

Smelling the difference: hermit crab responses to predatory and nonpredatory crabs

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ARTICLE INFO

Article history:

Received 29 January 2009

Initial acceptance 18 February 2009

Final acceptance 11 May 2009

Published online 30 July 2009

MS. number: A09-00069R

Keywords:

Cancer productus
chemical cue
chemical ecology
Crustacea
hermit crab
Pagurus granosimanus
predator avoidance
predator recognition
Pugettia producta
signalling

Many aquatic invertebrates alter their behaviour in response to chemical stimuli from predators. Less is known about how finely prey can discriminate between stimuli from predatory and related non-predatory species, even in well-studied hermit crabs. We tested the time to emerge from the shell after disturbance (hiding time) of a common intertidal hermit crab, *Pagurus granosimanus* was exposed to effluent from two large-bodied brachyuran crabs: the durophagous, predatory red rock crab, *Cancer productus*, and the herbivorous kelp crab, *Pugettia producta*, in a controlled laboratory setting. Hiding times were a dramatic 41% shorter in the presence of *Cancer* effluent than when exposed to *Pugettia* effluent, which did not differ from a sea water control. Therefore hermit crabs can distinguish between chemical effluent from predatory and nonpredatory brachyuran crabs, which could include crab-specific compounds or metabolites from recently consumed prey, and adjust their behaviour accordingly. Shorter hiding times probably decrease the risk of being eaten by a shell-breaking predator because hermit crabs may be better able to elude them, either by running rapidly away or by abandoning their shell before it is crushed. Individual tests with three video stimuli (control, predatory crab, herbivorous crab), and combined tests with video and chemical stimuli, revealed a consistent generalized response to the presence of video but no differences among video treatments.

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Aquatic animals live awash in a complex cocktail of chemical stimuli (Brönmark & Hansson 2000). For many invertebrates, chemical stimuli are a major, if not the primary, source of information about their aquatic environment (Dill 1987; Chivers & Smith 1998; Kats & Dill 1998). Different stimuli elicit different behaviours including aggregation, spawning, attraction to mates, searching for food, homing in on suitable microhabitats, and appropriate responses to potential predators, such as hiding or fleeing. Therefore, at any particular moment, an individual must not only monitor these diverse stimuli, but it must also rank the value of potential behavioural responses to decide which response is most appropriate (Dill 1987; Kats & Dill 1998; Dicke & Grostal 2001).

A major challenge faces animals that depend on chemical stimuli released by predators to guide their behaviour: how do they distinguish among stimuli from related species? For example, not all large-bodied crabs are predators. Inappropriate responses, like fleeing from a harmless herbivorous crab, may be costly, as they reduce time to feed or mate (Ydenberg & Dill 1986; Dill & Gillett 1991; Scarratt & Godin 1992; Dill & Fraser 1997) and may increase the risk of encounter with another predator. Natural selection should therefore favour individuals that can distinguish among predatory and nonpredatory species. But how finely can they do so?

Many invertebrates do appear able to assess risk levels based on chemical stimuli (Kats & Dill 1998). For example, marine snails can distinguish between predatory and nonpredatory brachyuran crabs (Marko & Palmer 1991), starfish (Schmitt 1981) and snails (Dix & Hamilton 1993) as well as between crabs fed conspecific or other snail species (Jacobsen & Stabell 2004). Freshwater snails respond differently to the scent of different predators (fish or crayfish) fed conspecific snails (Turner et al. 1999). Barnacles can distinguish between predatory and nonpredatory snails and starfish (Palmer et al. 1982). Mussels can distinguish between predatory crabs and herbivorous urchins (Cote 1995), and burrowing bivalves can

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distinguish between feeding and starved crabs (Griffiths & Richardson 2006; Smee & Weissburg 2006). Similarly, snails (Stenzler & Atema 1977), polychaete worms (Watson et al. 2005) and crabs (Hazlett & McLay 2005) can all distinguish chemical stimuli released by damaged conspecifics from those released by more distantly related prey. Finally, individuals from populations not normally exposed to a predator may respond differently to predator scents than individuals that normally encounter that predator (Geller 1982; Trussell & Nicklin 2002), which suggests that such abilities may be learned or may evolve rapidly.

