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Effects of backswimmer (*Notonecta*) predation on crayfish (*Pacifastacus*) young: autotomy and behavioural responses

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The effects of predatory adult backswimmers (*Notonecta lutea*) on young-of-the-year of the signal crayfish (*Pacifastacus leniusculus*) were examined. Laboratory experiments showed that crayfish juveniles (2 months old, carapace length 14 mm) resorted to cheliped autotomy to escape predation by backswimmers. Autotomy proved to be a successful tactic, since no crayfish young were killed by the backswimmers, in spite of many attempts. The number of lost chelipeds was higher in experiments with backswimmers and without shelter, but the time of day had no effect. However, the crayfish young did not alter their sheltering behaviour in the presence of a backswimmer. In seminatural nursery ponds the proportion of crayfish juveniles with cheliped regeneration was highest in the pond with the highest *Notonecta* predation pressure. In all ponds the crayfish with regenerated chelipeds were smaller than intact individuals. Moreover, crayfish survival rate was lowest in the high predation pressure pond. This study indicates that although cheliped autotomy is an effective escape mechanism for signal crayfish young, predation by backswimmers, through nonlethal injuries, reduces individual growth rate and resource holding potential in crayfish.

1. Introduction

Antipredatory responses of prey animals may be costly in terms of reduced opportunities to other activities and thus may result in reduced growth and reproductive success (Sih 1987, Lima & Dill 1990). Optimal balancing between conflicting demands predictably changes during ontogeny, and this is reflected in alterations in behaviour. Predation is an important source of mortality in the life of juvenile crayfish (reviews Hogger 1988, Huner 1988). In crayfish the risk of predation by fish is inversely correlated to crayfish size (Stein 1977) and, moreover, with chela size (Stein 1976, 1977). Accordingly, indirect antipredatory responses are inversely correlated with body size in crayfish (Stein & Magnuson 1976, Stein 1979) and lobsters (Wahle 1992). In addition, crayfish are able to escape predatory attacks (Webb 1979, Bellman & Krasne 1983) and actively defend themselves against predators in various ways (Stein & Magnuson 1976, Saiki & Tash 1979), but unsuccessful predation may lead to cheliped losses through autotomy (Skurdal et al. 1988) (chelipeds are the first and largest thoracic limbs of crayfish, with the two outer joints modified as massive pincerlike claws, the chelae).

In many animals, autotomy seems to be an adaptation toward increasing the probability of surviving a predatory encounter (McVean 1982, Harris 1989). Balanced against an increase in survival is the loss of an organ that is often important for many vital functions (Harris 1989). Decapods can make use of cheliped autotomy as an escape mechanism that increases survival probability (Robinson et al. 1970, McVean 1982), but subsequently leads to slower growth rate (Bowler & Brown 1977). In addition, the regenerated limb will be much below its proper size (McVean 1982), consequently reducing resource holding potential and many other components of individual fitness (Bovbjerg 1953, 1956, Ingle & Thomas 1974, Stein 1976, 1977, Stein & Magnuson 1976, McVean 1982, Ranta & Lindström 1992a).

Aquatic insect predators have a significant adverse impact on crayfish juveniles in many fishless waters, in the littoral zones of lakes with low fish densities, in aquaculture (Dye & Jones 1975, Barr & Huner 1977, Barr et al. 1978) and under laboratory conditions (Gydemo 1989, Jonsson 1992). Although there are many reports available on fish induced behavioural changes in crayfish juveniles (Stein & Magnuson 1976, Stein 1977, 1979, Saiki & Tash 1979, Hamrin 1987, Appelberg & Odelström 1988), little is known of their behavioural responses to insect predators. However, Jonsson (1992) found that second stage crayfish young did not react to the presence of a predatory dragonfly. Aquatic insect predators, such as backswimmers (*Notonecta*) and larval dragonflies, are close to the size of crayfish young. Thus, it seems probable that the predator-prey interaction between these animals changes considerably during crayfish growth.

