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ANTI-PREDATOR BEHAVIOURS OF A FRESHWATER CRAYFISH (*PARANEPHROPS ZEALANDICUS*) TO A NATIVE AND AN INTRODUCED PREDATOR

Summary: The anti-predator behaviours of a New Zealand freshwater crayfish (*Paranephrops zealandicus*) to the native long-finned eel (*Anguilla dieffenbachii*) and the introduced brown trout (*Salmo trutta*) were investigated. Crayfish modified their behaviour in the presence of both trout and eels. However, a significantly greater number of defensive chela displays and swimming responses were made to eels than trout. Crayfish were able to use chemical cues from skin mucus to detect eels but not trout. *Paranephrops zealandicus* is able to make some appropriate defensive behavioural responses to the introduced brown trout as well as to its native predator, the long-finned eel. However, crayfish may be at greater risk from the introduced predator because of their apparent inability to detect trout using non-contact chemical cues. This may be a reflection of the different co-evolutionary histories crayfish have had with trout and eels.

Keywords: anti-predator behaviour; freshwater crayfish; native and introduced predators; chemical cues; co-evolutionary history.

Introduction

There is mounting evidence that New Zealand's freshwater communities have changed after the introduction in the second half of the nineteenth century of aggressive predators such as brown trout (*Salmo trutta* L.) (Crowl, Townsend and McIntosh, 1992). Among the species affected are crayfish (*Paranephrops* spp.), and early this century Archey (1915) suggested that as a result of trout predation "the restriction of crayfish to such places as cannot be inhabited by these fish [brown trout] is only a matter of time". More recently McDowall (1968) commented that it was difficult to find freshwater crayfish in areas with adult trout populations and expressed doubts about the continuing coexistence of the species in New Zealand. Several studies have indicated that crayfish can be an important component of trout diet (Cairns, 1942; Allen, 1951). Trout are already held responsible for the local extinction of one of New Zealand's two crayfish species (*P. planifrons* White) from Lake Waingata in the North Island (Fish, 1966). The second indigenous species, *P. zealandicus* White, is also thought to have declined in both numbers and distribution in the South Island due to predation by brown trout.

Reasons for the dramatic impact of brown trout on native species may include the fact that the indigenous fauna lack appropriate defences developed during a common co-evolutionary history (McDowall, 1968; Crowl *et al.*, 1992). The long-finned eel (*Anguilla dieffenbachii* Gray) and the short-finned eel (*A. australis schmidtii* Phillips) are New Zealand's only large native fish predators, and both feed extensively on crayfish (Cairns, 1942; Burnet, 1952). Because crayfish have a long co-evolutionary history with eels in New Zealand (McDowall, 1964), they should have evolved defences to these predators, such as detection and avoidance behaviours or effective escape responses.

For prey to actively avoid predators they must be able to detect them either by direct tactile or visual cues, by non-contact chemical cues, or by mechanical (vibrational) stimuli. Other genera of crayfish are known to use all three cues to avoid their predators (Wine and Krasne, 1982; Hazlett 1985; Blake and Hart, 1993).

There are advantages in being able to detect a predator using non-contact cues, since prey may then avoid the predator effectively before a direct interaction can occur. The ability to use trout skin mucus as a cue has previously been demonstrated by some freshwater invertebrates (Williams, 1986) so similar non-contact cues from both trout and eels may be available to crayfish.

Once a predator has been detected, prey can behave in various ways to decrease their vulnerability. In response to predators some crayfish have been found to reduce activity (Hamrin, 1987;

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Blake and Hart, 1993) and to show increased use of refuges (Stein and Magnuson, 1976; Stein, 1977), at least in the case of American and European species. The distinctive chela display of crayfish, used in intraspecific encounters (Bovbjerg, 1953), may also be a deterrent against fish predators. Finally, crayfish can employ one of several escape responses, including walking away and swimming using the characteristic "tail-flip" (Wine and Krasne, 1982).

Set against the benefit of reducing predation risk, avoidance behaviours and escape responses can have associated costs. Time spent avoiding predators is time lost from other essential activities such as feeding and breeding. Natural selection should therefore favour prey which make more precise anti-predator responses, the "precision" of a response being "the degree to which the response is commensurate with predation risk" (Sih, 1986). Ideally, prey should assess the risk from different predators and modify their responses accordingly. A prey organism unfamiliar with a particular predator species (in an evolutionary sense) may make inappropriate responses, including unnecessarily avoiding a safe predator or ignoring one that is dangerous.

