



Chemically mediated avoidance of *Hemigrapsus nudus* (Crustacea) by *Littorina scutulata* (Gastropoda): effects of species coexistence and variable cues

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Some gastropods can respond to waterborne chemicals released from predators and injured conspecifics with avoidance behaviour. We examined the avoidance response of the intertidal snail *Littorina scutulata sensu lato* to chemical cues from the predatory crab *Hemigrapsus nudus*, both from the Pacific coast of Canada, using two-choice laboratory experiments. *Littorina scutulata s. l.* from a site with *H. nudus* (Ross Islets) avoided water containing chemical cues from the predator, but snails from a site without *H. nudus* (Prasiola Point) did not. The avoidance behaviour of *L. scutulata s. l.* from the 'crab site' strengthened with increasing perceived predation threat. We found a risk hierarchy, with risk increasing from control sea water (no risk), to predator cues (low risk), to injured-conspecific cues (intermediate risk), to a combination of predator and injured-conspecific cues (high risk). This risk gradient seems logical, because the sole presence of predators does not necessarily represent an immediate predation threat, whereas predator and injured-conspecific cues together may indicate that predation is actually occurring nearby. These results are important for understanding the effects of chemically mediated predator–prey interactions on intertidal distribution patterns of littorinids.

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Predator–prey interactions are important in establishing marine community structure (Duffy & Hay 2001). When prey are a limiting factor, their abundance can affect populations of predators; likewise, predators can affect prey abundance. Detection of a predator can, therefore, be essential for the survival of prey. Responses to detection by prey can include escape or avoidance behaviours; the former is a response to contact with a predator, whereas the latter is a response to substances diffused from a predator, which are used by prey to detect the predator from a distance (Phillips 1977). Avoidance responses can constitute an adaptation for slow-moving organisms to find refuge before a predator is too near; if contact is made, they are often unable to escape.

Organisms have met the challenge of predator detection in various ways, including photosensory, chemosensory or auditory modes, or their combination (Stachowicz 2001). Several studies have shown the ability of benthic

invertebrates to detect predators by chemical means. An example is the blue crab, *Callinectes sapidus*, which was found to avoid water containing predator (*Fundulus heteroclitus*) effluent (Díaz et al. 1998). Similarly, Chiussi et al. (2000) found that the hermit crab *Clibanarius antillensis* oriented itself directly away from a target representing a predator only in the presence of odour from a predatory fish (*Sphoeroides testudineus*), which indicates that chemical cues can have a strong effect on behaviour. Similar results have been found for gastropods. For example, *Tegula* snail species respond with an avoidance behaviour to chemical stimuli from predators such as octopuses, sea stars (class Asteroidea), and crabs of the genus *Cancer* (Schmitt 1981; Geller 1982; Fawcett 1984).

Different populations of a given gastropod display varying levels of evasive response to similar chemical cues. McCarthy & Fisher (2000) found that two *Physella heterostropha* (freshwater snail) populations from separate locations showed differing responses to odour from a predatory crayfish, *Procambarus clarkii*, possibly due to variations in community structure between locations. Prey populations living in the presence of a predator are likely to show markedly different responses to the

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predator's odour than populations living in its absence, as the latter never would have been exposed to the predator. Geller (1982) found significantly different responses of *Tegula funebris* to predator (*Cancer antennarius*) odour based on the presence or absence of *C. antennarius* where the groups of snails were collected.

In addition to previous exposure to a predator, apparent risk may also influence an individual's decision to respond to odour from a predator. Other than predator odour, chemical cues released by conspecifics when they are abused or crushed can also elicit an avoidance response by prey (Chivers & Smith 1998). Avoidance responses by prey species can be costly; therefore, some animals assess the risk associated with an encounter with a predator before responding to it, to minimize wasted energy (Marko & Palmer 1991; Vadas et al. 1994; McCarthy & Fisher 2000). For example, McCarthy & Fisher (2000) found progressively stronger responses in *P. heterostropha* to a risk gradient increasing from predator (crayfish) odour, to odour from crushed conspecifics, to both of these factors combined.

Littorina snails are marine gastropods that can be important herbivores in intertidal communities, and may have significant effects on the density of seaweeds. Kim & DeWreede (1996) found that *Littorina* snails may be partially responsible for controlling seaweed (*Mazzaella parksii*) abundance in intertidal habitats. In a similar way, *Hemigrapsus nudus*, a predatory shore crab that feeds on intertidal invertebrates, can influence the distribution of these snails in a community. *Hemigrapsus nudus* is known to prey on *L. scutulata* in British Columbia, Canada. In areas where predatory crabs and *Littorina* coexist, *Littorina* is found higher in the intertidal zone as a result of greater mortality due to predation in the lower areas and of prey seeking safer intertidal areas (Behrens Yamada & Boulding 1996; Rochette & Dill 2000).