The aim of this study is to assess the relative importance of lethal and nonlethal effects of predation by backswimmers on crayfish juveniles. My general predictions include a gradual change in the amount and quality of predation risk as the crayfish young grow larger. Firstly, I predict that the probability and relative importance of mortality caused by direct predation decreases as crayfish juveniles grow larger. Secondly, at the same time, the relative proportion of predator-mediated physical injuries, such as cheliped losses, are expected to increase. This is based on the assumption that larger crayfish have a more exposed lifestyle and prefer defensive strategy against threat (Krasne & Wine 1977). The cost of injury is lower growth rate due to energy diverted to limb regeneration. Moreover, individuals with cheliped deficiency are more susceptible to predation (Stein 1976, 1977) and cannibalism (Bovbjerg 1953), leading to higher mortality. Thirdly, the importance and intensity of behavioural responses that enhance survival, but reduce growth rate, are expected to decrease with increasing crayfish size. This is derived from the fact that predation avoidance responses in animals tend to be inversely correlated with body size (Stein 1977, 1979, Sih 1987, Wahle 1992). Here, I focus on approximately two month old signal crayfish (*Pacifastacus leniusculus* Dana) reared in nursery ponds, and their interactions with adult notonectids (*Notonecta lutea* L.) coexisting in the same habitats.

2. Materials and methods

2.1. Animals in laboratory experiments

Juvenile *P. leniusculus* were collected in mid July from nursery ponds at the Porla fish hatchery, southern Finland, where they had been stocked in mid May as second stage juveniles. Crayfish young used in the experiments had two symmetrically grown chelipeds. They were physically intact and active and in the intermoult stage. As a measure of crayfish body size I used the length of the carapace, from the tip of the rostrum to the posteriomedial rim of the cephalothorax, taken to the nearest mm, using vernier calipers. Mean carapace length in the crayfish used was 13.9 mm (*SD* = 1.1, range 11.0–17.2, *n* = 130). Before and between the experiments the crayfish were kept in two aquaria (80×45×35 cm) filled with dechlorinated tap water to a depth of 18 cm, a layer of gravel on the bottom and perforated bricks offering an excess of shelters. The crayfish young were fed once a day with chironomid larvae.

Adult *N. lutea* were collected from large fish and crayfish culture ponds at the Porla hatchery. Some additional individuals were collected from rock-pools near the Tvärminne Zoological Station, on the southern coast of Finland. Backswimmers from the two localities were chosen randomly for the experiments. Before and between the experiments backswimmers were kept individually in small plastic containers (15×10×10 cm) filled with dechlorinated tap water. The containers were provided with a small stone on the bottom and a floating leaf as resting sites. Between the experiments *Notonecta* were fed with dead insects, but before every test they were starved for 24 hours.

2.2. Experimental design

To study direct predation by *Notonecta* on crayfish young I used a factorial design in ANOVA. The factors used were: predator (present/absent), shelter (present/absent) and the time of day (day/night). There were eight replicates per cell. The behavioural responses of the crayfish were analysed using a similar procedure, with one exception: here the three factors were predator, the time of day, and the time elapsed from the beginning of an experiment (2×2×4 design).

Experiments were made in July–August 1991 with ambient water temperatures ranging between 15–17°C. In accordance with the natural light regime, I used artificial illumination from 6 am to 10 pm (16 h light : 8 h dark). The experiments were run in aquaria (47×25×34 cm) that were filled with dechlorinated and aerated tap water to a depth of 15 cm. As substrate there was a thin layer of gravel which the crayfish were not able to burrow into. The first set of aquaria contained a brick (270×70×125 mm) with 48 holes (diameter 15 mm). Another set of aquaria had no bricks and thus no shelters.

