacus* by *P. leniusculus*.

**Key words** Competition · Predation · Indirect effects  
Crayfish · Fish

### Introduction

The processes of competition and predation have long received much attention. Numerous studies show that both these factors can be important structuring forces in natural communities (see reviews by Connell 1983, Schoener 1983; Sih et al. 1985). Most studies on the effects of competition and predation have emphasized direct effects, but there is a growing awareness that interactions between competition and predation can result in important indirect effects. Indirect effects occur when one species affects the interaction between two other species (Miller and Kerfoot 1987). Often predation is viewed as a factor which reduces the intensity of competition, either by lowering prey densities or by removing superior competitors, and thereby promotes coexistence of competing prey (e.g. Brooks and Dodson 1965; Paine 1966; Dayton 1975; Morin 1983). However, predators may also have important indirect effects on prey through altering prey behaviour. Prey species show a variety of behavioural responses to avoid encounters with their predators (reviewed in Kerfoot and Sih 1987). Such antipredator responses, including shifts in habitat use or changes in activity times, may involve costs in terms of reduced feeding or growth rates that can significantly affect prey competitive ability (e.g. Stein and Magnuson 1976; Sih 1982; Werner et al. 1983; Mittelbach 1986; Resetarits 1991). Furthermore, a restriction of prey to habitats providing shelter may intensify competition with other refuging prey (Jeffries and Lawton 1984; Mittelbach 1988; Turner and Mittelbach 1990).

The distribution of the only native crayfish species in Sweden, *Astacus astacus* L., has been considerably reduced during the last century due to a lethal fungus disease, the crayfish plague (*Aphanomyces astaci* Schikora). In the 1960s the plague-resistant North American crayfish, *Pacifastacus leniusculus* Dana, was intro-

B. Söderbäck<sup>1</sup>  
Institute of Limnology, Uppsala University, Norbyvägen 20,  
S-752 36 Uppsala, Sweden

Present address:

<sup>1</sup> Department of Environmental Assessment,  
Swedish University of Agricultural Sciences, Box 7050,  
S-750 07 Uppsala, Sweden

duced into Sweden, and today this species has spread into many waters from which *Astacus astacus* has disappeared. However, in some Swedish lakes the two species coexist. Observational studies of coexisting populations indicate that *P. leniusculus* is gradually replacing *A. astacus* (Svärdson et al. 1991; Söderbäck 1993), but the mechanism behind the replacement is unclear. The crayfish plague cannot explain a gradual replacement, since a plague outbreak in an *A. astacus* population causes almost complete mortality within a few weeks (Unestam 1965; K. Söderhäll, personal communication). Abrahamsson (1983) assumed that *P. leniusculus*, because of more aggressive behaviour, higher fecundity and a higher growth rate, would be able to competitively exclude *A. astacus* when the two species meet, but his assumption was not substantiated by any experiments or studies of sympatric populations.

Crayfish are vulnerable to fish predation, and juvenile crayfish often constitute an important part of the diet of inshore predatory fish (Stein 1977; Gowing and Momot 1979; Dehli 1981; Quinn and Janssen 1989; Rabeni 1992). Several recent studies examining the mechanisms behind observed species replacements among crayfish have emphasized the importance of both direct and indirect effects of fish predation (Lodge et al. 1986; Olsen et al. 1991; DiDonato and Lodge 1993; Hill et al. 1993; Mather and Stein 1993). In Swedish lakes the European perch (*Perca fluviatilis* L.) is one of the most important crayfish predators (Vallin 1942; Appelberg 1986). Different fish predation on *A. astacus* and *P. leniusculus* in sympatric populations might explain the observed replacement. However, in a pond experiment with single-species groups, the two species did not differ markedly in vulnerability to perch predation (Söderbäck 1992). Moreover, the two species showed strong and similar antipredator responses to perch. These predator-induced behavioural modifications may interact with interspecific competition to produce important indirect effects.

The purpose of the present study was to examine the potential impact of interspecific competition and predation on the dynamics and relative densities of sympatric populations of *A. astacus* and *P. leniusculus*. In three experiments with young-of-the-year (YOY) crayfish, I documented: (1) the dominance relationship between the two species when competing for a limited shelter supply, (2) the effects of interspecific competition on growth and survival of the two species, and (3) the relative predation vulnerability of the two species in mixed-species groups.

