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The effect of weed cover on juvenile signal crayfish (*Pacifastacus leniusculus* Dana) exposed to adult crayfish and non-predatory fish

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In the laboratory we investigated the effects of weed cover on the activity, growth and survival of juvenile signal crayfish (*Pacifastacus leniusculus* Dana) exposed to adult signal crayfish and white aspe (*Leucaspius delineatus* Heckel), a non-predatory cyprinid. Juvenile crayfish showed no preference for habitats containing weed cover as opposed to habitats with no weed. However, real weed (*Elodia* sp.) improved juvenile growth and also reduced juvenile mortality. Both adult crayfish and white aspe reduced juvenile activity and survival. Juveniles in control tanks were more active at night. Juveniles became increasingly nocturnal in response to white aspe but were diurnal in response to adult crayfish. This suggests that non-predatory fish may affect juvenile crayfish activity and distribution in a similar way as do predatory fish. The results also suggest that adult crayfish influence juvenile survival indirectly by altering juvenile activity and growth as well as directly via cannibalism.

1. Introduction

Predation can be viewed as a sequence of predator behaviour associated with increasing predation risk, beginning with an encounter and ending in the consumption or escape of prey (Endler 1991). Prey defend themselves against predation by interrupting the sequence of predator behaviour. If the behavioural sequence is interrupted at an early stage, then the risk of death to the prey and the energetic costs of the defence employed by the prey are reduced. To avoid encountering predators, prey behave so as to appear rare (Endler 1991). Prey may achieve this by changing their diel activity, shelter and habitat use and, by detecting predators at a greater distance than they can be detected by predators.

Crayfish, particularly juveniles, have numerous predators with various predation strategies; these predators include many fish, mammalian and avian species (Svärdson 1972, Dehli 1981, Hogger 1988 for review, Svensson 1993, Neveu 1992), invertebrates including Odonata nymphs, Dytiscidae, and adult notonectids (Dye & Jones 1975, Qvenild et al. 1989, Gydemo et al. 1990, Jonsson 1992, Hirvonen 1992) and also adult conspecifics (Capelli 1980).

Crayfish modify their distribution and activity in response to predatory fish; they become more nocturnal and choose shelters that provide the maximum protection from predation (Stein & Magnuson 1976, Stein 1977, Hamrin 1987, Appelberg & Odelström 1988). Nyström (pers. obs.) found that juvenile crayfish are also less active in the presence of white aspe (*Leucaspius delineatus* Heckel); these are small cyprinid fish rarely more than 120 mm in length. Conversely, juvenile crayfish fail to show avoidance behaviour in response to predatory Odonata nymphs and adult notonectids (Jonsson 1992, Hirvonen 1992).

Predators can limit prey populations directly through predation, or indirectly by influencing the habitat use, activity and growth of prey (Stein 1979, Sih 1987). Crayfish are restricted to shelter-providing substrata by predators (Stein & Magnuson 1976, Stein 1977, Collins et al. 1983). Juvenile crayfish are often found in greatest numbers in the shallow littoral margins associated with favourable substrata or weed cover (Rabeni 1985, Appelberg 1986, Nyström 1989). Weed cover reduces largemouth bass (*Micropterus salmoides* Lacépède) predation on *Orconectes causeyi* (Saiki & Tash 1979), cunner (*Tautogolabarus adspersus* Walbaum) predation on juvenile lobsters *Homarus americanus* Milne-Edwards (Johns & Mann 1987), and perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* L.) predation on *Asellus aquaticus* L. (Matilla 1992).

Crayfish avoidance behaviour has a cost in terms of reduced feeding activity and hence slower growth (Appelberg & Odelström 1988). Rapid growth is at a premium in juvenile crayfish as this quickly excludes them from the diet of many predators (Momot et al. 1978). Therefore, weedy habitats may not only benefit juvenile crayfish survival by offering shelter from predation, but may also improve juvenile growth rates if food availability increases in association with weed cover.