Knowledge on the response of *Littorina* species to chemical cues for predator detection and avoidance is limited, but it is progressively accumulating (Behrens Yamada et al. 1998; Jacobsen & Stabell 1999). We investigated the response of *L. scutulata sensu lato* (see Methods for taxonomy) to predator odour from *H. nudus* and odour from crushed conspecifics. We hypothesized that (1) *L. scutulata s. l.* co-occurring with *H. nudus* would show an avoidance behaviour in response to chemicals diffused from this crab, that (2) *L. scutulata s. l.* from areas without *H. nudus* would not show an avoidance response to predator odour, and that (3) avoidance behaviour would increase with increasing risk: from water with predator odour only, to water containing crushed conspecifics, to a combination of these two factors.

METHODS

Study Sites

We collected *L. scutulata s. l.* from a 'crab site', Ross Islets (48°52'N, 125°37'W), and from a 'no-crab site', the east side of Prasiola Point (48°49'N, 125°10'W), in southern Barkley Sound, Vancouver Island, British Columbia,

Canada. We collected *H. nudus* from Ross Islets. These sites are subjected to moderate (Prasiola Point) to low (Ross Islets) wave exposure, compared with sites elsewhere in Barkley Sound. Exposure differences between our sites possibly explained the absence of *H. nudus* at Prasiola Point. The highest tidal amplitude in this region is about 4 m and mean monthly surface sea water temperature ranges between 8.6°C in winter and 16.1°C in summer (Scrosati 2001).

Study Species

Littorina snails are herbivorous marine gastropods that feed on microalgae and macroalgae and may influence algal distribution in areas where the snails are abundant (Voltolina & Sacchi 1990; Kim & DeWreede 1996). There are four species of *Littorina* in the northeast Pacific coast (Boulding & Harper 1998), of which two sister species (*L. scutulata sensu stricto* and *L. plena*) are morphologically very similar. These two species are difficult to distinguish and have been referred to as the *L. scutulata* complex (Mastro et al. 1982; Murray 1982; Chow 1987; Rugh 1997) or as *L. scutulata sensu lato* (Boulding et al. 1999). Both species are sympatric; their distribution broadly overlaps gradients of intertidal elevation and wave exposure (Hohenlohe 2003a, b). Recent studies have improved species identification based on molecular and morphological characters (Kyle & Boulding 2000; Hohenlohe & Boulding 2001), but the visual distinction is still not always clear-cut. Because of this, we will refer to our specimens as *L. scutulata sensu lato*. *Littorina scutulata s. l.* is abundant along the west coast of Vancouver Island, occurring primarily in the mid to upper intertidal zone on wave-exposed and wave-sheltered shores. We collected approximately 200 individuals from the intertidal zones of Ross Islets and Prasiola Point. The shell length of tested individuals ranged from 7 to 10 mm. We maintained the snails within mesh boxes in a flow-through sea water table, with the macroalga *Fucus gardneri* available for feeding at all times. Each animal was used only once, within 3 days after collection, and returned to the field immediately after tests.

Purple shore crab, *H. nudus*, is also common in the west coast of Vancouver Island. It is a predatory brachyuran crab that feeds largely on barnacles, but also on other intertidal invertebrates, including *Littorina* species. *Hemigrapsus nudus* occurs in the mid to low intertidal zone of rocky shores from the Gulf of California to Alaska (Wan 1990) and can often be found hiding under rocks and gravel. This crab is usually easily recognizable by its reddish to purple coloration. As the range of *H. nudus* often overlaps with that of the yellow shore crab, *H. oregonensis*, and coloration can be sometimes vague, we confirmed the identity of *H. nudus* by the presence of purple spots on the chelipeds and the absence of leg hairs (Kozloff 1996). Maximum carapace widths of crabs used were between 3 and 4 cm; both males and females were tested. We collected 16 crabs, which were kept in a 10-litre aquarium with running sea water, in individual mesh boxes to prevent fighting. The crabs were fed mussels

(either *Mytilus californianus* or *M. trossulus*) overnight every second evening, out of the aquarium, to prevent contamination of test water with any chemicals released by the mussels. Crabs were used within 3 days of capture and returned to the field immediately after tests.