## Materials and methods

*A. astacus* and *P. leniusculus* are ecological homologues with high interspecific overlap along important niche dimensions (Abrahamsson 1971, 1973, 1983; Westman and Pursiainen 1979). The two species are similar in size, morphology, and life history. They are opportunistic omnivores with a nocturnal activity pattern, occurring in the same type of habitat in lakes and streams, primarily in the littoral zone on stony bottoms or other substrates which of-

fer some form of refuge. Both species reach maturity when their body length is about 75 mm, usually at an age of 2–4 years (Cukerzis 1988; Lowery and Holdich 1988). The two species show an almost synchronous breeding period in autumn when the water temperature falls to about 10°C (Söderbäck 1994). Within a couple of weeks after mating, the females extrude their eggs and carry them under the abdomen until hatching in June–July the following year. Hatching occurs 2–3 weeks earlier in *P. leniusculus* than in *A. astacus* (B. Söderbäck, unpublished data) and the body mass of *P. leniusculus* hatchlings (10–17 mg) is lower than that of *A. astacus* hatchlings (21–27 mg) (A. Agerberg, personal communication; Cukerzis 1988). The earlier start of growth in *P. leniusculus* probably results in nearly equal-sized hatchlings of the two species at the time when those of *A. astacus* are released. The density of juvenile crayfish in dense populations can locally exceed 40 individuals m<sup>-2</sup> in the middle of July (B. Söderbäck, unpublished data).

## Experimental animals

At the beginning of June 1988 and 1990, egg-bearing females of *A. astacus* and *P. leniusculus* (10–20 specimens of each species) were collected from sympatric populations in Lake Skillötsjön, approximately 50 km SW of Stockholm, Sweden. The females of the two species were caged in separate outdoor wading pools for hatching of eggs. Hatching occurred between 12 June and 1 July in *P. leniusculus* and between 28 June and 10 July in *A. astacus*. When hatchlings were released about one week after hatching, the females were removed from the pools. To reduce handling mortality and problems with species recognition, the hatchlings were reared in the pools for about one month before the pool experiments started. During this period, the crayfish were additionally fed frozen zooplankton twice a week.

The perch used in the predation experiment were collected from Lake Erken about one week before the experiment started. They were kept in an outdoor wading pool and fed live earthworms daily. The only crayfish species occurring in Lake Erken is *P. leniusculus*. Thus, the perch had previous experiences with *P. leniusculus* but not with *A. astacus*.

## General methods for pool experiments

The pool experiments were performed outdoors, in an array of 15 rectangular plastic wading pools (1.5×1.2 m×0.25 m) at the Lake Erken Laboratory during the summers of 1988 and 1990. Pool substrate consisted of a 1 cm layer of sand. The pools were filled with water taken from the nearby mesotrophic Lake Erken in the middle of May of each year. A net bag with 0.3 kg (wet weight) of tightly packed leaf litter raked from the bottom of a nearby pond was added to each pool to provide detritus food and an inoculum of benthic micro-organisms. Each pool also received zooplankton, algae and other microorganisms from an inoculum collected with a 400 µm mesh net from the same pond. Pebbles (diameter 2–5 cm) and a brick with 32 holes (each of diameter 2 cm) were placed in each pool to provide refuges for the crayfish. The pebbles were enclosed in four PVC tubes (diameter 16 cm, height 2.5 cm) with Plexiglas bottoms covered with a layer of sand. Thus, each tube of pebbles was movable and easy to search for crayfish. Each tube of pebbles could theoretically hold more than 20 juvenile crayfish. However, the number of crayfish observed in a tube during the experiments seldom exceeded 10. In the predation experiment, a PVC cylinder (diameter 16 cm, length 35 cm) provided a refuge for the perch. Screen lids (mesh size 1 mm) were placed on the pools to exclude external predators and to prevent organic matter from falling down into the pools. Water temperature in four of the pools was automatically registered every 6th hour during the experiments.

### Experiment 1: competition for shelter

This laboratory experiment was performed in order to examine the dominance relationship between the two species in interference competition for shelter. In October 1988, YOY *A. astacus* and *P. leniusculus*, reared in wading pools during the summer, were placed in two large indoor plastic tanks with circulating water from Lake Erken (6°C). The two species were separated and the crayfish were fed potatoes and oats weekly. The experiment was performed in February 1989. The mean ( $\pm$ SD) wet weight of crayfish used in the experiment was 360  $\pm$ 33 mg for *A. astacus* and 390  $\pm$ 25 mg for *P. leniusculus*.

One mixed-species pair of equal-sized *A. astacus* and *P. leniusculus* (weight difference less than 25 mg) was placed in each of fifteen 2-l glass beakers (bottom diameter 12 cm), containing 1 l water from the holding tanks and one PVC shelter (diameter 8 mm, length 25 mm), the latter large enough to hold only one crayfish. The crayfish were placed in the beakers at 1700 hours and acclimatized to experimental conditions until 0900 hours the following day, when shelter use for each crayfish was recorded on six occasions occurring at 2 h intervals. Water temperature during the experiment was 14°C. To compare the two species' independent shelter use, ten crayfish of each species were placed singly in similar beakers and shelter use was recorded as above. All observations were made during daylight. Like most other crayfish species, these two species are night-active regardless of predator presence (Söderbäck 1992). This is often assumed to be a fixed antipredator behaviour (Stein 1979) and, accordingly, shelter should constitute an important resource during daylight for avoidance of visual predators.