Momot (1993) found that adult crayfish (*O. virilis* Hagen) were a major factor limiting the recruitment of juvenile crayfish to the population; this in turn limited the overall size of the population. Rabeni (1985) found that large crayfish modify the distribution of smaller size classes, and Momot (1993) suggested that adults increase juvenile mortalities by inhibiting juvenile feeding rather than by direct predation; a reduction in feeding may lead to an increase in moult failure. In enclosure experiments, adult crayfish reduced juvenile crayfish growth, but did not increase mortality, however, juvenile growth was enhanced by cover and low conspecific densities (Maxwell, 1988 cited by Momot 1993).

Our study had two main aims. Firstly, to determine whether weed cover is beneficial to juvenile crayfish survival and growth and secondly, to investigate further the avoidance behaviour of juvenile crayfish in response to both adult crayfish and white aspe. These two aims were combined in the following two experiments.

2. Materials and methods

2.1. Experimental animals

Newly independent (Stage II) juvenile crayfish were obtained from gravid females caught in Rögle Ponds in southern Sweden (described by Abrahamsson 1966). The juveniles were reared in a hatchery at Simontorp Aquaculture A.B., Blentarp, Sweden. White aspe measuring 50 to 80 mm in total length were caught from a local crayfish pond at the Simontorp Estate. Recently moulted adult male crayfish measuring 64 to 80 mm were trapped in Rögle Pond 3 during the last week of May. Juvenile crayfish and white aspe were fed a 150 ml suspension of either liquidised egg, peas and earthworm or chironomid larvae, every second day, supplemented occasionally by a liquidised suspension of green algae (*Chlorella* spp.).

2.2. Experimental design

The following two experiments were conducted at the Simontorp Hatchery in southern Sweden. All the tanks were made of fibre-glass, had a bottom area of 0.92 m^2 (2.2 m by 0.42 m), and were filled to a depth of 0.15 m. The tanks were supplied by recirculation systems which were supplemented by an additional inflow of well water so that 10% of the water was changed each week. The water temperature ranged between 15 and 20°C, and the tanks were illuminated on a 9:15 hr., light:dark light regime. The lights did not fade in or out.

2.2.1. *Juvenile habitat use*

Juvenile crayfish were offered a choice between a plain pebble substratum (no weed cover), a pebble substratum covered with artificial (plastic) weed, and a pebble substratum with real weed cover. The juveniles were allowed to select their preferred habitat: a) in control tanks with no predators, b) in tanks containing one adult male crayfish, and c) in tanks containing three white aspe. Over a two week period, between 30 May to 13 June 1992, eight replicates of the three experimental treatments were run in twelve tanks. Each replicate lasted one week. The tanks were arranged in two stacks, 3 tanks long by 2 deep, which were all fed by the same recirculating water system.

The habitats were presented to crayfish on three 0.572 m^2 circular trays placed in each tank. Each tray contained a 20 mm deep layer of pebbles measuring 12 to 29 mm diameter (n = 25). Sixty 300 mm strands of Canadian pond weed *Elodea canadensis* from Rögle ponds were attached to the pebble substratum in one tray of each tank so that the strands floated over the tray. Sixty plastic strips, 10 mm wide and 300 mm long, were attached to a second pebble substratum in each tank in a similar way. The third pebble filled tray in each tank was left with no cover. The three habitat trays were arranged randomly with respect to each other and tank inlet and outlets. One hundred juvenile crayfish were placed in each tank. After 24 hours, either white aspe or adult male crayfish were added to the tanks except for the control treatments. After six days we counted the number of surviving crayfish that were on each habitat and on the bare tank floor. Using Two Factor ANOVA, we examined the effects of predator and habitat on the survival and distribution of juvenile crayfish. Data for these analyses were log transformed. Tukey's Test was used for posthoc comparisons between treatments.

2.2.2. *Juvenile survival, activity and growth*

This experiment consisted of nine treatments arranged in a 3 × 3 design. Juvenile crayfish were placed in indoor tanks on one of three habitats; no weed (control), plastic weed (shelter only), and real weed (shelter and food), and were exposed to either adult crayfish, white aspe or no predators. Fifty-four tanks were used. These were arranged in 6 stacks, each stack being 3 tanks long and 3 tanks deep. Levels of illumination varied between stacks (H = 11.81. df = 5. $P <$ 0.05) and with tank height (H = 45.13, df = 2, $P <$ 0.001). The mean illumination of all 54 tanks was 181 Lux (SD = 97). Separate recirculation systems each supplied 2 stacks (18 tanks); water was pumped into the top tanks in each stack and ran through the tanks below. To minimise the effect of water from one treatment flowing into a different treatment, similar predator treatments were conducted in tanks above each other (3 tanks deep).