In the present study the anti-predator responses of a crayfish to two predator species, one native and one introduced, were evaluated. It was predicted that *P. zealandicus* should modify its behaviour in the presence of long-finned eels and trout since both present a predatory threat. However, crayfish may differ in their ability to detect eels and trout using chemical cues, and may make more inappropriate responses to trout because of their relatively short co-evolutionary history.

Methods

Experimental animals

Juvenile crayfish, ranging in size from 16.0 - 22.0 mm in carapace length, were caught by hand net from Orokonui Stream, 20 km north of Dunedin (NZMS 260 I44 224911). Both brown trout and long-finned eels are present in this stream. All crayfish were held in the laboratory under natural light conditions for a least 72 hr and fed *ad libitum* on lettuce before being used in a trial.

Predators were obtained by electric fishing. The trout (total length 205-228 mm) were collected from Evansdale Stream (NZMS 260 I44 205967) and eels (total length 552-593 mm) from the Water of Leith (NZMS 260 I44 173794). Two trout-eel pairs were used in alternate trials during Experiment 1. One of these pairs was retained to supply skin mucus for Experiment 2. Predator pairs were matched on gape size, rather than body length, as it is this measurement which affects the size of prey that can be taken.

Experiment 1: Crayfish responses to the chemical and physical presence of predators

Design and protocol

Two plastic pools (1.4 m x 1.3 m) were lined with white polythene to facilitate observation of animals under red light and filled with tapwater to a depth of 25 cm. Each pool was divided into two sections (A and B) by a water-permeable but opaque net barrier (double-thickness, mesh size = 1 mm^2). Fitted shade cloth lids, through which behaviours could still be observed, were used to cover the pools during experiments. In Section A of each pool, four perspex shelters (12 cm x 13 cm x 2 cm), modelled after those used by McNeely, Futrell and Sih (1990), provided cover for the crayfish in a regular arrangement. Two adjacent sides of each shelter were closed and the two open sides faced towards the centre of the tank. Windows of the experimental room were blacked out and experiments were carried out under diffuse red light provided by fluorescent tubes wrapped in red cellophane and suspended 2.35 m above each tank. Previous studies have shown that the behaviour of brown trout is unaffected by such light (Chaston, 1968; McIntosh, Townsend and Crowl, 1992) and no effects of the light on eel behaviour were observed in this experiment.

Four crayfish were individually marked with typewriter correction fluid and placed in Section A of each pool to acclimatise for approximately 10 hr before a trial was to begin. Eight salmon pellets were provided as food for the crayfish in each pool.

Observations began at dusk using the following regime:

1. Six crayfish behaviours were recorded (see Table 1) every thirty seconds for 15 minutes using an instantaneous scan sampling method (Martin and Bateson, 1986). These observations provided baseline, control data.
2. Following the baseline measurements, one predator (either an eel or a trout) was introduced to Section B, with the net barrier up. Immediately, a second 15 minute period of observations of crayfish behaviours commenced, as in step 1. In this period, crayfish were exposed only to chemical stimuli from the predator. The mesh net prevented mechanical stimuli such as movements of water from reaching the crayfish.
3. The net barrier was removed and the predator was allowed to swim through into Section A of the pool. Following this the barrier was

Table 1: *Description of crayfish behaviours.*

Behaviour	Description
Under cover	Crayfish is positioned with at least half of its body under the perspex shelter
Stationary	Crayfish is flat on the substrate with no observable movement of any body parts
Walking	Crayfish walks along the substrate with chelae not raised but held forward and parallel to the central axis of the body
Upright	Crayfish raises itself up on its hind walking legs extending its chelae forwards and upwards
Swimming	Crayfish propels itself backwards up off the substrate and through the water column by flicking motions of the tail up under the abdomen
Feeding	Crayfish transfers food to its mouth using its cheliped or maxilliped; crayfish is otherwise stationary

replaced, confining the predator and crayfish to Section A. A further 15 minute period of scan sampling began, again recording crayfish behaviours. In this period, crayfish were exposed to chemical, visual, and physical stimuli from the predator. All-occurrences sampling (Martin and Bateson, 1986) was also used to record every instance of a direct predator-crayfish interaction during this 15 minute period.

