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Predator avoidance and vulnerability of two co-occurring crayfish species, *Astacus astacus* (L.) and *Pacifastacus leniusculus* (Dana)

Björn Söderbäck

Söderbäck, B., Institute of Limnology, Uppsala University, Box 557, S-751 22 Uppsala, Sweden

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Juveniles of the native crayfish *Astacus astacus* and the newly introduced crayfish *Pacifastacus leniusculus* were reared separately in artificial ponds in the presence and absence of a predatory fish, the European perch (*Perca fluviatilis*), to measure the effects of this predator on the behaviour and survival of the two species. The two species responded strongly and similarly to the presence of perch by changing microhabitat use, thereby reducing their exposure to the predator. Crayfish that were observed outside of shelter did not tend to stay closer to shelter in the presence of perch than in perchless controls. The presence of perch increased the mortality of both species, but there was no significant difference in predation vulnerability between the two species. The prediction that *A. astacus*, because of a common evolutionary history with perch, should show stronger and more effective antipredator responses and therefore suffer a lower mortality rate than *P. leniusculus* was not supported. The juvenile growth rate is slower in *A. astacus* than in *P. leniusculus* and, consequently, *A. astacus* is at a predation-vulnerable size for longer. The total risk of mortality due to predation during the whole juvenile period may therefore be higher for *A. astacus* than for *P. leniusculus*.

1. Introduction

Predation plays an important role in determining composition and structure of natural communities (see review by Sih et al. 1985). Prey species have evolved a variety of behavioural responses to avoid encounters with their predators. Typical antipredator responses include reduction in activity, shifts in habitat use or changes in activity times (e.g., Stein & Magnuson 1976, Peckarsky 1980, Sih 1982, 1986, Werner et al. 1983, Semlitsch 1987, Pierce 1988). The obvious direct benefit of these types of behaviour is increased survival. However, predator avoidance may also involve a cost for the prey in reduced feeding or growth rates (e.g., Stein & Magnuson 1976, Sih 1982, Mittelbach 1986). Prey should avoid predators, but only when the increased probability of survival outweighs the cost of the antipredator behaviour. Thus, natural selection should favour prey that show "precise antipredator responses" (sensu Sih 1986), i.e., prey that can make appropriate decisions between mortality risk and energy gain. Indeed, several studies suggest that animals are sensitive to the degree of predation risk and can vary their antipredator responses in adaptive ways with variation in the magnitude of predation risk (e.g., Dayton et al. 1977, Peckarsky 1980, Dill & Fraser 1984, Sih 1986).

Most crayfish species show a nocturnal activity pattern, regardless of the presence of predators (Webb 1983). This is often assumed to be a fixed antipredator behaviour, the evolutionary result of long-term predation pressure (Stein 1979). Other antipredator behaviours are reactive, occurring only when a predator is detected. Stein & Magnuson (1976) and Stein (1977) showed that the crayfish *Orconectes propinquus* (Girard) responded to a fish predator by reducing activity and by selecting substrates affording most protection. Reduction in crayfish activity in response to predatory fish has also been reported for *Pacifastacus leniusculus* (Dana) (Appelberg & Odelström 1988) and *Cambarus bartonii* (Fabricius) (Resetarits 1991).

Crayfish often constitute an important part of the diet of inshore predatory fish (Stein 1977, Dehli 1981, Quinn & Janssen 1989). The European perch *Perca fluviatilis* L. is, together with eel *Anguilla anguilla* (L.), regarded as one of the most important crayfish predators in northern European lakes (Vallin 1942, Appelberg 1986). Perch is a visually dependent predator with diurnal and crepuscular feeding activity (Thorpe 1977). Crayfish are most vulnerable to perch predation during juvenile stages; when adult crayfish are consumed by perch it is often during molting (Dehli 1981).