Hermit crabs respond differently to different chemical stimuli in their environment. They can distinguish their own scent from that of other individuals (Benoit et al. 1997; Gherardi et al. 2005). Predator effluent may interfere with mating (Hazlett & Rittschof 2000), and odours from living (Hazlett 1996b), damaged or dead snails (Rittschof 1980), or conspecific hermit crabs (Rittschof et al. 1992) attracts them or increases shell grasping behaviour. Hermit crabs also respond to visual stimuli in their environment, and these responses may be modulated by olfactory cues (Chiussi et al. 2001; Dalesman & Inchley 2008).

Shell-breaking crabs are important predators of hermit crabs (Vermeij 1978). Although hermit crabs clearly respond to the effluent from predatory crabs (Hazlett 1996a; Rittschof & Hazlett 1997), whether they can distinguish between predatory and non-predatory crabs remains unclear. We therefore tested whether the hermit crab *Pagurus granosimanus* would show different behaviours in response to chemical and visual stimuli from two different, large-bodied brachyuran crabs: a shell-breaking predatory crab, the red rock crab *Cancer productus* (Cancroidea, Cancridae), and an herbivorous crab, the kelp crab *Pugettia producta* (Majoidea, Epialtidae).

METHODS

Collection and Holding of Specimens

The grainy-handed hermit crab, *Pagurus granosimanus*, is a common intertidal hermit crab of northeastern Pacific shores, and prefers to inhabit large snail shells into which it may withdraw completely (Jensen 1995). We collected 400 individuals from the mid-intertidal shore of Scott's Bay (48°50'N, 125°05'W) near Bamfield Inlet on Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada. Intermediate-sized individuals of roughly the same size were collected on 11 August 2005 and held in the laboratory until experiments began on 13 August. The 30 largest and 30 smallest hermit crabs were eliminated from the group of 400 to minimize size variation. In addition, only hermit crabs bearing *Tegula funebris* shells were used. Two red rock crabs, *Cancer productus*, and two kelp crabs, *Pugettia producta*, were collected from shallow water near Scott's Bay. *Cancer* crabs measured 12–15 cm, and were collected on 11 August. All hermit crabs were allowed to acclimatize for at least 12 h in the laboratory before testing, and were evenly distributed among eight mesh containers roughly 20 × 20 × 10 cm held in a water table with running sea water prior to testing. Hermit crabs were fed small pieces of frozen fish every other day.

Prior to the experiments, each large crab was held individually in a separate approximately 15 litre, glass-walled aquarium with a steady supply of running sea water. Like Dalesman & Inchley (2008), who fed squid to their predatory crab, we fed the *Cancer* crabs frozen fish every other day so that their effluent would not be contaminated with metabolites released following consumption of crustacean prey. *Pugettia* were fed seaweed from the bay where they were collected.

Chemical and Visual Stimuli

Hermit crabs were exposed to three types of chemical stimuli: (1) control: incoming sea water from the Bamfield Marine Sciences Centre sea water system, (2) predatory crab: sea water in which *Cancer productus* had been held and (3) nonpredatory crab: sea water in which *Pugettia producta* had been held. For each crab stimulus, an individual crab was transferred to a plastic bucket filled with approximately 5–8 litres of aerated sea water, and left to sit there without flow, for 1.75 h. The crab was then transferred back to its original tank and 4.5 litres of water from the plastic bucket were transferred to the testing arena.