4. Finally, predator activity (distance travelled) was sampled for a 5 minute period by tracing the movements of the predator onto a small-scale plan of the pool.

This procedure was completed first with four crayfish in one pool with the trout and then with four different crayfish in the second pool with the eel, constituting one trial. This consistent ordering of the two predator species was chosen because of the preferred feeding times of dusk for trout (Allen, 1951) and later in the evening for eels (Burnet, 1952). Pools were drained and thoroughly scrubbed between trials. Crayfish, predators and treatments were randomly assigned between the two pools over a total of ten trials, with replication through time. Individual crayfish were used only once, with either trout or eels, before being returned to the wild.

Analysis of behaviours

The number of sampling periods during which an animal was observed performing a particular behaviour was divided by the total number of sampling periods (n = 30) to estimate the percentage of time each crayfish was engaged in each behaviour under the different treatments.

Because each crayfish was individually identifiable it was possible to calculate changes in behaviour brought about by the introduction of each new stimulus type. Three new categories, representing the differences between each of the treatment conditions (chemical cues only present, CC; all cues present, AC) and the control (no predator present, NP), as well as the difference between the two treatment conditions (CC and AC), were created. These three categories, henceforth termed “cue types”, are denoted as:

(a) CC-NP: the percentage time performing a behaviour under the chemical cues condition, minus the percentage time spent performing that behaviour in the no predator condition;
(b) AC-NP: the percentage time performing a behaviour under the all cues condition, minus the percentage time spent performing that behaviour in the no predator condition;
(c) AC-CC: the percentage time performing a behaviour under the all cues condition, minus the percentage time spent performing that behaviour in the chemical cues only condition.

All variables were examined for homogeneity of variance and in no case was transformation of the data necessary.

A separate analysis was then performed for the percentage of time spent engaged in each behaviour with each of these three different cue types, using a nested balanced ANOVA to test for a main effect of predator type (trout or eel). Individual predators (trout 1 and 2, eel 1 and 2) were nested within predator type, and crayfish group (values from the four crayfish together in the pool during a particular trial) was nested within each of these. By performing such an analysis it was possible to separate out the variation in the response within each crayfish group from the variation between individual predators, and the latter was used to assess the significance of the variation between predator types (trout and eels). In all tests significance was taken at the 5% level.

To test for differences between the number of direct predator-crayfish interactions (i.e., contacts) for each predator and the movement of each predator (i.e., distance travelled) we again employed a nested ANOVA to look for differences both between the two individuals of each predator species and between the two different predator types.

Experiment 2: Crayfish responses to "contact" and "non-contact" chemical stimuli

Design and protocol

Experiments were conducted in the laboratory using a series of clear perspex tanks 310 mm long x 390 mm wide x 300 mm deep. Each tank was filled with tap water at room temperature (±18°C) to a depth of 150 mm. A single crayfish was introduced to each tank an hour before observations began. All trials were carried out during daylight.

Presentation of stimuli involved use of a wooden probe shaped at one end to resemble a fish's head and varnished so that mucus applied could not soak into the wood. Mucus preparations were made by scraping 0.5 cm^3 of skin mucus off a predator into a glass petri dish where it was mixed with 1 cm^3 of distilled water. New mucus preparations were made for each series of presentations, with the maximum age of any preparation being approximately twenty minutes. The experimenter did not operate the probe "blind" (i.e., without knowing what, if any, mucus had been applied) but made every effort to ensure that presentations were standardised across treatments.

Each of 24 crayfish was exposed to four series of presentations thirty minutes apart. A series consisted of three presentations of the probe to the antennules of the crayfish under three treatments: no mucus, trout mucus and eel mucus. The antennules, the shorter antennae, are the site of reception of chemical stimuli for several other genera of freshwater crayfish (Hazlett, 1990; Oh and Dunham, 1991) and were assumed to be sites of chemoreceptors in *P. zealandicus*. Presentation order to each crayfish was randomised, with the time between each presentation in a series being approximately five minutes.