All tanks were supplied with four building bricks, each containing 24 holes which acted as crayfish shelters. Bricks were either rested on: a) sixty 300 mm long strands of Canadian pond weed which floated around the brick (real weed cover), b) on 60 strands of black plastic 10 mm wide and 300 mm long arranged in a similar fashion to the weed (plastic weed cover), or c) on the bare tank floor (no cover). One hundred juvenile crayfish were placed in each tank. After 24 hours, four white aspe, one adult male crayfish, or no predators (control), were added to the respective tanks. After 26 days, white aspe and adult crayfish were removed from each tank and the surviving juvenile crayfish were counted. The minimum number of juveniles surviving in any one tank was 17. The weights (mg) of these crayfish and of 17 juvenile crayfish randomly chosen from each of the other 53 tanks were recorded. Individual crayfish were weighed to the nearest mg after excess moisture had been removed using absorbent paper. Experimental trials were run between the 15 June to 14 July 1992.

During two periods of the experiment, days 4 to 7 and 14 to 17, and on the penultimate and last day of the experiment, days 25 to 26, juvenile crayfish activity was monitored by counting the crayfish exposed in a 0.25 m^2 area of each tank at

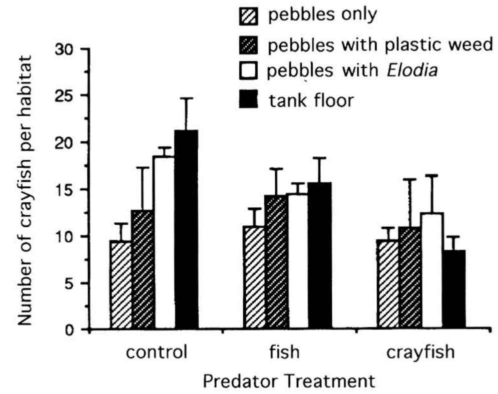

Fig. 1. Mean number (±*SE*) of juvenile crayfish using each habitat and exposed on the tank floor in Experiment 2.2.1 in control tanks, tanks with white aspe and tanks with adult crayfish.

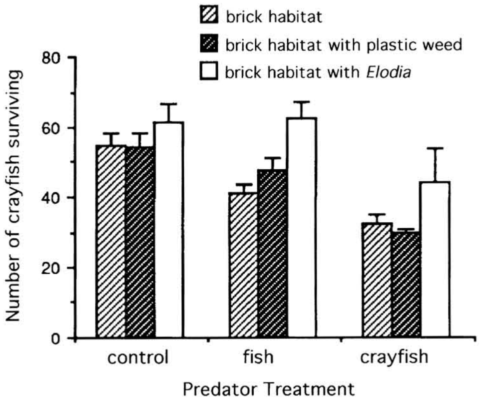

Fig. 2. The mean number (±*SE*) of juvenile crayfish surviving in control tanks, tanks with white aspe and tanks with adult crayfish (Experiment 2.2.2).

11.00 and 19.30 hours. The area chosen was free from any real or plastic weed cover. On the last day of the experiment, juvenile activity is expressed as the percentage of the surviving juveniles that were found exposed on 0.25 m^2 of the tank floor at 11.00 (light) and 19.30 hours (dark).

A Two Factor ANOVA was used to examine the effects of predator and habitat on juvenile crayfish survival and growth; the data was log transformed for these analyses. Tukey's Test was used for posthoc comparisons between treatments. A nonparametric Two Factor ANOVA and posthoc comparisons between treatments (Meddis 1984) were used to analyse the effect of predator and habitat on the percentage of the surviving crayfish that were exposed at 11.00 and also at 19.30 hours on the last day of the experiment. Within each predator treatment, Wilcoxon pairwise comparisons were used to compare numbers of crayfish exposed between 11.00 and 19.30 hours on each of the three observation periods. Habitat treatments were combined for this analysis.