### Experiment 2: effects of interspecific competition on survival and growth rate

A pool experiment with mixed- and single-species groups of *A. astacus* and *P. leniusculus* was performed to examine whether interspecific competition affected the two species differently. In August 1988, YOY of the two species were introduced into the experimental pools in three different treatments; the two species separately at initial densities of 90 YOY per pool, or both species together at densities of 45 YOY per species and pool (50 individuals m<sup>-2</sup> in all three treatments). The mean ( $\pm$ SD) wet weight of individual crayfish at the start of the experiment was 55 $\pm$ 7 mg for *A. astacus* and 46 $\pm$ 15 mg for *P. leniusculus*. Mean ( $\pm$ SD) water temperature during the experiment was 17.4 $\pm$ 1.4°C.

The three treatments were each replicated 5 times, except the *A. astacus* single-species treatment which was only replicated 4 times because of a shortage of animals. The experiment lasted for 35 days, and I sampled the pools on day 8, 16, 23, and 35. During a sampling event all crayfish were collected with a small dip-net and counted, and 30 randomly selected crayfish per species and pool were weighed before they were released again.

Crayfish growth rate and survival were used as response variables. The null hypothesis tested in this experiment was that the effects of intra and interspecific competition were equally strong. Growth curves for each species were constructed by plotting mean weight (mg wet weight) against time (day). The data were fitted to the power equation  $W_t = W_0 e^{at}$ , where  $W_0$  = mean weight at time zero,  $W_t$  = mean weight at time  $t$ , and  $a$  = the instantaneous coefficient of growth. I estimated  $a$  by least-squares regression of logarithmic transformed means. Survival (percent of the number introduced that were alive on day 35) was arcsin-square root transformed to normalize the data. I performed  $t$ -tests to examine whether  $a$  and survival differed between treatments.

### Experiment 3: vulnerability to perch predation in mixed-species groups

The effect of perch on *A. astacus* and *P. leniusculus* survival in mixed-species groups was studied in a pond experiment in August

1990. Twenty five YOY of each species were placed in each of ten pools (27.8 individuals/m<sup>2</sup>). The mean ( $\pm$ SD) wet weight of *A. astacus* was 42 $\pm$ 9 mg and of *P. leniusculus* 47 $\pm$ 15 mg. After 2 days one perch (170–210 mm standard length) was added to each of five randomly chosen pools. On day 3 and 9 following the introduction of the fish, the perch were removed and kept in a storage pool, while all crayfish in each pool were collected with a small dip-net, counted, and then released again. After 2 hours of reacclimatization by the crayfish a randomly chosen perch was added to each of the fish treatment pools. The *A. astacus* survival on day 9 was zero in four of the perch treatment pools, and therefore the experiment was terminated. Mean ( $\pm$ SD) water temperature during the experiment was 16.9 $\pm$ 2.3°C. The data were analysed with non-parametric methods because of unequal sample variances.

## Results

### Experiment 1: competition for shelter

When a mixed-species pair competed for a single shelter, *P. leniusculus* was strongly dominant over similar-sized *A. astacus* (Fig. 1). In 14 out of 15 mixed-species pairs, *P. leniusculus* occupied the shelter more often than *A. astacus* (Wilcoxon matched-pairs signed-ranks test,  $P < 0.01$ ). In beakers with a single crayfish, the frequency of shelter use was higher for *A. astacus* than for *P. leniusculus* (Mann-Whitney  $U$ -test,  $P < 0.02$ ) (Fig. 1).

### Experiment 2: Effects of interspecific competition on survival and growth rate

The replacement of half of the number of each species in the single-species treatments with an equal number of the potentially competing species in the mixed-species treatment, did not have any significant negative effects on growth or survival of either species (Fig. 2). There was a tendency for *A. astacus* to grow more slowly in