Hermit crabs were also exposed to three types of visual stimuli: (1) neutral video: a single video of an aquarium with rocks and algae but no crab, (2) predatory crab: a single video of a *Cancer productus* moving about and (3) nonpredatory crab: a single video of a *Pugettia producta* moving about. These videos were created by filming an aquarium habitat that included rocks, shells and algae from the natural environment of the hermit crabs. The same tank and arrangement were used for each of the three videos; the movement of the crab was the only variable. When filming the crabs, a hand-held camera was aimed directly at the tank from a low angle to mimic the perspective of a hermit crab. Video sequences of 100 s were played back to the hermit crabs during visual treatments.

Behavioural Assays

An individual hermit crab was exposed to one of eight treatments: (1) control sea water, (2) neutral video, (3) *Pugettia* video, (4) *Cancer* video, (5) *Pugettia* effluent, (6) *Pugettia* effluent + *Pugettia* video, (7) *Cancer* effluent or (8) *Cancer* effluent + *Cancer* video. All trials were conducted in a small glass aquarium (15 × 30 cm) containing 4.5 liters of stationary, unaerated sea water (either control or treatment) at 11.5–13 °C. During trials with chemical stimuli, the aquarium was surrounded in opaque black plastic on all four sides but open to artificial light at the top. For trials involving a video stimulus, a 30 cm wide colour video monitor was placed immediately adjacent to the long side of the aquarium, but the remaining three sides remained covered in black plastic.

For each trial, an individual hermit crab was removed by hand from its holding tank and placed inside the experimental arena. This handling caused the hermit crab to withdraw into its shell and exposed it briefly to air (the process took less than 2 s). If, after placement in the experimental arena, the hermit crab did not emerge within 10 s, it was removed from the experiment. After 100 s of acclimation to the chemical and/or video stimuli, during which time the hermit crab wandered about the experimental arena, we firmly tapped its shell with a blunt glass rod. Hiding time, the time elapsed from the moment of the tap until the hermit crab emerged fully from its shell, was recorded to the nearest second with a digital stopwatch. Each individual hermit crab was used only once and placed in a separate holding tank after testing so it would not be confused with untested hermit crabs. Extraneous sound, vibrations and visual stimulation were minimized during the experiment, and all trials were conducted between 1130 and 1700 hours. The sea water was unchanged for 40 trials and kept between 11.5 and 13 °C. The *Cancer* crab effluent experiment was conducted on 13 August, within 2 days of *Cancer* crab collection. The *Cancer* crab video and neutral video were taped on 14 August, as were the *Cancer* video and effluent-and-video trials, so all trials involving *Cancer* crab were completed in 2 days. The control trial and the neutral video trials were completed 15 August. The experiments with *Pugettia* were conducted 22 August, 48 h after *Pugettia* were collected.

Hiding times were log-transformed to normalize distributions and homogenize variances prior to analysis. Differences among

treatments were analysed using SuperANOVA (Ver. 1.11, Abacus Concepts, Berkeley, CA, U.S.A.). Two individuals with hiding times of zero were excluded from the analysis (one from *Cancer* video, one from *Pugettia* effluent + video) because a true 'zero' hiding time was too difficult to score reliably.

Ethical Note

Hermit crabs and the stimulus crabs (*C. productus* and *P. producta*) were collected from the field, held in fresh running sea water except for a few minutes at a time when effluent was being collected or when hermit crabs were being tested. All crabs were provided with food throughout their stay in the laboratory (as noted above) and were released back into the field after tests were done. These experiments were conducted with invertebrates, for which Animal Use Protocols are not required by the Canadian Council on Animal Care.

RESULTS

Log transformation normalized the distribution of hiding times and also homogenized the variances (Fig. 1; see two-factor ANOVA results below for details). Mean hiding times varied by a factor of two (range 3.4–6.8 s) among the eight treatments (Fig. 1), and these differences were highly significant (one-way ANOVA: $P < 0.001$; Table 1). Although slight differences were apparent among the three video-only treatments (neutral video, *Pugettia* video, *Cancer* video; Fig. 1, bars 2–4), these differences were not significant statistically (one-way ANOVA: $P = 0.21$, analysis not shown), so data from these three treatments were pooled as a single 'video only' treatment for a more robust two-factor analysis.