3. Results

3.1. Juvenile habitat use

Not all of the surviving juvenile crayfish were found on the habitat trays; in each of the tanks some juveniles were also found on the tank floor (Fig. 1). Predators affected juvenile survival ($F_{2,84}$ = 3.58, P = 0.032) but habitat had little effect on the distribution of the surviving crayfish ($F_{3,84}$ = 2.21, P = 0.094). There was no interaction effect ($F_{6,84}$ = 1.027, P = 0.436). Using Tukey's multiple comparisons test, the only difference found was between the number of juveniles exposed on the tank floor in the control and crayfish treatments ($P < 0.1$). One Factor ANOVA tests between predator treatments (all habitats combined) indicated that adult crayfish reduced juvenile survival by comparison to control tanks with no predators ($F_{2,21}$ = 6.43, $P < 0.01$; Tukey test between adult crayfish and control tanks, $P < 0.01$). Also, proportionally more of the surviving juvenile crayfish occupied habitat trays in tanks with adult crayfish by comparison to control tanks ($F_{2,21}$ = 2.91, P = 0.077; Tukey test between adult crayfish and control tanks, $P < 0.1$). The data were log transformed for the former analysis and arcsine transformed for the latter.

3.2. Juvenile survival, activity and growth

3.2.1. Survival

Juvenile crayfish survival differed significantly between treatments and was influenced by both predators ($F_{2,45}$ = 22.26, $P < 0.001$) and by habitat ($F_{2,45}$ = 8.52, $P < 0.001$; Fig. 2). Adult crayfish reduced juvenile survival on no weed and plastic weed habitats by comparison to control treatments with no ($P < 0.05$), plastic ($P < 0.01$) and real ($P < 0.001$) weed. Also, less juveniles survived in adult crayfish tanks containing no weed and plastic weed by comparison to fish treatments containing plastic and real weed (fish/plastic v crayfish/none, $P < 0.1$; crayfish/plastic, $P < 0.025$; fish/weed v crayfish/none, $P < 0.001$; crayfish/plastic, $P < 0.001$). Further, in tanks with adult crayfish, real weed enhanced juvenile survival by comparison to plastic weed ($P < 0.1$). White aspe increased juvenile crayfish mortality in tanks with no weed cover by comparison to control and white aspe tanks containing real weed (both $P < 0.1$).

The light levels in each tank were not correlated with either the mean weight of the surviving juvenile crayfish in each tank or with juvenile crayfish survival (Spearman's Rank Correlation $P > 0.05$). The mean weight of juveniles from each tank was, however, correlated with juvenile survival (Spearman's Rank correlation; $R = 0.41$, $n = 53$, $P < 0.01$).

3.2.2. Activity

Predators significantly reduced juvenile activity at 11.00 h ($H = 35.00$, $df = 2$, $P < 0.001$) and at 19.30h ($H = 19.34$, $df = 2$, $P < 0.001$; Fig. 3); habitat had no effect. By day, white aspe reduced juvenile activity on all three habitats by comparison to controls with no weed (all $P < 0.001$) and plastic weed (control/plastic v fish/none, $P < 0.025$; fish/plastic, $P < 0.1$; fish/weed, $P < 0.1$). Juveniles were also more active in response to adult crayfish/no weed treatments by comparison to fish/none ($P < 0.025$), fish/plastic ($P < 0.025$), and fish/weed ($P < 0.01$) treatments. At night, juveniles were less active in response to adult crayfish in all three habitats by comparison to juveniles in control tanks with no weed (control/none v crayfish/none, $P < 0.1$; crayfish/plastic, $P < 0.001$; crayfish/weed, $P < 0.001$). Juveniles were also less active on real weed habitats with crayfish than with white aspe ($P < 0.1$). Throughout the experiment, juveniles in control tanks tended to be nocturnal (Fig. 4a). Juvenile crayfish exposed to white aspe strongly favoured nocturnal activity (Fig. 4b), but this preference was reversed in response to adult crayfish (Fig. 4c).