In Sweden, the two crayfish species *Astacus astacus* and *Pacifastacus leniusculus* commonly co-occur with perch, but they differ in their historical contacts with this predator. *Astacus astacus* is the only native crayfish species in Sweden and it has a common evolutionary history with perch. The distribution of *A. astacus* has been considerably reduced during the last century due to a lethal fungus disease, the crayfish plague (*Aphanomyces astaci* Schikora). In the 1960's, the plague-resistant crayfish *P. leniusculus* was introduced into Sweden, a species native to North America, west of the Rocky Mountains (Bott 1950). Prior to its introduction in Sweden it had no contact with European perch, and probably no contact with North American percoid species, since these species originate from areas east of the Rocky Mountains (Craig 1987). *Astacus astacus* and *P. leniusculus* are ecological homologues with high interspecific overlap along important niche dimensions (Westman & Pursiainen 1979, B. Söderbäck unpubl. data). The two species are similar in size, morphology, and life history. They are opportunistic omnivores, occurring in the same type of habitat in lakes and streams, primarily on stony bottoms or other substrates which offer some form of refuge. Today, *P. leniusculus* has been introduced into many waters from which *A. astacus* has disappeared due to the plague, but in some Swedish lakes the two species occur sympatrically.

This study was conducted to assess the potential impact of a common predatory fish on population dynamics and relative densities of sympatric populations of *A. astacus* and *P. leniusculus*. In a pond experiment, the antipredator responses and predation vulnerability of young-of-the-year of the two crayfish species when confined with perch were analysed. It seemed that *A. astacus*, because of its lengthy coexistence with perch, should be better at avoiding perch predation than *P. leniusculus*. The main objectives of the study were (1) to quantify how microhabitat use, activity, and survival of the two crayfish species is affected by the presence of perch; (2) to test whether *A. astacus* shows stronger antipredator responses to perch than *P. leniusculus*; and (3) to test whether *A. astacus* suffers lower predation mortality than *P. leniusculus*.

2. Material and methods

2.1. Experimental ponds and experimental animals

The experiment was performed outdoors in an array of 12 artificial ponds (rectangular plastic wading pools, 1.5 × 1.2 m and 0.25 m deep) at the Lake Erken laboratory of Uppsala University in June 1989 and was repeated with the same design in August 1989. The substrate of the pools consisted of a 1-cm layer of sand. The pools were filled with water from the nearby mesotrophic Lake Erken in the middle of May. A net bag with 0.3 kg (wet weight) of tightly packed leaf litter raked from the margin of a nearby pond was added to each pool to provide a detrital food base. Each pool also received zooplankton, algae, and other microorganisms from a 0.5-l inoculum collected with a 400 µm mesh net from the same pond. In each pool four piles of pebbles (diameter 2–5 cm) and a brick with 32 holes (diameter 2 cm) were placed to provide refuges for the crayfish. The pebbles were enclosed in a PVC tube (diameter 16 cm, height 2.5 cm) with a plexiglass bottom, which made the whole pile movable and easy to search for crayfish. A 30-cm-long PVC tube in each pool provided a refuge for the perch.

The crayfish used in the experiment were young-of-the-year *A. astacus* and *P. leniusculus* without previous experiences of predators. In June, one-month-old crayfish from two commercial hatcheries were used. The crayfish used in August originated from egg-bearing females of the two species, collected at the beginning of June from sympatric populations in Lake Skillötsjön, approximately 50 km SW of Stockholm. They hatched in the middle of June and were reared in wading pools at the Lake Erken laboratory. The perch were collected from Lake Erken about one week before the experiment started and were kept in an outdoor wading pool and fed live earthworms daily until the start of the trials.

2.2. Experimental design

The experiment was designed to quantify changes in microhabitat use, activity times and survival of the two crayfish species in response to perch. Single-species groups of *A. astacus* and *P. leniusculus* were reared in the presence or absence of perch. The perch treatments and controls were each replicated three times for a total of 12 experimental pools. The experiment was performed from 3 June to 22 June 1989 and repeated with the same design from 4 August to 23 August 1989. The mean (± *SD*) wet weight of individual crayfish at the start of the June experiment was 38.8 ± 3.8 mg for *A. astacus* and 24.6 ± 4.3 mg for *P. leniusculus*. In the August experiment the starting weights were 68.8 ± 10.6 mg for *A. astacus* and 162.0 ± 41.1 mg for *P. leniusculus*. Water temperature in four of the pools was automatically registered every six hours during the experimental periods. The mean (± *SD*) water temperature was 14.2 ± 3.1°C in June and 16.7 ± 3.8 °C in August.