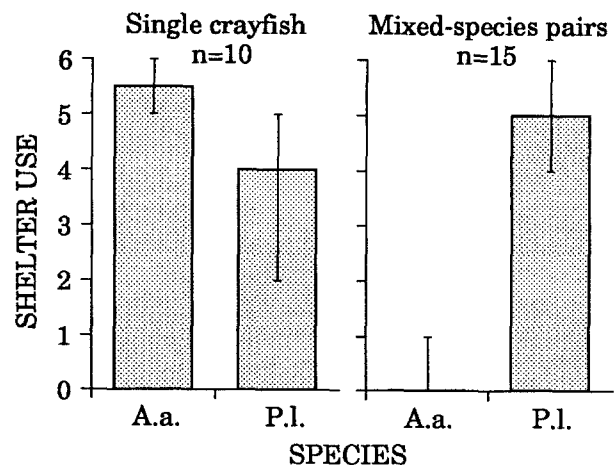
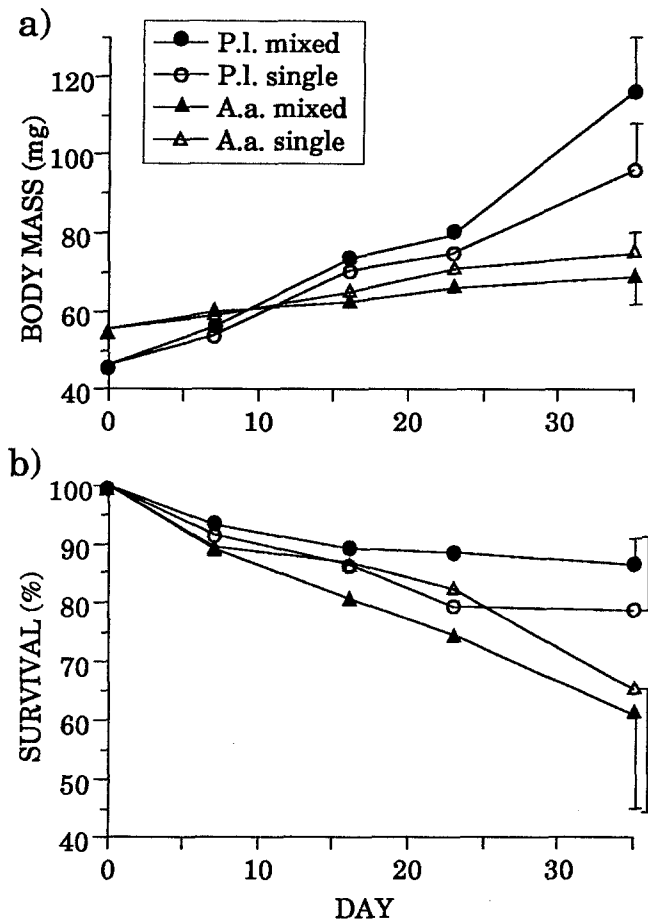


Fig. 1 Shelter use (number of observations when crayfish occupied shelter) of YOY *Astacus astacus* (A.a.) and *Pacifastacus leniusculus* (P.l.) in beakers with one shelter and a single crayfish or a mixed-species pair. Each beaker was observed on six occasions at 2 h intervals (median and interquartile range,  $n$  = number of replicates)



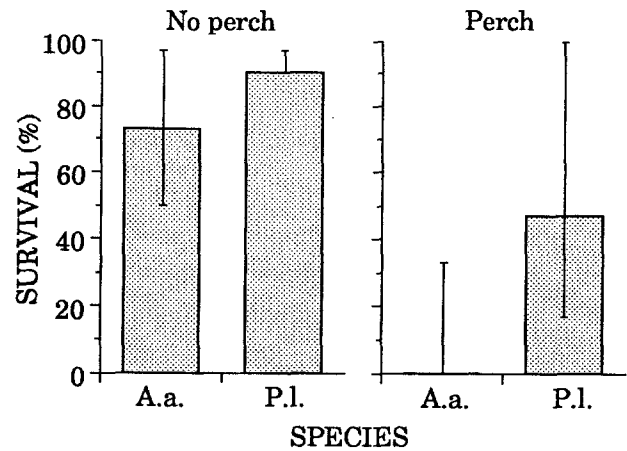
**Fig. 2** a Growth curves for and b survival of YOY *Astacus astacus* and *Pacifastacus leniusculus* in single- and mixed-species groups. Each point represents the mean value of four (*A. astacus* single) or five replicates. Bars denote 1 SD at the last sampling date

**Table 1** Juvenile growth rate at the end of experiment 2, in which YOY *Astacus astacus* and *Pacifastacus leniusculus* were kept in single- and mixed-species groups for 35 days. Mean values are shown, with 1 SD in parentheses. Tests of significance are given in the Results section

Species	<i>n</i>	Growth rate ( $a \times 10^3$ )
<i>Astacus astacus</i> , single	4	8.88 (1.22)
<i>A. astacus</i> , mixed	5	5.94 (3.02)
<i>Pacifastacus leniusculus</i> , single	5	21.25 (3.18)
<i>P. leniusculus</i> , mixed	5	24.95 (2.38)

mixed-species groups than when alone (Table 1; Fig. 2a), suggesting an effect of interspecific competition, but the difference was not significant ( $t$ -test,  $P=0.12$ ). In contrast to *A. astacus*, *P. leniusculus* grew significantly faster in mixed-species groups than when alone ( $t$ -test,  $P<0.05$ ) (Table 1; Fig. 2a). Survival did not differ between mixed- and single-species groups for either species ( $t$ -test,  $P>0.5$  for *A. astacus*,  $P>0.3$  for *P. leniusculus*) (Fig. 2b).