First the crayfish were put in the aquaria, 10 individuals per aquarium (corresponding to 85 ind./m^2), corresponding to the highest stocking density in the rearing ponds. The crayfish were allowed to settle for one hour. Every experiment lasted for 10 hours. Daytime experiments were started at 10 am, and the night-time experiments at 10 pm, respectively, when the positions of the crayfish were observed and one backswimmer was added to each experimental aquarium. To examine whether the crayfish changed their sheltering behaviour during the trials, the animals were observed again after 30 min, 60 min and at the end of the experiments. *Notonecta* and control experiments were run simultaneously. All observations of contacts between the backswimmers and the crayfish were recorded on audiotape as a description of the behaviour. After each trial the crayfish were counted and their condition was checked. All injured individuals ($n = 33$) and a sample of normal crayfish ($n = 97$) were taken to measure their carapace length.

2.3. Field observations

The backswimmers and crayfish were observed in three small natural food ponds at the Porla hatchery. From the ponds available I chose the ones which were most similar to each other in other respects than the predators, in order to use them as replicates. However, this was not completely achieved, although the ponds were also situated close to each other. Initially the ponds were stocked as follows: pond A, 3000 crayfish on May 18th; pond B, 2000 crayfish on May 16th; and pond C, 1500 crayfish on May 16th. The area of ponds A, B and C was 35 m^2, 28 m^2 and 23 m^2, respectively. Thus, the respective stocking densities were about 85, 70 and 65 ind./m^2. In practice, crayfish densities in ponds B and C can be considered as equal, but the density in pond A is slightly higher, so that this density difference might affect the results obtained. The maximum depths of ponds A, B and C were 48, 40 and 32 cm, with a slow exchange rate of water. In each pond there were about 35 perforated bricks offering shelters for the crayfish.

The ponds were drained in September and the remaining crayfish were sampled before and during drainage. The sampling dates for different ponds are as follows, the last date is the drainage date: pond A September 17th, 23rd and 24th, pond B September 11th, pond C September 17th, 23rd and 26th. The crayfish from each sample were classified into two groups, individuals with normal chelipeds and those with cheliped regeneration. All individuals with regenerated chelipeds and a random sample of normal crayfish were taken to measure their carapace length. Individuals lacking chelipeds were excluded, because it was not known whether the loss was due to injury during sampling. For each pond the data from different sampling dates were pooled, since there were no within-group differences in crayfish carapace lengths between the samples (*t*-tests, $P > 0.1$).

The density and activity of *N. lutea* adults in different ponds were measured on five different days from 28th August to 9th September. The abundance and movements of backswimmers in each pond were observed in four one m^2 squares, one at a time. Two of the squares in each pond were located in the middle and two at the edge of the pond. The squares in each pond were at least one metre apart from each other. I measured the time that each observed *N. lutea* spent in one square during the 10 minute observation period. On each day the observations were started from a randomly chosen square in a randomly chosen pond. If the observations started, say, from the middle square in pond A, the observations were continued in a randomly chosen middle square in pond B or C. According to this procedure each square was observed once per day. The mean of the cumulative values from the samples forms an index of backswimmer density indicating predation pressure in the ponds.

3. Results

3.1. Laboratory experiments

According to ANOVA, shelter use by the crayfish was not affected by predator absence or presence, the time of day or time elapsed from the beginning of an experiment (Table 1). Similarly, no interactions between these factors were significant. Only the interaction between the time of day and predator presence tended to show some effect (*P*

Table 1. ANOVA table for examining how the presence or absence of a *N. lutea* predator, the time of day (day/night) and the sequence time elapsed from the beginning of the experiment (0/30/60/600 min) affects shelter use by signal crayfish young.

Source	*SS*	*df*	*MS*	*F*	*P*
Predator	0.834	1	0.834	0.16	0.688
Time of day	0.459	1	0.459	0.09	0.766
Sequence	7.964	3	2.655	0.52	0.677
Predator × Time	16.293	1	16.293	3.16	0.079
Predator × Sequence	17.856	3	5.952	1.16	0.331
Time × Sequence	16.470	3	5.490	1.07	0.368
Pred × Time × Sequence	3.089	3	1.030	0.20	0.895
Error	473.91	92	5.151		

Table 2. Summary of the number of signal crayfish young (mean ± *SE*) out of shelter (brick-holes) in different experimental treatments: the time of day (day/night), predator (absent/present) and sequence time from the beginning of the experiment.