Experimental Design

We performed the tests as choice experiments in July 2002. We designed a simple apparatus, giving snails an equal choice between each of two treatments. The apparatus, henceforth referred to as the choice plate (Fig. 1), was constructed with transparent Plexiglas and silicone. Two channels, each 3 cm wide, were separated by a Plexiglas divider on a Plexiglas base. The choice plate was on a slight incline (about 10°) to keep water flowing down the gradient and to allow for *Littorina's* tendency to go up in the intertidal zone when threatened, and to climb out of the water when handled. Two treatments were compared simultaneously, with each treatment running down one of the channels of the choice plate, creating a thin film of water along each channel. The flow rate was kept equal between both channels as much as possible. For each trial, we placed one snail at the base of the divider between the two channels (Fig. 1), with equal opportunity of choosing to go left or right.

We used four different water treatments, progressively increasing in risk: (1) 'control water', which was a constant source of running sea water (no risk), (2) 'predator water', which was sea water with chemicals diffused from *H. nudus*, obtained by siphoning water from the 10-litre

aquarium with the crabs using a continual supply of running sea water (low risk), (3) 'snail water', which was sea water with chemicals diffused from crushed conspecifics, obtained by diluting 1.6 g of crushed *L. scutulata s. l.* (about 10 snails with a mean size of 8.5 mm) in 5 litres of sea water (intermediate risk), and (4) 'predator plus snail water', which was sea water with odours from both predators and crushed snails, obtained by diluting 1.6 g of crushed *L. scutulata s. l.* in 5 litres of predator water (high risk). Water temperature was the same as that for coastal waters in the area in July (about 13–14°C; Scrosati 2001).

To test hypothesis 1, we tested snails from the crab site (Ross Islets) for a response to predator water against control water. To test hypothesis 2, we tested snails from the no-crab site (Prasiola Point) for a response to predator water against control water. We compared these results to determine whether locality of origin affected the snails' responses to predator chemical cues. We also tested snails from the no-crab site for a response to snail water against control water. To test hypothesis 3, we tested snails from the crab site for a response to snail water (intermediate risk) against control water, predator plus snail water (high risk) against control water, and snail water against predator water. The experiments were done during daytime hours under natural light equivalent to cloudy conditions. Choice for a particular treatment was determined when the snail moved to that particular side of the plate and remained there. A total of 30 different snails were used in each experiment. We analysed the results through chi-square (goodness-of-fit) tests (Howell 1992).

RESULTS

Response by Site

Littorina scutulata s. l. from the crab site (Ross Islets) significantly avoided predator water, but specimens from the no-crab site (Prasiola Point) did not (Table 1). Snails from the no-crab site, however, significantly avoided snail water (Table 1).

Response by Risk

As mentioned above, snails from the crab site displayed an avoidance behaviour to predator water. Snails from the crab site showed a stronger avoidance response to snail water (Table 1) and an even stronger avoidance response to predator plus snail water (Table 1). To verify the positions of predator water and snail water in the risk gradient for snails from the crab site, we ran an experiment with predator water and snail water as choices: snails avoided snail water significantly (Table 1), showing that snail water is a stronger threat indicator than predator water.

DISCUSSION

Our results support the hypothesis that *L. scutulata s. l.* from a site with *H. nudus* avoids water containing

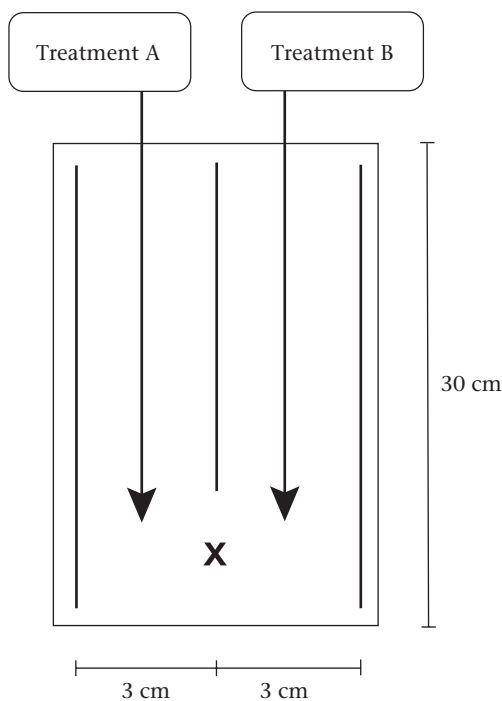


Figure 1. Top view of the choice plate used in the experiments. For each trial, one snail was initially placed at X. The arrows indicate the direction of water flow from each treatment tank.