A two-factor ANOVA testing for differences in log-transformed hiding times between effluent treatments (sea water only, *Pugettia* effluent, *Cancer* effluent) and video stimuli (absent, present)

Table 1

Results from a one-factor ANOVA testing for differences in hermit crab hiding times among all eight treatments

Source	df	Mean square	F	P
Group	7	0.456	8.87	<0.001
Error	307	0.051		

See Fig. 1 for treatment means.

revealed a highly significant effect of effluent ($P < 0.001$) and a highly significant effect of video stimulus ($P = 0.001$), but no interaction between these effects ($P = 0.88$; Table 2). Overall, residuals from cell means did not depart from normality ($P > 0.1$; skew = -0.17 , kurtosis = -0.15 , $N = 315$), and variances did not vary significantly among groups (effluent treatments: $P = 0.15$; video treatments: $P = 0.07$; effluent-by-video interaction: $P = 0.45$; Levene's two-factor heterogeneity of variance test on absolute values of residuals). Adding a video stimulus decreased hiding time in all three effluent treatments by an average of 19.5%, regardless of the effluent stimulus (22.7%, 19.3% and 16.6% for sea water only, *Pugettia* effluent and *Cancer* effluent, respectively). Post hoc tests of the effluent effects (both Fisher's protected least squares difference and Duncan's new multiple range) revealed no significant difference between the sea water-only and *Pugettia*-effluent treatments, so the highly significant effect of effluent stimulus was due almost entirely to the *Cancer*-effluent treatment. The presence of *Cancer* effluent reduced hiding times by a dramatic 41% with no video stimulus, and by nearly the same amount (36.8%) when a video stimulus was present (Fig. 1).

DISCUSSION

Brachyuran crabs frequently prey on hermit crabs (Reese 1969; Bertness 1981), so how hermit crabs respond to them may have a large impact on fitness. On the other hand, not all large-bodied