	Predator	Time elapsed (min)			
		0	30	60	600
Day	Absent	2.17 ± 0.95	1.17 ± 0.31	1.83 ± 0.31	4.00 ± 0.97
	Present	3.13 ± 1.13	2.50 ± 1.20	2.88 ± 1.08	2.88 ± 0.74
Night	Absent	3.50 ± 0.99	2.67 ± 0.88	3.17 ± 1.08	3.17 ± 0.75
	Present	2.43 ± 0.57	2.71 ± 0.81	2.29 ± 0.42	1.57 ± 0.57

= 0.079). The maximum proportion of crayfish out of shelter was observed at the end of the daytime experiments without the predator. By contrast, the strongest sheltering took place at the end of the night-time experiments with *Notonecta* present (Table 2).

Although the notonectids frequently attacked *P. leniusculus* young, no crayfish were killed in any experiments. However, the tail-flip escape tactic was not used as a primary escape tactic. If defensive behaviour, i. e. chelae display against the attacking backswimmer, did not succeed, the crayfish successfully made use of cheliped autotomy to escape capture by the backswimmer.

Most of the time the backswimmers were resting on the surface. Occasionally the notonectids dived down to the bottom to search for prey. The crayfish either did not respond to the insect until a physical contact occurred, or they tried to defend themselves by chela display (Stein & Magnuson 1976), i. e. raising their chelipeds with spread chelae towards the backswimmer. Usually this resulted in a brief fight between the animals without any losses on either side. Sometimes, however, the backswimmer succeeded in sticking its rostrum into one of the cheliped joints of the crayfish. The crayfish responded by vigorously shaking its chelae in an attempt to force the backswimmer to lose contact. If this did not succeed within a few seconds, the crayfish autotomized its cheliped. The backswimmer subsequently swam to the water surface with the cheliped and sucked out its fluids.

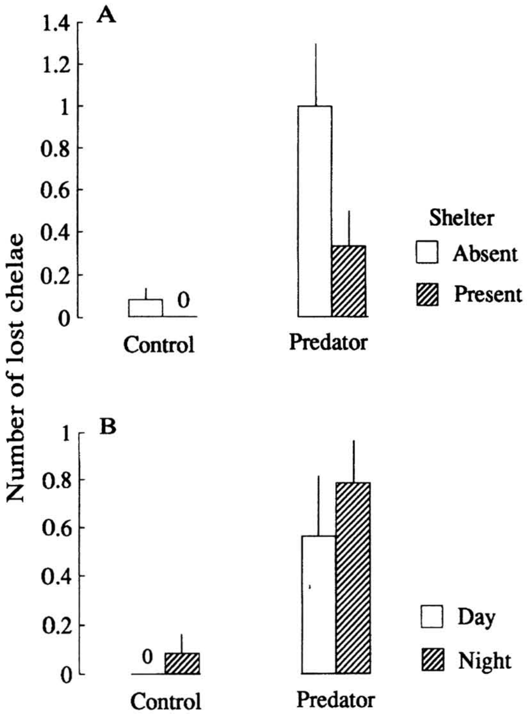

Fig. 1. Number of lost chelae per ten young-of-the-year signal crayfish (mean ± *SE*) in 10 hour laboratory experiments. — A. Results of same experiments with and without a *N. lutea* backswimmer when the aquaria were and were not provided with shelter (day- and night-time data were pooled). — B. Results from day-time and night-time experiments when a backswimmer was absent (control) and present (predator) (shelter and non-shelter data were pooled).

The crayfish lost significantly more chelipeds in experiments with the *Notonecta* present and shelter absent, but the effect of the time of day was not significant (Fig. 1, Table 3). Crayfish vulnerability to attacks by *N. lutea* was not affected by crayfish size. The carapace length of injured crayfish (mean = 13.8, $SD = 1.02$, $n = 33$) did not differ from the size of the intact individu-

Table 3. ANOVA table for examining how the presence of a *N. lutea* predator, shelter and the time of day affects cheliped losses among the signal crayfish young in laboratory experiments.