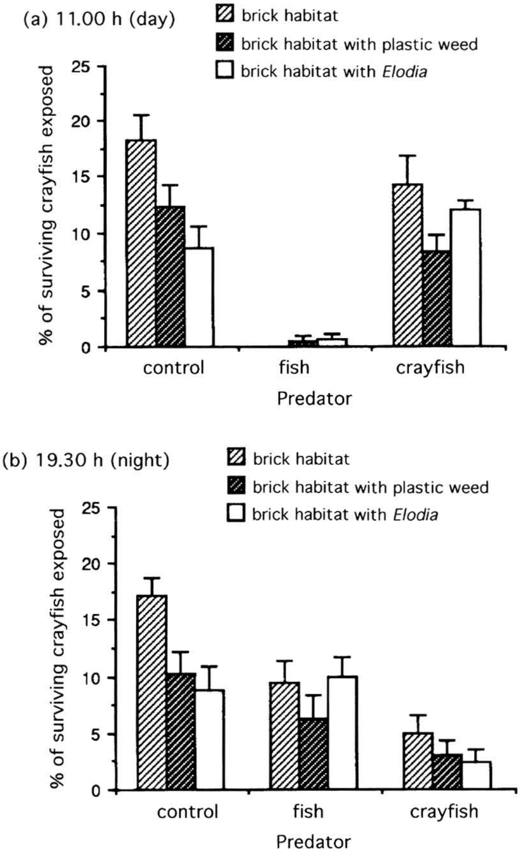

Fig. 3. Crayfish activity in response to different predators in Experiment 2.2.2, at a) 11.00 and b) 19.30 hours. Values are means (±*SE*) of the percentage of surviving crayfish which were exposed in 0.25 m^2 of each tank.

3.2.3. Growth

Juvenile weights differed between habitats ($F_{2,909} = 19.26$, $P < 0.001$) but not predator treatments ($F_{2,909} = 2.09$, $P = 0.124$), although there was an interaction effect of the two variables ($F_{4,909} = 4.354$, $P < 0.01$; Fig. 5). Within both control and fish treatments, crayfish from real weed habitats weighed more than crayfish from either the plastic weed or no weed habitats (control/weed v no weed, $P < 0.01$; plastic weed, $P < 0.001$; fish/weed v no weed and plastic weed, both $P < 0.001$). Juvenile weights did not differ between habitats when adult crayfish were present. Within the weed habitats, juveniles weighed less when adult