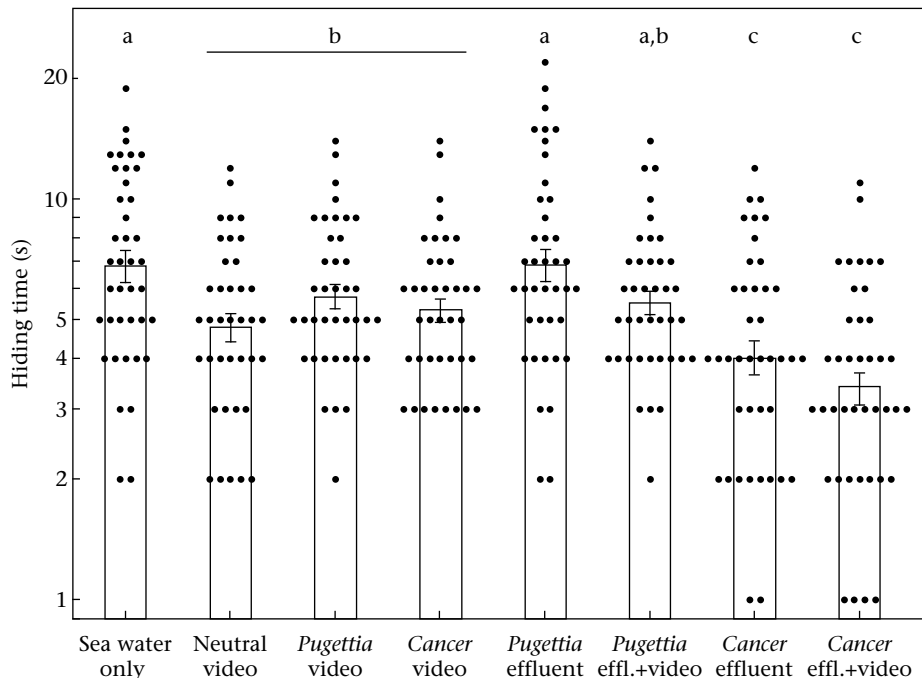


Figure 1. Hiding times of hermit crabs, *Pagurus granosimanus*, exposed to different experimental conditions in a laboratory aquarium. Each dot represents the hiding time for a single observation on an individual hermit crab. Bars represent treatment means (\pm SE) that were computed from log-transformed hiding times and backtransformed prior to plotting. Note that the Y axis is a logarithmic scale. Sample sizes were as follows: $N = 40$ for treatments 1, 5, 7 and 8; $N = 39$ for treatments 3, 4 and 6; $N = 38$ for treatment 2. Treatment means with the same letter above them did not differ significantly from one another; treatment means not sharing the same letter differed significantly (the same groupings were obtained for Fisher's protected least squares difference and Duncan's new multiple range post hoc tests).

Table 2

Results from a two-factor ANOVA testing for differences in hermit crab hiding times between chemical (sea water only, *Pugettia* effluent, *Cancer* effluent) and video stimuli (present, absent)

Stimulus	df	Mean square	F	P
Chemical (C)	2	1.3287	25.86	<0.001
Video (V)	1	0.6005	11.69	0.001
C × V interaction	2	0.0068	0.13	0.88
Error	309	0.0514		

See Fig. 1 for treatment means.

brachyuran crabs are predators. Therefore, because of costs associated with inappropriate behaviours (Dill 1987; Dicke & Grostal 2001), natural selection should favour the ability to distinguish between predatory and nonpredatory crabs. *Pagurus granosimanus* appears to be able (1) to distinguish the effluents from predatory and nonpredatory crabs and (2) to alter their behaviour (hiding time) in an appropriate manner.

Hiding time (time to emerge from the shell after disturbance) is a convenient behaviour of hermit crabs because it is easy to score quantitatively (Scarratt & Godin 1992) and it is a useful measure of response to predation risk (Palmer et al. 1982; Dill & Fraser 1997; Jennions et al. 2003). Hiding times of hermit crabs might increase either in the presence of predators that are unlikely to break through their gastropod-shell retreat, or in the presence of visually orienting predators that cue on prey motion (Scarratt & Godin 1992; Hazlett 1997). Alternatively, hiding times might decrease in the presence of slower-moving durophagous predators because active movement away from the predator may be a more effective defence than withdrawing into the shell (Scarratt & Godin 1992; Jackman 1998).

Hermit crabs respond to visual stimuli from predatory crabs either by increasing their rate of locomotion (Hazlett 1997) or by ceasing to feed (Dalesman & Inchley 2008). In the present study, video stimuli did significantly decrease hiding times of *Pagurus granosimanus*. However, the 20% shorter hiding times in response to video stimuli appeared unrelated to the content of the video, as hiding times did not differ among the video-only treatments (Fig. 1, bars 2–4): moving crabs elicited the same response as the neutral video and the identity of the crab appeared to be irrelevant. We hesitate to give too much weight to our conclusion about lack of a response to different crab visual stimuli, as only a single video sequence of each crab was presented to hermit crabs, and factors like visual angle and rate or direction of motion of a moving object may influence how crustaceans respond to visual stimuli (Zeil & Hemmi 2006). We suspect that the hermit crabs in the experimental arena were responding more to altered light level introduced by the video monitor or some other property of the video stimulus rather than the video content, but additional tests would be required to confirm this.

Many hermit crabs respond to the effluent of predators by altering their behaviour. They may increase the rate of locomotion in the presence of shell-breaking crabs (Hazlett 1996a; Rittschof & Hazlett 1997), increase both the response distance and the distance of flight from a moving predator (Dalesman & Inchley 2008), decrease the rate of locomotion in the presence of visual predators (Hazlett 1997), reduce the rate of pair formation when mating (Hazlett & Rittschof 2000), or alter their orientation response to visual cues about potential refuges (Chiussi et al. 2001). Despite this extensive literature on hermit crab responses to visual and chemical stimuli, our study is the first to show that hermit crabs can distinguish between predatory and nonpredatory crabs based on their effluent.