Source	*SS*	*df*	*MS*	*F*	*P*
Predator	6.400	1	6.400	13.52	0.0006
Shelter	2.268	1	2.268	4.79	0.034
Time of day	0.376	1	0.376	0.79	0.378
Predator × Shelter	1.375	1	1.375	2.90	0.095
Predator × Time	0.078	1	0.078	0.17	0.686
Shelter × Time	0.066	1	0.066	0.14	0.712
Pred × Shelter × Time	0.006	1	0.006	0.01	0.911
Error	21.780	46	0.474		

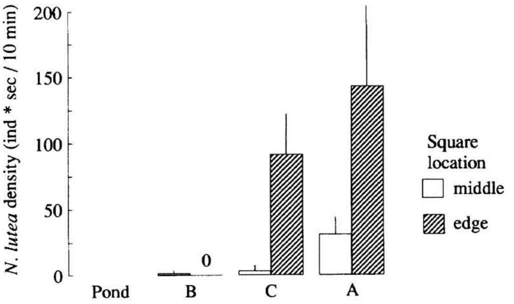

Fig. 2. Activity scaled density index of *N. lutea* (mean ± *SE*) which indicates the potential predation pressure on crayfish in the two pond zones (middle, edge) of the three different ponds A-C.

als (mean = 14.0, *SD* = 1.16, *n* = 97; *t* = 0.76, *df* = 128, *P* = 0.4).

3.2. Observations in ponds

The amount of potential predation pressure by backswimmers on the crayfish young in the stocking ponds was estimated by measuring the activity scaled density of backswimmers in the three ponds. ANOVA for ranked data shows that all three ponds and the two pond zones differed in the degree of predation pressure, which is indicated by the activity scaled density index of *N. lutea* (Table 4). *Notonecta* density was clearly highest in pond A (high crayfish density), intermediate in pond C and almost negligible in pond B (Fig. 2). The backswimmers spent much more time at the edges (Fig. 2), mainly attached to macrophytes surrounding the pond edges. I wish to point out that the *N. lutea* densities were natural, i.e. they were not manipulated.

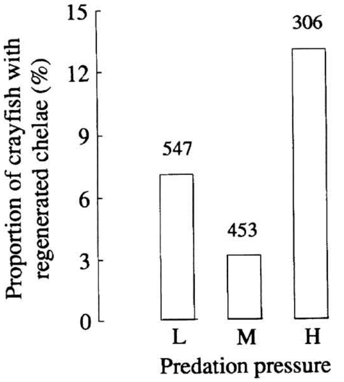

Fig. 3. Proportion of signal crayfish young with regenerated chelae of all young in the three different ponds with different *N. lutea* predation pressures (L = low, M = medium, H = high, see Fig. 2). Numerals above the columns show the sample sizes for each pond. The significances of χ^2-tests between pond types are: L:M, 0.007, M:H, <0.001; L:H, 0.006.

The proportion of crayfish individuals with one or two regenerated chelipeds was highest in the pond with the highest density index value of *Notonecta* (Fig. 3). In contrast to my prediction, there were significantly more cheliped losses in the low-pressure pond than in the pond with intermediate predation pressure. This implies that factors other than backswimmer predation may account for the observed cheliped losses in crayfish young.

Losing chelipeds retards crayfish growth (Fig. 4). In all three ponds, young with cheliped regeneration were significantly smaller than normal individuals (Mann-Whitney *U*-test; pond B with low predation *P* = 0.0000; pond C with medium predation *P* = 0.005; pond A with high predation *P* = 0.0002).

Table 4. ANOVA table for ranked data for examining how pond type and pond zone (middle/edge) affect the activity scaled density index of *N. lutea*. Ranked data was used to normalize the distributions.