In the single-species groups, the growth rate of *P. leniusculus* was significantly higher than that of *A. astacus*



**Fig. 3** Survival of YOY *Astacus astacus* (*A.a.*) and *Pacifastacus leniusculus* (*P.l.*), reared in mixed-species groups in the presence or absence of perch for 9 days (median and range,  $n=5$ )

( $t$ -test,  $P<0.05$ ) (Table 1; Fig. 2a), while there was no difference in survival between the two species ( $t$ -test,  $P=0.25$ ) (Fig. 2b).

### Experiment 3: Vulnerability to perch predation in mixed-species groups

The presence of perch in mixed-species groups of *A. astacus* and *P. leniusculus* reduced total crayfish survival, but the two species differed considerably in vulnerability to perch predation. Survival of *A. astacus* on day 9 was significantly lower in perch treatment pools than in fish-free controls (Mann-Whitney  $U$ -test,  $P<0.01$ ) (Fig. 3). In fact, no *A. astacus* individuals survived until day 9 in four of the five perch pools. Survival of *P. leniusculus* in the perch pools on day nine was highly variable, probably a result of behavioural differences between perch individuals. *P. leniusculus* survival appeared lower with perch compared to the fish-free controls, but the difference was not significant (Mann-Whitney  $U$ -test,  $P=0.14$ ) (Fig. 3). Overall, in 9 days, perch predation converted the mixed crayfish population to one comprised of virtually 100% *P. leniusculus*.

### Discussion

The strong effect of a common predatory fish on the relative densities of *A. astacus* and *P. leniusculus*, as documented in this study, suggests that predation can be an important mechanism in the observed in situ replacement of *A. astacus* by *P. leniusculus*. This result is particularly interesting since Söderbäck (1992), in similar experiments with single-species groups, did not find the two species to differ in vulnerability to perch predation. The different results of these two experiments indicate a strong behavioural indirect effect (*sensu* Miller and Kerfoot 1987) of interactions among the two crayfish

species and the fish predator resulting in increased predation on *A. astacus*.

In a previous study I documented strong antipredator responses of YOY of the two species (Söderbäck 1992). Both species reduced activity and changed microhabitat use to substrates providing the best shelter in the presence of perch. Such predator-induced concentrations of vulnerable prey within refuges may intensify both intra- and interspecific interactions (Werner et al. 1983; Mittelbach 1986; Werner 1986, 1992; Persson 1993). In Experiment 1, YOY *P. leniusculus* were strongly dominant over similar-sized *A. astacus* in competition for shelter. Although the mechanism by which *P. leniusculus* monopolized the shelter was not identified, competition for shelter should presumably involve aggressive interactions (cf. Schoener 1983). The plausible mechanism behind the increased predation vulnerability of *A. astacus* in mixed-species groups is that *P. leniusculus*, because of their dominance in interference competition for shelter, displace *A. astacus* from the refuges and thereby increase their exposure to the predator.

I could not ascertain whether *A. astacus* YOY were more exposed than *P. leniusculus* in experiment 3 because it was not possible to separate the two species by visual observations in the ponds. However, during visual observations before the first sampling event, no crayfish were observed outside the shelters in the perch treatment, neither in daylight nor in darkness. In the absence of perch, the number of exposed crayfish was high during darkness, and some exposed crayfish were also observed in daylight. Thus, the antipredator responses of both species were similar to those observed in single-species groups (Söderbäck 1992). Despite the strong microhabitat shift to refuges, *A. astacus* suffered high predation by perch. Sih et al. (1988) suggested that high predation rates can occur even when few prey are observed outside of refuges, if high rates of prey emergence from refuges are accompanied by high attack rates. It seems probable that interference interactions within refuges increased the emergence rate of *A. astacus*, and this could explain the high predation rate on this species.

To prey species sharing a common refuge to avoid predators and interfering within the refuge, indirect effects of competition and predation may have important implications for prey population dynamics and even persistence in the system. At least two other studies have documented similar indirect effects. Huang and Sih (1990) studied indirect interactions between two prey organisms, salamander larvae (*Ambystoma barbouri*) and isopods (*Lirceus fontinalis*), that used a shared refuge to avoid a predatory fish. They found that salamander larvae tended to drive isopods out of refuges and, as a result, isopods suffered higher predation rates with than without salamanders. Similarly, Rahel and Stein (1988) documented predator-prey interactions among a small prey fish (*Etheostoma nigrum*) and two predators (the crayfish *Orconectes rusticus* and the predatory fish *Micropterus dolomieu*). The prey fish reduced activity and

increased refuge use in the presence of the predatory fish. When both predators were present, the prey fish were often forced to move by approaching crayfish, and they were often evicted from shelters by intruding crayfish. Thus, crayfish increased the vulnerability of the small fish to the predatory fish by evicting them from refuges and causing increased activity.