The nearly 40% decrease in hiding times we observed in *Pagurus granosimanus* when exposed to *Cancer* crab effluent was clearly a biologically significant response compared to that elicited by plain sea water or by sea water containing *Pugettia* effluent. *Pugettia*

effluent did not affect hiding time: hermit crabs responded to *Pugettia* effluent as if it were merely sea water (compare bars 1 and 5 and bars 3 and 6, Fig. 1). In addition, hiding times decreased roughly the same amount in both *Cancer*-effluent treatments (Fig. 1, bars 7 and 8) compared to the equivalent *Pugettia*-effluent treatments (Fig. 1, bars 5 and 6): 41% and 37.6%, respectively. Therefore the effect of *Cancer* crab effluent was both strong and repeatable.

We cannot say with confidence to what chemical stimuli *P. granosimanus* were responding in our tests. Because the predatory *Cancer* crabs were fed fish and the herbivorous *Pugettia* were fed algae, hermit crabs might have been responding to different metabolites released from the different foods rather than crab-specific (diet-independent) compounds. Nevertheless, metabolites from different foods are probably a good predictor of how great a risk a particular crab poses to a hermit crab, even if such stimuli would not allow a hermit crab to distinguish among different predatory crabs. In addition, we cannot rule out possible differences in metabolic rates between comparably sized herbivorous and predatory crabs that may have yielded different metabolite concentrations to which the hermit crabs were responding. However, we can say that hermit crabs were responding to scents released by a predatory crab that had not consumed conspecific hermit crabs, because the *Cancer* crabs were fed only fish for at least 48 h before testing. In addition, explicit tests with other prey taxa (clams) suggest that feeding rate is reduced in response to predator-specific scent rather than dietary metabolites, a strategy that would be more effective against generalist predators because recent past diet may be a less reliable predictor of predation risk (Smee & Weissburg 2006).

Our results add to the growing list of aquatic invertebrates that can distinguish chemical effluent released by predators from those released by related but nonpredatory species, including snails (Marko & Palmer 1991; Dix & Hamilton 1993) and barnacles (Palmer et al. 1982). The ability to distinguish such effluents is probably adaptive, in general, as an inappropriate defensive response to a nonthreatening stimulus may reduce time for other activities (Ydenberg & Dill 1986; Dill & Gillett 1991; Scarratt & Godin 1992; Dill & Fraser 1997). Reduced hiding time of hermit crabs in the presence of predatory crabs is consistent with elevated activity levels observed in other studies (Hazlett 1996a; Rittschof & Hazlett 1997). In addition, reduced hiding time when attacked by a shell-breaking crab is probably adaptive because hermit crabs will abandon their shell and flee when picked up by a large, shell-breaking *Cancer* crab (Jackman 1998).

Acknowledgments

We thank the director and staff at the Bamfield Marine Sciences Centre for their assistance, C. Bergstrom and M. Boeckner for statistical advice and comments on early drafts of this paper, I. Jong and two anonymous referees for helpful comments on the manuscript, and I. Jong and H. MacIntosh for kelp crabs and technical assistance. A.R.P. was supported by Natural Sciences and Engineering Research Council of Canada Discovery Grant A7245.

References

- Benoit, M. D., Peeke, H. V. S. & Chang, E. S. 1997. Use of chemical cues for shell preference by the hermit crab, *Pagurus samuelis*. *Marine and Freshwater Behaviour and Physiology*, **30**, 45–54.
- Bertness, M. D. 1981. Predation, physical stress, and the organisation of a tropical hermit crab community. *Ecology*, **62**, 411–425.
- Brönmark, C. & Hansson, L.-A. 2000. Chemical communication in aquatic systems: an introduction. *Oikos*, **88**, 103–109.
- Chiussi, R., Diaz, H., Rittschof, D. & Forward, R. B. 2001. Orientation of the hermit crab *Clibanarius antillensis*: effects of visual and chemical cues. *Journal of Crustacean Biology*, **21**, 593–605.
- Chivers, D. P. & Smith, R. J. F. 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. *Ecoscience*, **5**, 338–352.