Source	*SS*	*df*	*MS*	*F*	*P*
Pond	4689.4	2	2344.7	19.87	0.0000
Pond zone	1207.0	1	1207.0	10.23	0.0024
Pond × Zone	1131.3	2	565.6	4.79	0.0123
Error	6136.1	118	118.0		

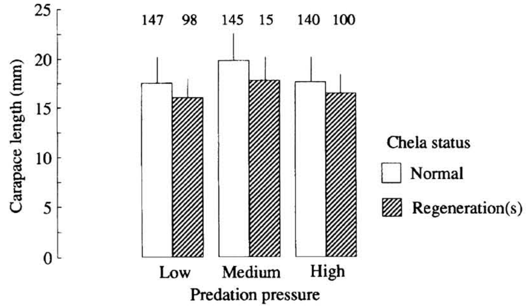

Fig. 4. Carapace length (mean ± *SE*) of normal signal crayfish young and those with regenerated chelipeds in different pond types in September. For explanations of pond types see Fig. 2. Numerals above the columns indicate the number of individuals measured.

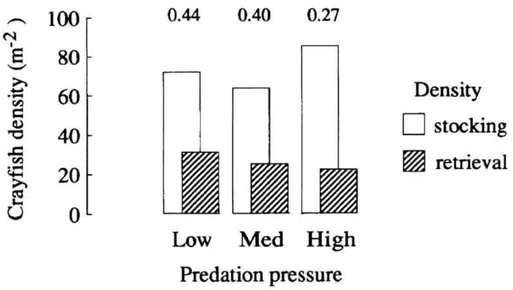

Fig. 5. Stocking and retrieval densities of young-of-the-year *P. leniusculus* in the ponds with three levels of *Notonecta* predation pressure (low, medium and high, see Fig. 2). Numerals above the columns indicate crayfish survival rate in each pond.

The survival rate of juvenile crayfish is considered here as the ratio between stocking density and retrieval density in each pond. The data suggest that the retrieval density was low when the predation pressure was high (Fig. 5). Crayfish survival rate was significantly lower (0.27) in the high *N. lutea* density pond A than in the two other ponds B and C (χ^2-test; $P = 0.0000$ in both cases), but these did not differ significantly from each other (pond C 0.40, pond B 0.44; χ^2-test; $P = 0.1494$). However, crayfish stocking density was also highest in pond A (85 ind./m^2).

4. Discussion

Antipredatory behaviour of prey includes predator avoidance before encounters and escape and defensive behaviour after an encounter (Sih 1987). As two month old signal crayfish young do not seem to avoid encounters with or escape attacks by notonectids, they use active defensive behaviour and an effective, although costly, escape behaviour to prevent capture.

In my laboratory experiments predator avoidance behaviour of the crayfish, i.e. the proportion of crayfish inside the shelter, was not influenced by the time of day. This contrasts with the suggestion that the nocturnal activity pattern of crayfish is an adaptation to avoid visual predation by fish (e.g. Westin & Gydemo 1988). However, when Wessman (1988) studied signal crayfish young in the Porla ponds, she found that from May to early July the crayfish were active throughout the day and night without any special pattern. From mid July, when the young were two months of age, onwards the crayfish were most active in the morning and evening dusk and a third peak was observed after sunset. My results show that the notonectids were as efficient predators during the night as during the daytime. In addition to constant crayfish behaviour, this was probably due to the fact that notonectids can detect their prey both visually and by mechanoreception (Ellis & Borden 1970, Wiese 1972, Goldsmith & Bernard 1974, Schwartzkopff 1974, Giller & McNeill 1981).