Two sets of trials employing different stimuli were conducted as follows:

1. Contact with mucus
   The probe, after being dipped in the appropriate mucus preparation, was gently brought into contact with the antennules and held there for two seconds. Behaviour of the crayfish at the time of presentation was recorded. The probe was thoroughly wiped to remove traces of mucus between each individual presentation.
2. Close approach with mucus
   The same method was used as above except that the probe was not brought into contact with the crayfish but held 1 cm from the head for two seconds.

Analysis of behaviours

Four different behaviours were recorded: stationary, upright, swim, and walk. Descriptions of these behaviours were as for Experiment 1.

Any time effect over the four presentation series within the two treatments ("contact with mucus" and "close approach with mucus") was assessed using a $\geq^2$ test. This analysis considered the number of crayfish performing each behaviour under the three conditions (no mucus, trout mucus and eel mucus) across the four series. No significant series effect was found in either the contact treatment (Tablewide $\geq^2 = 30.50$, d.f. = 33, $P > 0.05$) or the close approach treatment (Tablewide $\geq^2 = 16.35$, d.f. = 33, $P > 0.05$); i.e., crayfish behaviours did not change significantly with time within a series. Therefore, the responses of crayfish to each mucus condition within all four series were added in both cases.

The behaviours were then categorised further into "static" (stationary only) and "non-static" groups (upright, swim and walk responses) for final analysis. Contingency tables of the numbers of crayfish making static and non-static responses under each different stimulus condition were tested for significance using 2*3 G-tests with Williams' correction (to appropriately deal with the small sample sizes - Sokal and Rohlf, 1981).

Results

Experiment 1: Crayfish responses to the chemical and physical presence of predators

The activity of the predators across the different trials was assessed by comparing both the number of direct contacts each predator made with crayfish and the total distance travelled by each predator in a five minute period. No significant difference was found in either measure of activity between individual predators nor between predator species ($P > 0.25$ in all cases). We concluded that the different predators all behaved in a similar manner during the experiment, and so any differences in crayfish behaviour could not be attributed to predator activity differences.

Crayfish spent more time under cover as an increasing number of predatory cues became available, and in each case a greater percentage of time was spent under cover in response to eels than to trout (Fig. 1a). This difference in response between the two predator types was significant in the case of the change in behaviour from the control period to the