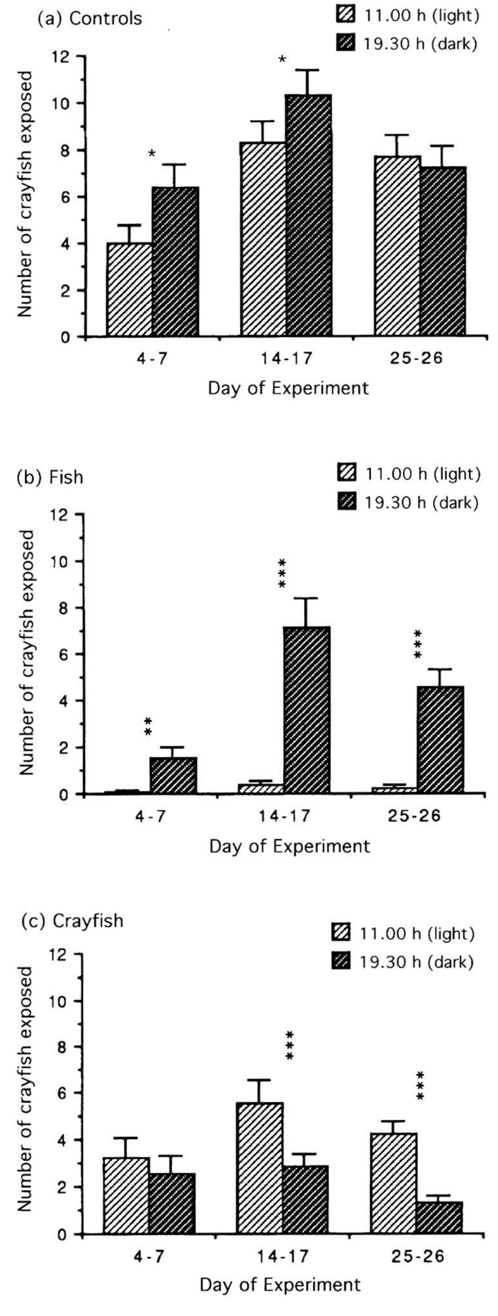

Fig. 4. Juvenile crayfish activity in response to changes in illumination. Values are means (±*SE*) of the number of crayfish exposed in 0.25 m^2 of each tank at 11.00 and 19.30, hours on three occasions during Experiment 2.2.2., in a) control tanks, b) tanks with white aspe, and c) tanks with adult crayfish. Levels of significance are for Wilcoxon comparisons, between 1100 (light) and 1930 (dark), and are: $P < 0.1^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.

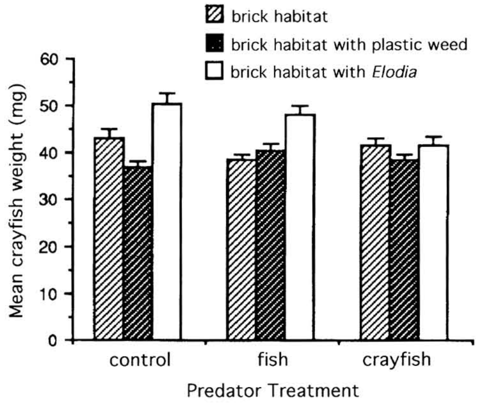

Fig. 5. Mean (±*SE*) weights (mg) of 17 juvenile crayfish taken from each of 54 tanks in Experiment 2.2.2. Mean weights are given for crayfish from control tanks, tanks with white aspe and tanks with adult crayfish.

crayfish were present than in controls with no predators ($P < 0.025$). This is the likely source of the interaction effect.

4. Discussion

Juvenile crayfish were evenly distributed between the three habitats to which they had access in Experiment 2.2.1; this was the case both in the presence and absence of predators. In laboratory experiments, Johns & Mann (1987) found that juvenile American lobsters preferred real as opposed to artificial weed, and that weed reduced fish predation on lobsters. They suggested that the preference for real weed was directed by chemical cues, but could not tell whether lobsters were reacting to the scent of the plants or of the organisms living on the plants. In our study, there was no evidence that juvenile crayfish differentiate between habitats on the basis of weed cover; nor did we find evidence that juvenile distribution was affected by differential predation on the three habitats. However, adult crayfish did reduce juvenile crayfish survival and increase the proportion of juveniles which were using shelter.

Juvenile crayfish growth is a product of food availability and of juvenile activity, which are regulated by water temperature, photoperiod, densities of adult and juvenile conspecifics, availability of shelter, and by predatory fish (Mason 1979, Appelberg & Odelström 1988, Figiel et al. 1991, Maxwell 1988 cited by Momot 1993). Real weed habitats (Experiment 2.2.2) reduced juvenile mortalities and enhanced juvenile growth. This indicates that shelter and/or food was more available in real weed habitats. As crayfish showed no preference for weed as opposed to no weed habitats, then the improved growth of juveniles in real weed habitats can only be considered a secondary benefit of sheltering within weed.

It is possible that the improved growth in association with weed in the second experiment was an artifact of the experimental set up. Such a result may be expected if an insufficient quantity of food was supplied to the juveniles, or if the weed provided a better quality or concentration of food. In treatments without predators the real weed habitats improved juvenile growth but did not improve juvenile survival by comparison to treatments with plastic or no weed. Conversely, when white aspe were present, real weed improved both juvenile growth and survival by comparison to plastic and no weed habitats. Crayfish activity did not differ between the three habitats. This suggests that weed may enhance juvenile survival by allowing juveniles to feed whilst sheltering within a protective environment. Thus juveniles may continue to grow whilst reducing the probability of being detected by predators.