Fifty crayfish were placed in each pool (corresponding to a density of 27.8 m^2). After two days acclimatization, one perch (150–210 mm standard length) was added to each of the six fish treatment pools. The experiment continued for 20 days after the perch were added and the pools were sampled on days 4, 12 and 20. On each sampling occasion, the number of exposed crayfish in each pool was counted in daylight (1600 h), at dusk (30–60 min after sunset) and at night (about 2400 h). Crayfish not exposed (not visible from above) were in the brick holes or in the piles of pebbles. During the night observations, the distance to the nearest refuge for each exposed crayfish was estimated. During the dusk and night observations, the pools were illuminated using a flashlight for approximately 2 min. The following day 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 into the pool from which they were collected. After 2 h reacclimatization, a randomly chosen perch was added to each of the fish treatment pools.

The crayfish exposure data from the three sampling occasions within each pool were treated as statistically independent and were combined in the analysis as the results did not suggest any effect of sampling date on the degree of exposure. Since the sampling interval was as long as eight days, and a randomly chosen perch was added to the fish treatment pools after each sampling event, the combination of data was justified. To avoid a strong influence by a single individual on the proportion of exposed crayfish, only exposure data from pools with more than five surviving crayfish were used in analyses.

3. Results

3.1. Behavioural responses

Juvenile *A. astacus* and *P. leniusculus* showed strong and similar responses to the presence of

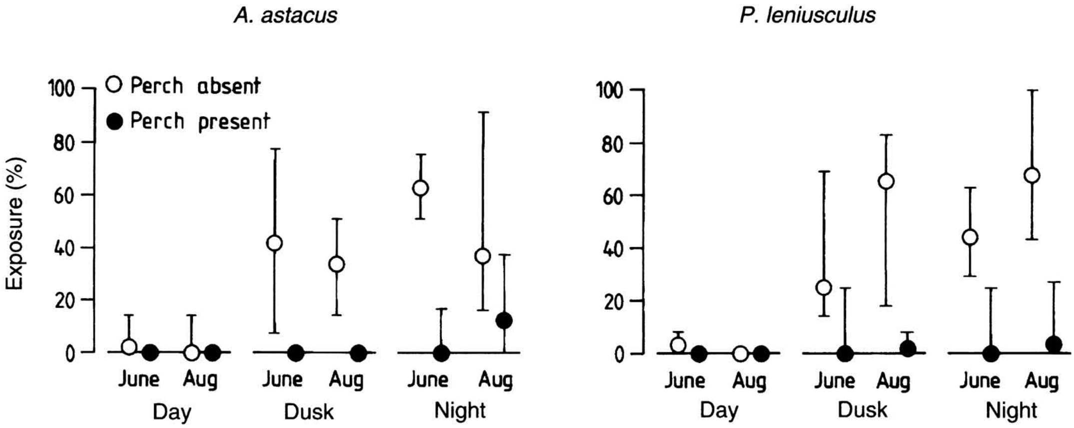

Fig. 1. The proportion of exposed juveniles of *A. astacus* and *P. leniusculus* in different light conditions in the presence and absence of perch in June and August (median and range, number of observations varied between 7 and 9).

perch by changing microhabitat use (Fig. 1). Kruskal-Wallis tests were performed separately for each light condition in the two experimental periods to determine whether the proportion of exposed crayfish differed among treatments. In daylight, exposed crayfish of both species were observed in fish-free controls, while no exposed crayfish were observed in any fish treatment pool, but the difference was not significant. In the dusk and night observations the overall test showed a significant treatment effect ($P < 0.001$). Multiple comparisons (Conover 1980:231) indicated, for both species, a significantly lower degree of exposure in perch treatments than in controls, both at dusk and at night ($P < 0.001$). In perch treatments there were no significant differences in exposure between the two species in any light condition. In control treatments *A. astacus* was more exposed than *P. leniusculus* at night in June and less exposed at dusk and night in August ($P < 0.05$), but these differences may be caused by differences in size and origin of the experimental animals.

No differences were found among treatments in the distance between exposed crayfish and shelter. Mean distances were nearly equal for all four treatments in both experimental periods, varying between 15 and 17 cm. The Kolmogorov-Smirnov two-sample test, performed separately for each species, showed no effect of perch presence on the observed distances ($P > 0.25$ for both species).