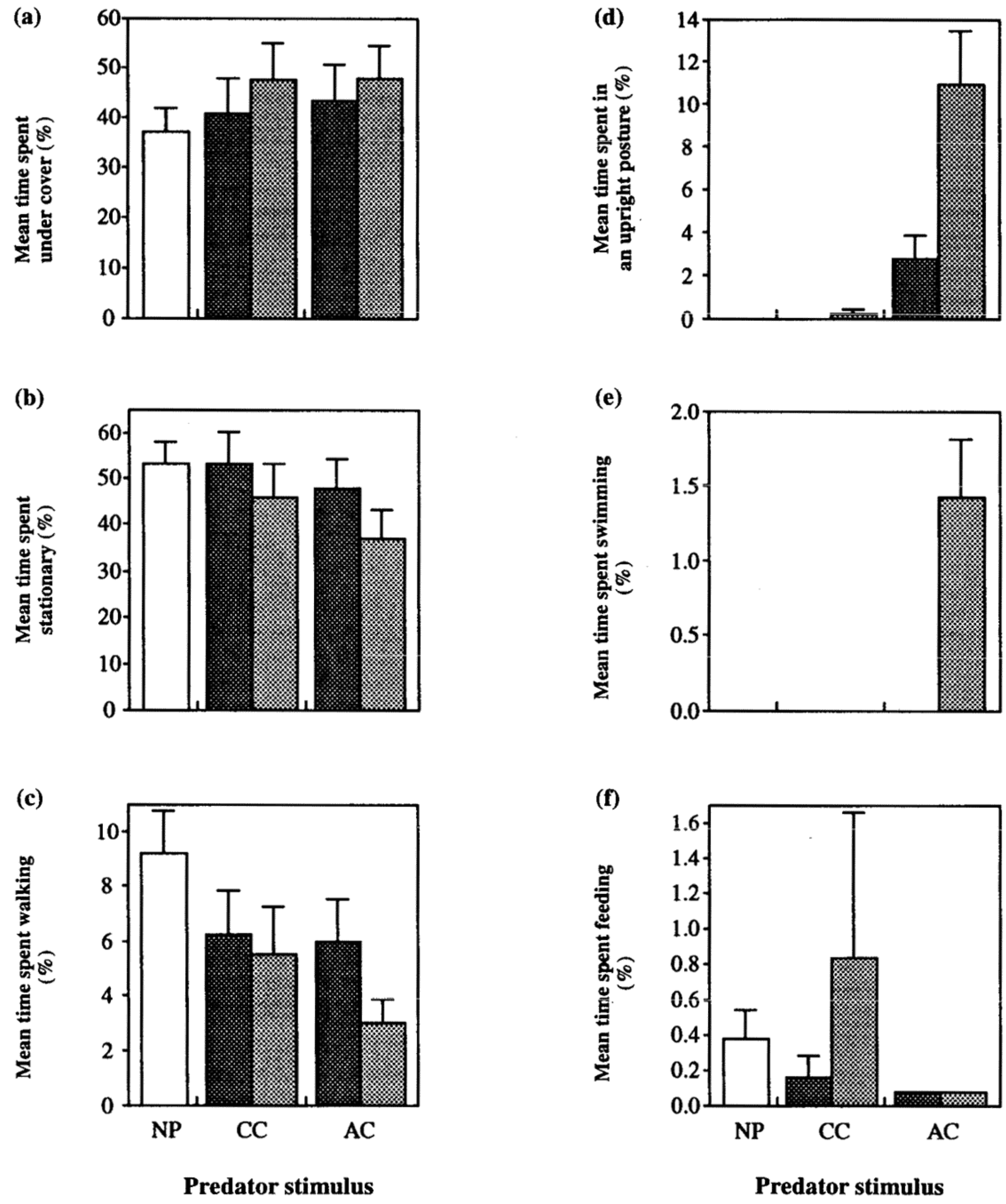

Figure 1: *The percentage of time crayfish spent performing each of six behaviours during the three periods in which different predator stimuli were available: no predator present (NP), chemical cues only (CC), all predatory cues (AC). Trout (*■*), eels (*□*). Error bars indicate one standard error for the mean percentage time across ten trials.*

Table 2: *Results of a series of nested ANOVAs used to test for a main effect of predator type (trout or eel) on the change in behavioural response by crayfish to three cue type situations. Behaviours as described in Table 1; for cue types see text. Where* P *< 0.10 the probability value is presented; NS denotes* P *≥ 0.10. • denotes that the denominator of the F-test = 0.*

		Behaviours					
	Cue type	Cover	Stationary	Walk	Upright	Swim	Feed
Between predator types (d.f. = 1)	CC-NP	0.026	NS	NS	0.099	•	NS
	AC-NP	0.098	0.086	0.000	0.005	0.030	0.050
	AC-CC	NS	NS	NS	0.005	0.030	NS
Between individual predators (d.f. = 2)	CC-NP	NS	NS	NS	NS	•	NS
	AC-NP	NS	NS	NS	NS	NS	NS
	AC-CC	NS	NS	NS	NS	NS	NS
Between crayfish groups (d.f. = 16)	CC-NP	0.015	NS	NS	NS	•	NS
	AC-NP	0.028	NS	NS	NS	NS	NS
	AC-CC	NS	0.037	NS	NS	NS	NS

time when chemical cues only were available (Table 2). A similar but non-significant difference in response was seen in the comparison of time spent under cover in the control period and when all predatory cues were available. The difference in the increase in use of cover between the periods when chemical cues only were available to the period when all cues were available was reversed, with a greater increase being shown in response to trout than to eels, although this was not significant (Fig. 2a).

Crayfish showed a decrease in stationary behaviour in response to cues from both predators (Fig. 1b). A greater decrease in stationary behaviour was shown to eels than to trout, in each cue type combination (Fig. 2b), although these differences were not significant (Table 2). Crayfish also showed a decrease in time spent walking when predatory cues were present (Fig. 1c). Again this decrease was larger in response to eels than trout under each cue type (Fig. 2c), although it was significant only when comparing the change in response between the period when all predatory cues were available to the crayfish and the control period (Table 2).