Table 1. Results of two-choice tests

Snail origin	Control water	Predator water	Snail water	Predator plus snail water	χ^2 (<i>P</i>)
C	21	9			4.8 (<0.005)
NC	13	17			0.5 (>0.05)
NC	24		6		10.8 (<0.005)
C	23		7		8.5 (<0.005)
C	29			1	26.1 (<0.005)
C		27	3		19.2 (<0.005)

The sites of snail origin were Ross Islets (C = 'crab site') and Prasiola Point (NC = 'no-crab site'). Numbers in treatment columns indicate the number of snails that chose a particular treatment. Statistical differences between treatments were evaluated with the χ^2 statistic and its corresponding *P* value. For all of the tests, *N* = 30 snails.

chemicals diffused from the predatory crab. The results coincide with those from similar studies on the avoidance behaviour of other marine gastropods. Geller (1982) found that *T. funebris* avoided water containing exudates from a predatory crab, *C. antennarius*. Also, a study concerned with the avoidance behaviour of *Nucella lamellosa* found that this species avoids water containing chemical cues from *C. productus* (Marko & Palmer 1991).

The hypothesis that *L. scutulata s. l.* from a site without *H. nudus* does not show an avoidance response to chemical cues from the crab is also supported by our study. Similar findings have been reported for *T. funebris* from an area without *C. antennarius* (Geller 1982) and for the freshwater snail *P. heterostropha* from an area without a predatory crayfish (McCarthy & Fisher 2000). There are a couple of possible explanations for the avoidance response only appearing in snail populations that are sympatric with a predator. First, there could be an inherent genetic trait involved, which has previously been suggested by Geller (1982). At sites where crabs occur, individuals with a stronger predisposition to avoid chemical cues from predatory crabs may have a higher chance for survival, providing a strong local selection for animals possessing that trait. At sites lacking crabs, there would be no such selection for the avoidance trait, and thus an avoidance response would not be predominant in that population. Second, the avoidance of chemicals from a predator could be a learned response. However, this view has been criticized for two reasons: it is unlikely that many snails would survive an attack by a crab and retain that experience with an inclination to turn away from crab chemical cues in the future, and it is also unlikely that snails can observe a crab attacking another snail and then associate chemicals from that crab species with predation threat (Geller 1982).

Our results also show that there is a hierarchy of risk eliciting increasingly stronger avoidance responses in *L. scutulata s. l.* The hierarchy increases in risk from control water (no risk), to predator water (low risk), to snail water (intermediate risk), to predator plus snail water (high risk). Such a gradient seems logical. Encounters with predators are not always negative, because predators are not always feeding. As avoidance responses can be energetically costly, and also costly in time lost from

foraging, it is beneficial for the prey to assess the risk of predation and only respond if the perceived threat is high. The next level of risk, alarm cues from crushed conspecifics, could indicate a number of threats, including various predators or other risks such as possible mortality caused by disturbance by nonpredatory organisms. Finally, the high-risk category appears to give a clear message that an actively foraging predator is nearby, and thus it is worth the effort and the associated cost to avoid the source of the chemical signal. Other snails, including whelks, *Nucella* spp., and other littorinids, have been found to similarly regulate their avoidance behaviour in response to their perception of predation risk (Marko & Palmer 1991; Vadas et al. 1994; Rochette et al. 1997; Behrens Yamada et al. 1998; Jacobsen & Stabell 1999; McCarthy & Fisher 2000). Such a risk gradient might even affect shell thickening rates on longer timescales, as shown for *L. obtusata* and two *Nucella* species in contact with crab and conspecific cues (Appleton & Palmer 1988; Palmer 1990; Trussell & Nicklin 2002).

Avoidance behaviour is an important component of the activities of many intertidal invertebrates and is, therefore, relevant in studies of community structure where predator-prey interactions are involved (Trussell et al. 2003). Future studies in this area could examine whether differences in response by snails from crab and no-crab sites are due to learned or genetic factors (see Magurran 1999 for pertinent studies on fish). Another direction to follow could be to look at possible effects of shell size on avoidance behaviour, to determine whether there is a size refuge beyond which snails are not threatened as strongly by predators. Focusing on predators, it would be relevant to study whether the age (Turner & Montgomery 2003) or concentration of their chemical cues affects avoidance behaviour in snails.

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