3.2. Survival and growth

The presence of perch reduced survival of both *A. astacus* and *P. leniusculus* (Fig. 2), despite their strong antipredatory responses. To test whether crayfish survival differed among treatments the Friedmans test was performed with several observations for each treatment in each block (Conover 1980:307), where the experimental periods (June and August) constituted the blocks. The overall test showed significant differences among treatments ($P < 0.005$). Multiple comparisons indicated lower survival in perch treatments than in controls for both A. *astacus* and *P. leniusculus* ($P < 0.005$ and $P < 0.001$, respectively).

Survival in control treatments differed between the two species and between the two experimental periods (Fig. 2). The low proportion of *P. leniusculus* surviving in controls in June was probably due to a combination of small, vulnerable crayfish and low temperature, which may have increased handling mortality. Because of variability of survival in controls, comparison of predation vulnerability between the two species was done by standardizing the absolute values of survival in perch treatments as percentages of mean values obtained in the appropriate controls. To test if predation vulnerability differed between the two species the block-partitioned data (June and August) were analysed using the Friedmans test. This test did not show any difference in vulnerability to perch predation between *A. astacus* and *P. leniusculus* ($P > 0.5$). To reduce bias due to behavioural differences between individual perch on crayfish survival, a randomly chosen perch was added to the fish treatment pools after each sampling. Nevertheless, survival in perch treatments showed large variation among replicates (Fig. 2). This variation makes the conclusion of equal predation vulnerability of the two species uncertain, but the results do not suggest any substantial difference between the two species in vulnerability to perch predation.

The low survival in perch treatments precluded any analyses of pools population means to test whether crayfish growth was affected by the presence of perch. The mean weights in perch treatment replicates overlapped the means in controls for both species in the two experimental periods. Thus, the results do not suggest any strong negative effect of the presence of perch on the growth rates of the two species, but such effects may have been masked by effects of reduced population densities in perch treatments.

4. Discussion

This study focused on differences between *A. astacus* and *P. leniusculus* in antipredator responses and vulnerability to perch predation. It seemed that *A. astacus*, because of an evolutionary history with perch, should show stronger and more precise antipredator responses and therefore have a lower mortality rate than *P. leniusculus*. However, the effects of perch on the two species were found to be very similar, thus providing no support for this conjecture. Juveniles of *P. leniusculus* showed diel and predator-induced microhabitat shifts similar to those in *A. astacus*, and they were no more vulnerable to perch predation than juveniles of *A. astacus*.

Successful avoidance of predation may depend on either highly precise antipredator responses to a specific predator or a more general but effective combination of fixed and reactive antipredator responses. Chemically-mediated detection of predators has been demonstrated in a variety of aquatic organisms, for example, mayflies (Peckarsky 1980), mosquito larvae (Sih 1986), isopods (Holomuzki & Short 1988) and amphibian larvae (Petranka et al. 1987). Crayfish have well developed visual (Bruski & Dunham 1987), as well as chemical (Hazlett 1985) sensory mechanisms. Thus, it seems likely that they may use a combination of visual and chemical cues for predator detection. Preliminary results from a laboratory study, performed together with M. Appelberg and T. Odelström, indicate that juvenile *A. astacus*, without previous exposure to predators, are able to detect perch by chemical cues. Therefore, it seems reasonable that *A. astacus* have evolved mechanisms for recognition of perch and also effective behavioural responses for avoidance of predation.

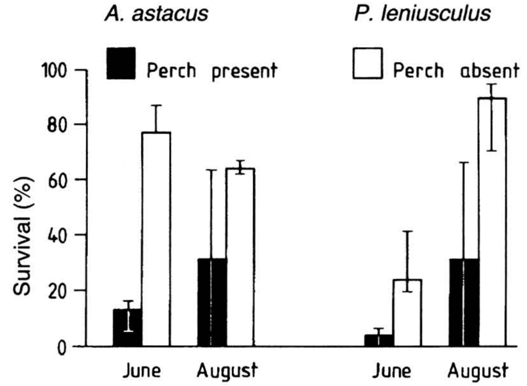

Fig. 2. Proportion of 50 juveniles of *A. astacus* and *P. leniusculus* surviving in the presence and absence of perch during 20 days in June and August (median and range, $n = 3$).