Clear differences were found in the frequency of upright responses between the different treatments (Fig. 1d). The percentage time spent performing upright postures was significantly different between predator types when all predatory cues were available to the crayfish; fewer upright behaviours were seen in the presence of trout than eels (Fig. 2d).

Crayfish were seen swimming in seven out of ten trials in which an eel was present, but never in the presence of trout (zero out of ten trials). All swimming responses occurred following direct contact by an eel (Fig. 1e).

Feeding by crayfish occurred at a low rate throughout the trials, and never accounted for more than a mean of 2% of the time budget. A slight decrease in feeding activity usually occurred when predatory cues increased. However, there was an increase in feeding during the period where eel chemical cues were available (Fig. 1f). Again in every case the greater change in response was to eels than to trout (Fig. 2f) and the difference in response to the two predators was almost significant when comparing feeding behaviour in the physical presence of predators to feeding during the control period ($P = 0.050$).

In only three instances was there a significant effect of crayfish group and for all behaviours and under all different cue types the response of crayfish to the two trout or the two eels was not significantly different (Table 2). It can therefore be concluded that the variability of crayfish response was greater between the two species of predator than it was to individuals of the same predator species.

Experiment 2: Crayfish responses to “contact” and “non-contact” chemical stimuli

A comparison was made between the frequency of behaviour under each stimulus type after combining the upright, swim and walk responses together into a “non-static” response category (Fig. 3). No significant difference was found between the number of non-static responses made to the three mucus treatments under the contact stimulus condition ($G = 5.48$; $P > 0.05$). However, significantly more non-static responses were given by crayfish to a close approach with eel mucus than with no mucus or trout mucus ($G = 14.1$; $P < 0.001$).