Furthermore, I failed to find any clear behavioural responses of *P. leniusculus* young to *Notonecta* presence in the laboratory experiments. In terms of optimal behaviour the degree of behavioural responses of prey to predators is inversely related to the risk of predation (Stein 1977, 1979, Sih 1982, 1987) and the trade-off between predation risk and food intake (Sih 1980, Bellman & Krasne 1983). Crayfish have been reported to change their behaviour in response to fish predators when the risk is high (Stein & Magnuson 1976, Stein 1977, Appelberg & Odelström 1988). Hence, the laboratory experiments in this study imply that the risk of *Notonecta* predation was too low to force the crayfish young to stay in shelters. Moreover, Jonsson (1992) reported that second stage crayfish *A. astacus* seemed to ignore the predatory larval dragonfly *Aeshna grandis*, although the crayfish suffered significant mortality due to predation from *A. grandis*. Therefore, it is possible that the crayfish juveniles do not consider insect predators as a threat at all. To answer this question further behavioural research is required.

This study indicates that signal crayfish young with a carapace length of about 14 mm are too large a prey to be killed by adult backswimmers. This is in agreement with the observations by Dye & Jones (1975) using notonectids and small juveniles of the crayfish *Orconectes virilis*. However, when attacked, after firstly defending themselves by chela display, the crayfish young did not repel the attack, but resorted to cheliped autotomy to escape the backswimmer. Previous studies have shown that small crayfish (Krasne & Wine 1975) and lobsters (Lang et al. 1977) prefer tail-flip escape behaviour at the cost of defensive behaviour, i.e. raised chelae, in response to a threat, but in larger animals the preference is reversed. In my experiments the crayfish young preferably resorted to defensive behaviour, although they were not large enough to defend themselves with complete success. However, they could switch to a very successful escape strategy, autotomy. Cheliped autotomy can be interpreted either as an adaptive mechanism, permitting the crayfish to rid itself quickly of an injured appendage, or as an escape mechanism (McVean 1982). The second explanation fits the results of my laboratory experiments.

Virtually all cheliped losses in the laboratory experiments can be interpreted as due to backswimmer predation (Fig. 1). However, several authors have reported that crayfish juveniles also lose their chelipeds in intraspecific conflicts both in the wild (Abrahamsson 1966, Skurdal et al. 1988) and in enclosures (Westman 1973, Mason 1979). In these cases cheliped loss has been linked to high crayfish densities, and a consequent shortage of food and shelter and an increase in aggressiveness. If these effects are not involved, cheliped losses due to intraspecific fights probably occur only infrequently (McVean 1982). Accordingly, autotomy caused by intraspecific fights was not an important phenomenon in my experiments. This could partly be due to the even size structure of the experimental crayfish population. Intraspecific conflicts probably more often lead to cheliped losses when size differences between individuals are larger (Abrahamsson 1966, Skurdal et al. 1988).

In the laboratory experiments the frequency of cheliped losses was lower when sheltering holes were available. When shelter was provided, the crayfish had less encounters with the notonectids and the former could probably defend themselves more successfully while inside the holes. There is little information available on the effect of shelter availability on cheliped loss, although several authors have reported that shelters increase crayfish survival. For example Jonsson (1992) found that in the presence of a larval dragonfly the mortality rate of second stage young of the crayfish *Astacus astacus* decreased when the crayfish had access to shelters, but he gave no data on nonlethal injuries. Capelli & Hamilton (1984) showed that in *Orconectes rusticus* aggressive interactions between individuals declined with the availability of shelters, but again no information on injury rates was provided.

The frequency of cheliped losses in the Porla ponds ranged from 3.2 to 13.1%. This loss rate is lower than those from pond populations of *A. astacus* in Sweden, where the frequency ranged from 11 to 32 percent (Abrahamsson 1966). He observed the highest frequences in dense, unexploited populations. Similar observations were made by Skurdal et al. (1988) in natural populations of *A. astacus* in Norway, where the loss range was 1.5–16.1%. In general, the frequency of nonlethal injuries has been used as an indicator of the intensity of predation pressure, although interpretation is not always unambiguous (Schoener 1979, Harris 1989). Furthermore, Mason (1979) found that the rate of cheliped loss was positively correlated with mortality rate in *P. leniusculus* young. The rate of injury is also likely to be positively related to prey density (Harris 1989). This is in accordance with the fact that in pond A with the highest predator and crayfish densities the proportion of crayfish with cheliped losses was higher than in the two other ponds (Fig. 3), although the lack of replicates does not allow firm conclusions to be drawn.