Quinn and Janssen (1989) suggested that the same type of interaction between competition and predation determined the relative abundance of two crayfish species, *Orconectes virilis* and *O. propinquus*, in Lake Michigan. *O. virilis* comprised about 40% of the eggs and juveniles, but accounted for only 20% of the adult population. The authors proposed that *O. propinquus*, because of its dominance in competition for shelter, displaced juvenile *O. virilis* from shelters, leaving them more vulnerable to fish predation. The relatively greater juvenile mortality of *O. virilis* did not result in displacement of that species, since it was offset by a greater individual fecundity, and also because *O. virilis* had a refuge from interspecific competition and size-selective predation by means of having a larger adult size than *O. propinquus*.

Observed species replacements among crayfish have often been explained by competitive exclusion, mediated through direct aggressive interactions (e.g. Penn and Fitzpatrick 1963; Bovbjerg 1970; Capelli and Munjal 1982; Capelli and Magnuson 1983). In a study of the dominance relationship between *A. astacus* and *P. leniusculus*, performed in aquaria with no resource for which crayfish could compete, *P. leniusculus* strongly dominated aggressive interactions with similar-sized *A. astacus* when the crayfish were older than YOY (Söderbäck 1991). In YOY pairs neither species dominated, and YOY crayfish were considerably less aggressive than crayfish from the larger size-groups. The dominance by YOY *P. leniusculus* in competition for shelter shown in the present study, suggests that also YOY *P. leniusculus* are aggressively dominant over similar-sized *A. astacus*. In situations where the abundance of some critical resource is limited, the benefit of dominance is obvious. Interference interactions can influence species resource use in such a way that subordinate species become restricted to suboptimal habitats or diets (Bovbjerg 1970; Hixon 1980; Berglund 1982; Peck 1985). This may reduce feeding and growth rates, and in the long run also survival of the subordinate species.

However, the present study provided no evidence for any strong direct effects of competition between YOY *A. astacus* and *P. leniusculus*, influencing the two species differently. Generally, it is assumed that asymmetrical competition should result if one species has a larger body size, faster growth rate, or greater impact on resource levels (Persson 1985; Morin and Johnson 1988; Peckarsky 1991). In experiment 2, the growth rate of *A. astacus* in single-species groups was lower than that of *P. leniusculus*. Furthermore, *P. leniusculus* growth rate was less affected by interspecific competition with *A. astacus* than by intraspecific competition, while growth

rate of *A. astacus* was at least equally affected by interspecific as by intraspecific competition. The higher growth rate of *P. leniusculus* in mixed-species groups than when alone could possibly be due to *P. leniusculus* predation on *A. astacus* individuals. However, this explanation seems unlikely since the corpses of most crayfish that died during the experiment were found intact and removed at the sampling occasions. I therefore suggest that the higher growth rate of *P. leniusculus* in mixed-species groups was an effect of reduced intraspecific competition, i.e. the effect of intraspecific competition in single-species groups was stronger than the effect of interspecific competition in mixed-species groups.

This indicates that competition between the two species is asymmetrical, favouring *P. leniusculus*. The predator-induced confinement of juvenile crayfish to refuges, documented in several studies (Stein and Magnuson 1976; Appelberg and Odelström 1988; Resetarits 1991; Söderbäck 1992) and also observed in experiment 3, may intensify competition and also reduce individual growth rate. The high predation rate on *A. astacus* in experiment 3 precluded any analysis of non-lethal effects of predation, but intensified competition within refuges may affect *A. astacus* more than *P. leniusculus* due to asymmetric effects.

Size-selective fish predation, more strongly affecting a smaller species or a species with a lower growth rate, has been suggested to contribute to species replacements among crayfish (Butler and Stein 1985; Lodge et al. 1986; Olsen et al. 1991; DiDonato and Lodge 1993; Hill et al. 1993; Mather and Stein 1993). The lower growth rate of YOY *A. astacus*, possibly further reduced by interspecific competition, implies that *A. astacus* spend a longer time in predation-vulnerable size than *P. leniusculus*. Hence, the probability of mortality during the juvenile stage should be higher in *A. astacus* than in *P. leniusculus*. Werner et al. (1983) have shown that a given reduction in growth rate during life stages when survival is already low (e.g. the juvenile stage) can have pronounced consequences for survival to reproduction.