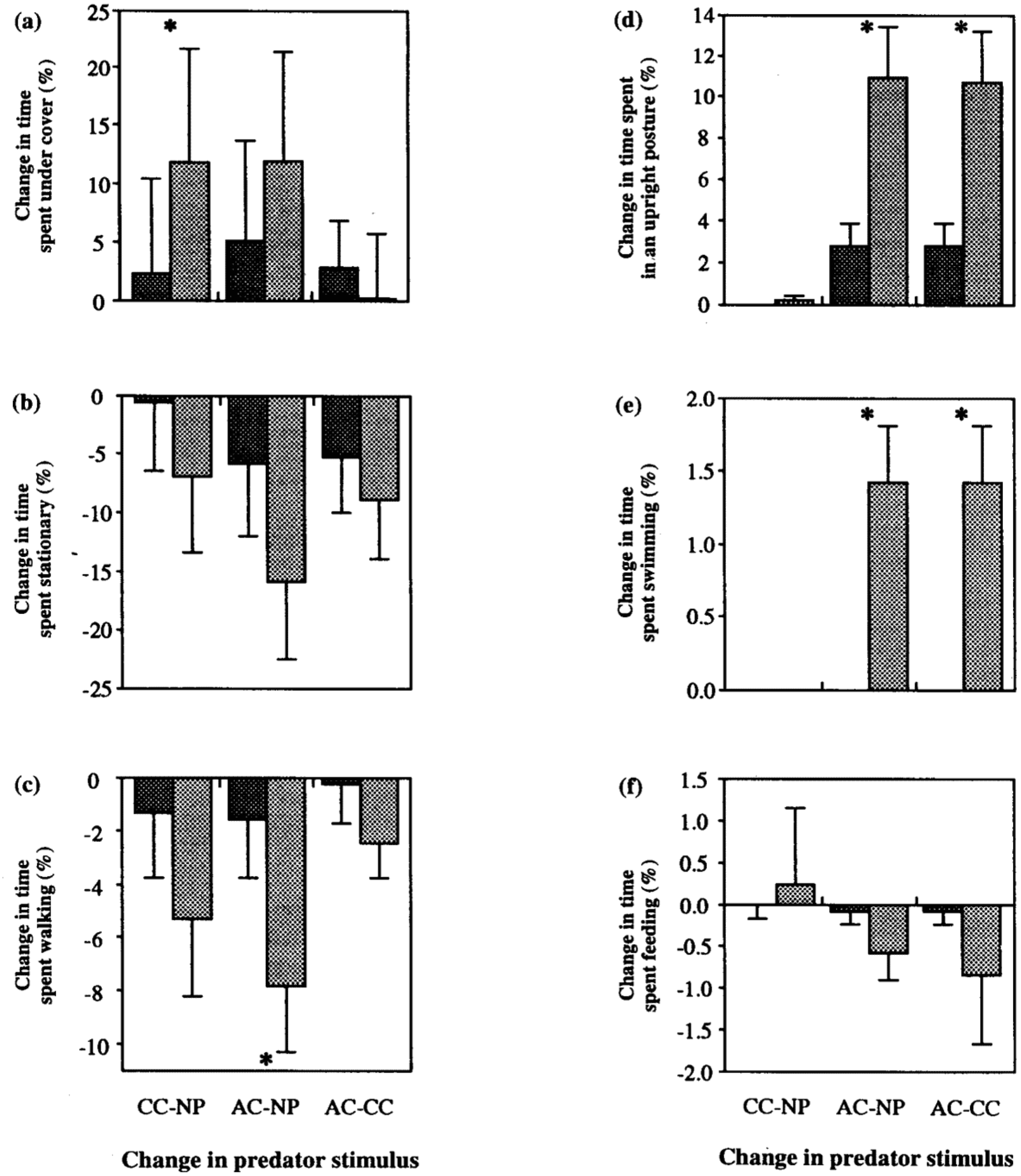

Figure 2: *The change in percentage time crayfish spent performing each of six behaviours between: when chemical cues were available and the control period (CC-NP); when all predatory cues were available and the control period (AC-NP); and when all cues were available and only chemical cues were available (AC-CC). The values are the mean change in response to trout (* ■ *) and to eels (* □ *) across the ten trials. Error bars indicate one standard error and asterisks denote significance at the 5% level.*

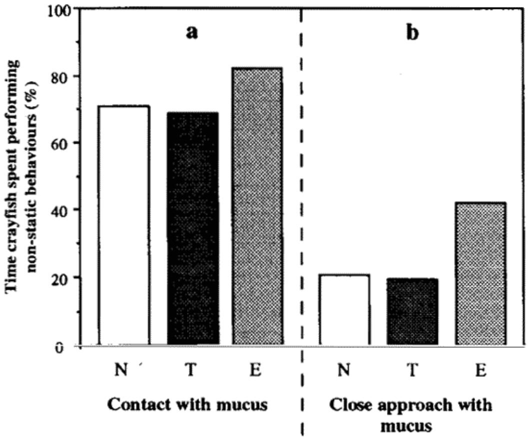

Figure 3: *The percentage of crayfish which performed "non-static" behaviours in response to (a) physical contact and (b) close approach only, under three different mucus conditions: no mucus (N), trout mucus (T), eel mucus (E).*

Discussion

Predator detection using chemical cues by crayfish

The first experiment showed crayfish modified their behaviour by using more cover and reducing their stationary and walking behaviours when only chemical cues from the two predators were presented. Whereas both eels and trout seemed to be perceived as presenting some risk there were few significant differences in responses to different predatory chemical cues. It is possible that the design of the first experiment may not have been ideal for chemical cue detection. The volume of water in each pool was large, and concentrations of predator chemicals may not have exceeded some lower detection threshold (Williams and Moore, 1985) necessary to stimulate a full reaction from the crayfish. As the experiment was carried out in standing water, dispersal of chemicals may also have been too slow to reach the crayfish in the fifteen minute experimental period.

Experiment 2 was carried out in an attempt to eliminate some of these difficulties by using a "point source" of slime to give high concentrations near the crayfish. No statistically significant evidence of detection of either trout or eel mucus was observed using a stimulus of contact with mucus. When stimulated by a close approach of the probe treated with eel mucus, however, an increased number of crayfish performed upright responses and significantly more crayfish made non-static responses to eel mucus than to no mucus or trout mucus. Thus, we concluded that *P. zealandicus* was able to detect eel skin mucus in high local concentrations, but it seems probable that physical contact masks the effect of skin mucus on anti-predator behaviours.