On the other hand, in the Porla ponds food shortage could have led to increased cannibalism and aggression in early summer due to the exceptionally cold, cloudy and rainy weather in May and June 1991 (Finnish Meteorol. Inst. 1991). This suggestion is supported by the fact that overall crayfish survival rate in the ponds was exceptionally low in 1991. Normal values with the stocking densities used in 1991 are about 50–80% (P. Ilmarinen, personal communication). The mortality rate of crayfish young has been reported as being higher in dense populations, both in the wild and in culture ponds (Abrahamsson 1966, Westman 1973, Dye & Jones 1975, Mason 1979, Pursiainen et al. 1983, Keller 1988). In the experiment by Pursiainen et al. (1983) *A. astacus* survival dropped from 68% to 32% as stocking density increased from 100 to 300 ind./m^2. Correspondingly, Keller (1988) observed that as stocking density increased from 200 to 800 ind./m^2 survival declined from 86% to 49%. These results indicate that crayfish density differences between the ponds used in my study (from 65 to 85 ind./m^2) could not account for the significant reduction in survival rate (from 44% to 27%). However, the threshold density, above which mortality is significantly higher, may vary due to many environmental factors including food availability and temperature. Still, I think that food scarcity caused by the exceptionally cold weather in May and June may have reduced the overall survival rates in the Porla ponds. Moreover, variation in the availability of alternative prey for the backswimmers may significantly affect their impact on crayfish young. Unfortunately, due to practical difficulties, no estimation of alternative prey densities was made.

I found no difference in size between the individuals injured by *Notonecta* and the intact ones in the laboratory experiments. On the contrary, Stein (1977) reported that crayfish mortality by predation from the smallmouth bass (*Micropterus dolomieui*) increased with decreasing size of the crayfish *Orconectes propinquus*. Moreover, when *O. propinquus* of similar carapace lengths were eaten by the bass, predation sequence was based on chela size. Bass ate crayfish in ascending order of chela length. Because females have smaller chelae than similar sized males, they were eaten first (Stein 1976). A similar morphometrical pattern has been observed in *Austropotamobius pallipes pallipes* when carapace length was above 25 mm (Bowler & Brown 1977), and in *A. astacus* (Abrahamsson 1966) and *P. leniusculus* (Ranta & Lindström 1992b) when carapace length was more than 40 mm. However, as the crayfish were smaller, the difference in ratio between carapace length and chela length between the two sexes was neglible. Thus, there was no reason to expect differential susceptibilities of the sexes on a morphometrical basis in this study.

The prediction that autotomy retards growth rate in crayfish juveniles with regenerated chelipeds was confirmed. This result is in accordance with those reported by Bennet (1973) for the crab *Cancer pagurus* L. and Bowler & Brown (1977) for the crayfish *A. p. pallipes*. Furthermore, Bowler & Brown (1977) showed that the retarded growth of injured individuals was due to energy allocation to cheliped regeneration at the cost of somatic growth. This mechanism, therefore, may account for the smaller size of the injured crayfish young in the Porla ponds. For a crayfish individual the consequences of slower growth and deficient chelipeds are manifold. Studies on several crayfish species have shown that large chelae and body size are an advantage in intra- and interspecific conflicts (Bovbjerg 1953, 1956, Stein 1976, Bruski & Dunham 1987, Söderbäck 1991, Ranta & Lindström 1992a, 1992b), and in reproductive behaviour (Ingle & Thomas 1974, Stein 1976) as well as in defence against predators (Stein 1976, 1977, Saiki & Tash 1979). Therefore, chela deficiency can make crayfish young more vulnerable to predators. Consequently, declined survival, chela losses and slower growth lead to lower productivity of crayfish aquaculture and stocking in natural waters.

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