Crayfish are most vulnerable and show the strongest responses to predatory fish during the juvenile stage (Stein and Magnuson 1976). Accordingly, the direct effect of predation and any indirect effect of competition and predation should be strongest among juvenile crayfish. The dominance by YOY *P. leniusculus* in competition for shelter, resulting in increased predation vulnerability of YOY *A. astacus*, may play an important role in the observed replacement of *A. astacus* by *P. leniusculus*. The importance of this mechanism should be strongly density-dependent. However, since crayfish populations are size-structured, interactions among YOY crayfish only constitute a subset of interactions that are potentially important for the dynamics of co-occurring populations of the two species. There are probably interactions among other size-classes, as well as between size-classes, that contribute to the observed pattern.

**Acknowledgements** I would like to thank Ulf Lindqvist, Tommy Odelström, Magnus Appelberg, and Kurt Pettersson for aid and encouragement in various aspects of this study. The manuscript benefitted from the comments of Magnus Appelberg, Rickard K. Johnson, David M. Lodge, Mikael Lönn, Birger Pejler and an anonymous reviewer. This work was financially supported by the National Swedish Board of Fisheries.

## References

- Abrahamsson SA (1971) Density, growth and reproduction in populations of *Astacus astacus* and *Pacifastacus leniusculus* in an isolated pond. *Oikos* 22:373–380
- Abrahamsson SA (1973) The crayfish *Astacus astacus* in Sweden and the introduction of the American crayfish *Pacifastacus leniusculus*. In: Abrahamsson S (ed) Freshwater crayfish 1. Studentlitteratur Lund, Sweden, pp 27–40
- Abrahamsson SA (1983) Trappability, locomotion, and the diel pattern of activity in the crayfish *Astacus astacus* L. and *Pacifastacus leniusculus* Dana. In: Goldman CR (ed) Freshwater crayfish 5. AVI Publishing Company, Davis, Calif, pp 239–253
- Appelberg M (1986) The crayfish *Astacus astacus* L. in acid and neutralized environments. Ph. D. thesis, Acta Universitatis Upsaliensis 23, Uppsala, Sweden
- Appelberg M, Odelström T (1988) Interaction between European perch (*Perca fluviatilis*) and juvenile *Pacifastacus leniusculus* (Dana) in a pond experiment. In: Goeldin P (ed) Freshwater Crayfish 7. Musee Zoologique Cantonal, Lausanne, Switzerland, pp 37–45
- Berglund A (1982) Coexistence, size overlap and population regulation in tidal vs. non-tidal *Palaemon prawns*. *Oecologia* 54:1–7
- Bovbjerg RV (1970) Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology* 51: 225–236
- Brooks JL, Dodson SI (1965) Predation, body size and composition of plankton. *Science* 150:28–35
- Butler MJ, Stein RA (1985) An analysis of the mechanism governing species replacements in crayfish. *Oecologia* 66:168–177
- Capelli GM, Munjal BL (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. *J Crustacean Biol* 2:486–492
- Capelli GM, Magnuson JJ (1983) Morphoedaphic and biogeographic analysis of crayfish distributions in Northern Wisconsin. *J Crustacean Biol* 3:548–564
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Cukerzis JM (1988) *Astacus astacus* in Europe. In: Holdich DM, Lowery RS (eds) Freshwater crayfish: biology, management and exploitation. Croom Helm Ltd, London, pp 309–340
- Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal community. *Ecol Monogr* 45:137–159
- Dehli E (1981) Perch and freshwater crayfish. (in Norwegian with English summary) *Fauna* 34:64–67
- DiDonato GT, Lodge DM (1993) Species replacements among *Orconectes* crayfishes in Wisconsin lakes: the role of predation by fish. *Can J Fish Aquat Sci* 50:1484–1488
- Gowing H, Momot WT (1979) Impact of brook trout (*Salvelinus fontinalis*) predation on the crayfish *Orconectes virilis* in three Michigan lakes. *J Fish Res Bd Can* 36:1191–1196
- Hill AM, Sinars DM, Lodge DM (1993) Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. *Oecologia* 94:303–306
- Hixon MA (1980) Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61:918–931
- Huang C, Sih A (1990) Experimental studies on behaviorally mediated, indirect interactions through a shared predator. *Ecology* 71:1515–1522