The importance of predation as a process structuring the distribution and abundance of Crustacea is difficult to assess. Momot (1967) and Momot et al. (1978) suggest that fish and invertebrate predators have little effect on juvenile crayfish survival. Appelberg (1987, 1990) suggested that perch were responsible for limiting *Astacus astacus* L. populations in Swedish lakes, but it was not known whether this was a direct or indirect result of predation. In dense populations, adult male *O. virilis* mainly regulate juvenile crayfish recruitment by suppressing juvenile growth (Momot 1993); cannibalism is less important.

Our study supports the suggestion that adult crayfish affect juvenile crayfish recruitment. We have shown in the laboratory that adult crayfish suppress juvenile activity, and, over the three weeks of the experiment, there was evidence to suggest that adult crayfish also reduced juvenile growth. Juveniles in the tanks with real weed and no predators were heavier than juveniles in tanks with real weed and adult crayfish. Also, the average juvenile weight did not differ between the three habitats when adult crayfish were present, whereas weed enhanced juvenile growth in tanks with white aspe and no predators.

Both adult crayfish and, to a lesser extent, white aspe reduced juvenile crayfish survival, although real weed habitats generally reduced juvenile mortality. Adult crayfish probably cannibalised juveniles. Momot (1993) found no evidence for cannibalism in analyses of adult crayfish stomachs from two Canadian lakes, and also observed that adult crayfish were unable to catch juveniles. Smith & Herrnkind (1992) and Wahle & Steneck (1992) report that decapod predators are inefficient at catching and handling lobster prey. Adult *O. virilis* were observed to prey on immobile, moulting juveniles in laboratory conditions (Momot 1993) and cannibalism has been reported in field populations of *O. propinquus*, where large numbers of inter-moult young were consumed (Capelli 1980). The experimental designs in this study are likely to have increased encounter rates between adult and juvenile crayfish and between juveniles themselves and would therefore tend to enhance cannibalism.

The improved survival of juveniles in tanks with real weed suggests that real weed protected juveniles from predation by adult crayfish, however, juvenile survival also improved in association with weed by comparison to no weed habitats in tanks with white aspe. Momot (1993) found that juvenile growth and mortality were inversely related in unexploited crayfish populations and suggested that adult crayfish suppress juvenile growth as a result of suppressing activity. Appelberg & Odelström (1988) found that perch reduced both the activity and growth of juvenile *A. astacus* in a similar way. In our study, it is likely that juvenile avoidance behaviour increased intraspecific competition for food and shelter, and that juvenile mortality increased as a result of an increase in aggressive conspecific interactions. Cappelli & Hamilton (1984) found that the availability of shelter and food influenced intraspecific aggression in *O. rusticus*. The type of food also influenced levels of intraspecific aggression but limited shelter had a greater effect. Limited shelter has been shown to increase juvenile crayfish activity and reduce juvenile survival whereas different diets had no effect (Mason 1979, Westin & Gydemo 1988). Therefore, in our study, intraspecific interactions between juveniles may have been reduced in habitats with real weed which provided more shelter and/or food than habitats with plastic or no weed cover.

Although weed improved juvenile survival in Experiment 2.2.2, predation had no effect on juvenile distribution in Experiment 2.2.1. There are several possible reasons for this difference. Firstly, Experiment 2.2.2 ran for three weeks as opposed to Experiment 2.2.1 which only ran for one week. Any effect of predation may have failed to materialise over the shorter time period. Secondly, juveniles were free to move between habitats in Experiment 2.2.1 which may have masked any effects of differential predation. Lastly, the pebble substrate used in Experiment 2.2.1 may have provided better protection from predation than the bricks used in Experiment 2.2.2. thus reducing the importance of weed cover.