The period of co-occurrence between *P. leniusculus* and European perch corresponds to less than ten generations of *P. leniusculus*. Assumably, this period is too short for the evolution of precise and specific antipredator responses to perch. Nevertheless, *P. leniusculus* apparently recognized perch as a potential predator and showed strong behavioural responses to its presence. In its original range, *P. leniusculus* co-occur with salmonids and other predatory fish species. The antipredator responses of *P. leniusculus*, shown in this study, appear to be generalized responses to any predatory fish. The results suggest that these generalized responses are equally effective for avoidance of predation by perch as are the responses of *A. astacus*. Further studies are needed to determine if the two species use the same stimuli for detection of perch and also if they differ in the precision of their antipredator responses.

Experiments show that the restriction of prey to microhabitats providing shelter may incur a cost in reduced growth rates, either directly if food quality or availability is lower within these microhabitats (Sih 1982, Holmuzki & Short 1988), or indirectly by increased competition for food or space (Stamps 1984, Mittelbach 1986). Furthermore, Stein & Magnuson (1976) found that predatory fish reduced feeding rates of juvenile crayfish, and they suggested that predators, by reducing daily ration, may lower crayfish growth rates. The results of the present study did not suggest lower growth rates of *A. astacus* and *P. leniusculus* as a result of their antipredator responses. However, from the results it cannot be determined if perch predation on the two species was size-selective, or if the reduction in crayfish densities due to predation counteracted any negative effects of increased competition within refuges. Thus, one can not exclude the conjecture that the strong antipredator responses of *A. astacus* and *P. leniusculus* also involved a cost in reduced growth rates.

No long-term studies on the population dynamics of sympatric populations of *A. astacus* and *P. leniusculus* have been reported, but there are some indications that *P. leniusculus* may gradually replace *A. astacus* (Svärdson et al. 1991, B. Söderbäck unpubl. data). The large proportion of crayfish in the diet of several predatory fish species (Stein 1977, Dehli 1981, Quinn & Janssen 1989) indicates that predatory fish can influence the abundance of crayfish through direct exploitation. The effects of perch predation on crayfish survival was probably exaggerated in the present study because of the small experimental units and the absence of alternative food for the perch. Stein & Magnuson (1976) suggested that predators accounted for more than 25% of total annual crayfish mortality in a lake with dense populations of inshore predatory fish. The results of the present study suggest that *A. astacus* and *P. leniusculus* juveniles do not differ substantially in vulnerability to perch predation, and one might conclude that the mortality caused by direct perch predation should not affect the relative proportions of the two species. However, the juvenile growth rate is slower in *A. astacus* than in *P. leniusculus* (B. Söderbäck, unpubl. data). This implies that *A. astacus* are in predation-vulnerable sizes for longer time , and the total risk of mortality due to predation during the whole juvenile period may therefore be higher for *A. astacus*.

The indirect effects of predator-induced behavioural modifications may be even more important than direct predation for the dynamics of sympatric populations of the two species. A restricted spatial distribution of crayfish, especially the smaller size classes most predation-vulnerable, to habitats providing shelter has also been observed in natural lakes (Stein 1977, Appelberg 1986, Quinn & Janssen 1989). If shelter availability is limited and/or if the resource level within these habitats is low, the risk of predation can increase the importance of competitive interactions. Because of the large similarities in the two species, it is reasonable to suggest that interspecific competition can play an important role in determining the development of sympatric populations. Predators can mitigate the strength of both inter- and intraspecific competition by reducing the total abundance of crayfish. However, since the two species have similar means of avoiding predation by changing habitat use, the mere presence of perch may force them to compete more strongly within a common refuge. Perch may, therefore, strongly influence the population dynamics and relative abundances of *A. astacus* and *P. leniusculus* by indirectly increasing the importance of inter- and intraspecific competition. In order to evaluate the potential impact predators can have on the development of sympatric populations of the two species, further experimental studies are needed that integrate the effects of predator-induced behavioural modifications with the effects of competition.

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