- Jeffries MJ, Lawton JH (1984) Enemy free space and the structure of ecological communities. *Biol J Linn Soc* 23:269–286
- Kerfoot WC, Sih A (1987) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH
- Lodge DM, Kratz TK, Capelli GM (1986) Long-term dynamics of three crayfish species in Trout Lake, Wisconsin. *Can J Fish Aquat Sci* 43:993–998
- Lowery RS, Holdich DM (1988) *Pacifastacus leniusculus* in North America and Europe, with details of the distribution of introduced and native crayfish species in Europe. In: Holdich DM, Lowery RS (eds) *Freshwater crayfish: biology, management and exploitation*. Croom Helm, London, pp 283–308
- Mather MA, Stein RA (1993) Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. *Can J Fish Aquat Sci* 50:1279–1288
- Miller TE, Kerfoot WC (1987) Redefining indirect effects. In: Kerfoot WC, Sih A (eds) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, NH, pp 33–37
- Mittelbach GG (1986) Predator-mediated habitat use: some consequences for species interactions. *Environ Biol Fish* 16:159–169
- Mittelbach GG (1988) Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* 69:614–623
- Morin PJ (1983) Predation, competition, and the composition of larval anuran guilds. *Ecol Monogr* 53:119–138
- Morin PJ, Johnson EA (1988) Experimental studies of asymmetric competition among anurans. *Oikos* 53:398–407
- Olsen TM, Lodge DM, Capelli GM, Houlihan RJ (1991) Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can J Fish Aquat Sci* 48:1853–1861
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–85
- Peck SK (1985) Effects of aggressive interaction on temperature selection by the crayfish, *Orconectes virilis*. *Am Midl Nat* 114:159–167
- Peckarsky BL (1991) Mechanisms of intra- and interspecific interference between larval stoneflies. *Oecologia* 85:521–529
- Penn GH, Fitzpatrick JF (1963) Interspecific competition between two sympatric species of dwarf crayfishes. *Ecology* 44:793–797
- Persson L (1985) Asymmetrical competition: are larger animals competitively superior. *Am Nat* 126:261–266
- Persson L (1993) Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos* 68:12–22
- Quinn JP, Janssen J (1989) Crayfish competition in southwestern Lake Michigan: a predator mediated bottleneck. *J Freshwat Ecol* 5:75–85
- Rabeni CF (1992) Trophic linkage between stream centrarchids and their crayfish prey. *Can J Fish Aquat Sci* 49:1714–1721
- Rahel FJ, Stein RA (1988) Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia* 75:94–98
- Resetarits WJ (1991) Ecological interactions among predators in experimental stream communities. *Ecology* 72:1782–1793
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Sih A (1982) Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* 63:786–796
- Sih A, Crowley P, Mcpeek M, Petranka JW, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Ann Rev Ecol Syst* 16:269–311
- Sih A, Petranka JW, Kats LB (1988) The dynamics of prey refuge use: a model with sunfish and salamander larvae. *Am Nat* 132:463–483
- Söderbäck B (1991) Interspecific dominance and aggressive interactions in the freshwater crayfishes *Astacus astacus* (L.) and *Pacifastacus leniusculus* (Dana). *Can J Zool* 69:1321–1325
- Söderbäck B (1992) Predator avoidance and vulnerability of two co-occurring crayfish species, *Astacus astacus* (L.) and *Pacifastacus leniusculus* (Dana). *Ann Zool Fenn* 29:253–259
- Söderbäck B (1993) Population regulation in two co-occurring crayfish species. Ph.D. thesis, Acta Universitatis Upsaliensis 434, Uppsala, Sweden
- Söderbäck B (1994) Reproductive interference between two co-occurring crayfish species, *Astacus astacus* L. and *Pacifastacus leniusculus* Dana. *Nord J Freshwat Res* (in press)
- Stein RA (1977) Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237–1253
- Stein RA (1979) Behavioral response of prey to fish predators. In: Clepper H (ed) *Predator-prey systems in fisheries management*. Sport Fishing Institute, Washington, DC, pp 343–353
- Stein RA, Magnuson JJ (1976) Behavioral response of crayfish to a fish predator. *Ecology* 57:751–761
- Svärdson G, Fürst M, Fjälling A (1991) Population resilience of *Pacifastacus leniusculus* in Sweden. *Finn Fish Res* 12:165–177
- Turner AM, Mittelbach GG (1990) Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71:2241–2254
- Unestam T (1965) Studies on the crayfish plague fungus *Aphanomyces astaci*. I. Some factors affecting growth in vitro. *Physiol Plant* 18:483–505
- Vallin S (1942) Kräftan. In: Andersson KA (ed) *Fiskar och fiske i Norden*, vol 2 (in Swedish). Stockholm, Sweden, pp 645–654
- Werner EE (1986) Species interactions in freshwater fish communities. In: Diamond J, Case TJ (eds) *Community ecology*. Harper and Row, New York, pp 344–358
- Werner EE (1992) Individual behavior and higher-order species interactions. *Am Nat* 140:S5–S32
- Werner EE, Gilliam JF, Hall DJ, Mittelbach GM (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548
- Westman K, Pursiainen M (1979) Development of the European crayfish *Astacus astacus* (L.) and the American crayfish *Pacifastacus leniusculus* (Dana) populations in a small Finnish lake. In: Laurent PJ (ed) *Freshwater crayfish 4*. Institut National de la Recherche Agronomique, Thonon-les-Bains, France, pp 243–250