Crayfish did not respond to trout skin mucus at all. This may mean that *P. zealandicus* was unable to detect the trout mucus, or that visual stimuli are more important for the detection of crepuscular predators such as trout, as found by Blake and Hart (1993). Alternatively, crayfish may have received chemical cues from the brown trout but not have produced an overt behavioural response. Rehnberg and Schreck (1986) found that chemical cues from a predator induced a physiological response from coho salmon but did not elicit a detectable behavioural response. It is also possible that crayfish do not perceive a 'distant' trout to be as great a threat as a 'distant' eel.

The possibility that trout mucus might degrade more quickly than eel mucus is not supported by the observations of Williams and Moore (1985), who reported a significant response by the amphipod *Gammarus pseudolimnaeus* to trout skin mucus that had been aged for 24 hours. The structural nature of the chemicals in skin mucus of the two predators may, however, be sufficiently different to affect their relative dispersal rates to the crayfish.

Predator avoidance responses

P. zealandicus significantly modified certain aspects of its behaviour in the physical presence of a predator. Both predators caused an increase in the use of a spatial refuge by *P. zealandicus*, although this was greater in the presence of eels than trout. This finding is in keeping with observations made on crayfish of other genera (Stein and Magnuson, 1976; Stein, 1977; Blake and Hart, 1993). However, crayfish did not reduce their activity (walking) or increase their time spent stationary significantly more in the presence of trout than eels, as might have been expected given the trout's greater reliance on visual cues in foraging (Allen, 1951).

Anti-predatory chela displays (upright responses) and swimming responses were never observed in control periods when no predator was present. Crayfish performed significantly more chela displays in response to an eel than to a trout, and use of swimming as an escape response by the crayfish was found only in trials with eels. Upright and swim responses were made in general only to a direct contact stimulus, but crayfish were observed to make chela displays when the stimulus involved a close approach only (*unpubl. data*).

Generally, different groups of crayfish exposed to the same treatment made similar responses. However, the finding that in some cases there is significant variation between different groups of crayfish has implications for the experimental design. It may therefore be incorrect to make the assumption that the behaviour of each crayfish within a group was independent of the other three individuals.

In all cases in Experiment 1 crayfish responded similarly to the two individuals of the same predator species but quite differently to the two predator types. So, while using a larger number of individual predators would further increase the external validity of this experiment, we feel confident that the responses displayed by crayfish to the individual predators can be generalised to those species as a whole.

Mistakes are expected to be more costly for prey than for predators. A missed opportunity for a meal is unlikely to have much effect on the life-long fitness of a predator but just one failed escape has obvious implications for the fitness of a prey organism: the "life-dinner principle" (Dawkins and Krebs, 1979). While the benefit of avoiding predators clearly lies in improved survivorship, there are also immediate energetic and temporal costs to the prey in making avoidance behaviours. Ideally, prey should respond appropriately in relation to the risk of predation in a particular situation while remaining sensitive to the costs of avoidance in terms of, for example, reduced feeding rates or mating opportunities (Sih, 1982).

Previous studies have reported a correspondence between prey response and predation risk. Some prey species have the ability to distinguish between predators and similar-looking non-predators (e.g., Peckarsky, 1980), between active and inactive predators (e.g., Phillips, 1978) and between predators that differ in predation ability (Ducey and Brodie, 1983), mode of feeding (Dodson, 1988), or diet (Keefe, 1992). The ability to perceive the risk presented by a particular predator and respond appropriately will depend on what experience the prey species has had with that predator species. In this respect *P. zealandicus* has had a long co-evolutionary history with the native long-finned eel (McDowall, 1964) but only about 120 years have elapsed since trout were introduced to New Zealand. However, we cannot state conclusively whether the greater responsiveness of crayfish to eels than trout is a reflection of the different evolutionary histories that the crayfish shares with the other two species or the relative contemporary risk posed by the two predators.

From an evolutionary perspective a prey species has three options (Thorp, 1986). It can either tolerate a predator, live only in environments in which that predator is absent, or adapt its anatomy, physiology or behaviour to counter the predator. Losses may be too high for *P. zealandicus* to tolerate brown trout as a predatory threat and the crayfish may be more successful in existing in areas where trout are excluded. *P. zealandicus* shows some suitable behavioural responses to the introduced brown trout, but may still be losing out in the "predator-prey arms race" by not having sufficient ability to detect trout using non-contact chemical stimuli.

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