Stein (1979) categorised two types of anti-predator avoidance behaviour, 'fixed' and 'reactive'. Fixed behaviours do not require the presence of predators to elicit them, and are assumed to be a result of long-term predation pressure acting over evolutionary time. Reactive behaviours only occur in response to the presence of a predator. Previous studies have reported that juvenile crayfish are principally crepuscular/nocturnal but may increase nocturnal activity and decrease diurnal activity in response to diurnal fish predators (Hamrin 1987, Appelberg & Odelström 1988). In our study, the preference for nocturnal activity shown by crayfish in control tanks can be described as fixed anti-predator behaviour. The stronger preference for nocturnal activity in the presence of fish and the increase in diurnal activity in response to adult crayfish demonstrate that the avoidance behaviour of newly hatched crayfish, which had no previous experience of predation, was highly reactive. Most prey live in environments containing many predators of which one is particularly dangerous. Lima (1992) suggests that the presence of less dangerous predators may significantly affect anti-predator behaviour. Based on our findings, white aspe could conceivably cause a similar effect on juvenile crayfish activity and hence, growth and survival as do predatory fish or adult crayfish.

Why did crayfish avoid white aspe? Newly independent crayfish are small and extremely vulnerable to predation, but rapid growth is an important means of lowering predation risk from fish and invertebrate predators (Stein 1977, Momot et al. 1978, Momot 1984). Similarly, Wahle & Steneck (1992) found that attacks by fish on tethered juvenile lobsters fell drastically with small increases in body size. Attacks fell from 60/hour for size classes between 4 to 5 mm carapace length, to less than 10/hour for size classes over 8 mm. Therefore, juvenile crayfish may be expected to spend the maximum possible time feeding when the threat of predation is low.

White aspe are zooplanktivores (Benndorf et al. 1984) but can also feed on smaller insect larvae (Boikova 1986). To our knowledge there are no reports of white aspe preying on crayfish. In the present study white aspe were never observed to attack juveniles and we consider that they were incapable of feeding on juvenile crayfish. Animals can assess and behaviourally influence their risk of predation (Lima & Dill 1990 for review). Adult crayfish (*Orconectes* spp.) quickly distinguish between restrained and free predators (Butler & Stein 1985). Also *O. propinquus* from lakes in Ontario are more nocturnal and more shelter bound if the lakes contain abundant predators, but this behaviour persists for at least three weeks in aquaria without predators (Collins et al. 1983).

Fish movement stimulates crayfish defensive behaviour (Blake & Hart 1993) but crayfish may not be able to distinguish between the visual characteristics of individual species (Blake 1993). Non-predatory fish such as white aspe may produce similar visual stimuli as fish slightly larger than white aspe which do prey on juvenile crayfish. Svensson (1993), found that roach between 90 to 170 mm long and perch 120 to 150 mm long both reduce juvenile *A. astacus* survival by 10 to 47% respectively. The survival in non-predator controls was between 88 and 92%. The effect of white aspe may he exaggerated as they are likely to have been in artificially close proximity to juvenile crayfish in experimental tanks, however, both tend to be found in the shallow littoral margins of lakes.

Crayfish defensive behaviour is also stimulated by chemical stimuli from predatory fish or disturbed conspecifics (Hazlett 1985, 1990, Appelberg et al. 1993, Blake & Hart 1993). It is possible that to some extent the behaviours we observed were a result of juveniles responding to the recirculated scent of fish, adult crayfish or damaged juveniles, but the distinct differences in the behaviour of the juveniles in tanks with white aspe and crayfish suggests a real difference in the response of juvenile crayfish. Appelberg et al. (1993) found that juvenile *A. astacus* can distinguish between predators and non-predators and between hungry and satiated predators based on chemical stimuli alone.

Signal crayfish were introduced into Western Europe in the 1960's (Lowery & Holdich 1988) and so have relatively little evolutionary experience of European predators, and may not have evolved the ability to distinguish between predatory and non-predatory species in Europe. This may explain the defensive response of juvenile *P. leniusculus* toward white aspe in our experiments. However, Söderbäck (1992) suggests that the antipredator responses of juvenile signal crayfish are generalised to any predatory fish. He found no difference in the antipredator responses of *A. astacus* and *P. leniusculus* juveniles to perch despite *A. astacus* and perch having a much longer common evolutionary history. We agree with Söderbäck (1992) of the need for further studies on the mechanisms of predator detection by native and introduced crayfish species. In addition our results indicate the need for further research into the reactivity of antipredator responses to different predators and non-predators.

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