- Cote, I. M.** 1995. Effects of predatory crab effluent on byssus production in mussels. *Journal of Experimental Marine Biology and Ecology*, **188**, 233–241.
- Dalesman, S. & Inchley, C. J.** 2008. Interaction between olfactory and visual cues affects flight initiation and distance by the hermit crab, *Pagurus bernhardus*. *Behaviour*, **145**, 1479–1492.
- Dicke, M. & Grostal, P.** 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. *Annual Review of Ecology and Systematics*, **32**, 1–23.
- Dill, L. M.** 1987. Animal decision-making and its ecological consequences: the future of aquatic ecology and behavior. *Canadian Journal of Zoology*, **65**, 803–811.
- Dill, L. M. & Fraser, A. H. G.** 1997. The worm re-turns: hiding behavior of a tubedwelling marine polychaete, *Serpula vermicularis*. *Behavioral Ecology*, **8**, 186–193.
- Dill, L. M. & Gillett, J. F.** 1991. The economic logic of barnacle *Balanus glandula* (Darwin) hiding behavior. *Journal of Experimental Marine Biology and Ecology*, **153**, 115–127.
- Dix, T. L. & Hamilton, P. V.** 1993. Chemically mediated escape behavior in the marsh periwinkle *Littoraria irrorata* Say. *Journal of Experimental Marine Biology and Ecology*, **166**, 135–149.
- Geller, J. B.** 1982. Chemically mediated avoidance response of a gastropod, *Tegula funebralis* (A. Adams), to a predatory crab, *Cancer antennarius* (Stimpson). *Journal of Experimental Marine Biology and Ecology*, **65**, 19–27.
- Gherardi, F., Tricarico, E. & Atema, J.** 2005. Unraveling the nature of individual recognition by odor in hermit crabs. *Journal of Chemical Ecology*, **31**, 2877–2896.
- Griffiths, C. L. & Richardson, C. A.** 2006. Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology*, **331**, 91–98.
- Hazlett, B. A.** 1996a. Organisation of hermit crab behaviour: responses to multiple chemical inputs. *Behaviour*, **133**, 619–642.
- Hazlett, B. A.** 1996b. Comparative study of hermit crab responses to shell-related chemical cues. *Journal of Chemical Ecology*, **22**, 2317–2329.
- Hazlett, B. A.** 1997. The organisation of behaviour in hermit crabs: responses to variation in stimulus strength. *Behaviour*, **134**, 59–70.
- Hazlett, B. A. & McLay, C.** 2005. Responses of the crab *Heterozius rotundifrons* to heterospecific chemical alarm cues: phylogeny vs. ecological overlap. *Journal of Chemical Ecology*, **31**, 671–677.
- Hazlett, B. A. & Rittschof, D.** 2000. Predation-reproduction conflict resolution in the hermit crab, *Clibanarius vittatus*. *Ethology*, **106**, 811–818.
- Jackman, R.** 1998. *Life at the Edge of the Sea* (video). New York: Thirteen/WNET.
- Jacobsen, H. P. & Stabell, O. B.** 2004. Antipredator behaviour mediated by chemical cues: the role of conspecific alarm signalling and predator labelling in the avoidance response of a marine gastropod. *Oikos*, **104**, 43–50.
- Jennions, M. D., Backwell, P. R. Y., Murai, M. & Christy, J. H.** 2003. Hiding behaviour in fiddler crabs: how long should prey hide in response to a potential predator? *Animal Behaviour*, **66**, 251–257.
- Jensen, G. C.** 1995. *Pacific Coast Crabs and Shrimp*. Monterey, California: Sea Challengers.
- Kats, L. B. & Dill, L. M.** 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**, 361–394.
- Marko, P. B. & Palmer, A. R.** 1991. Responses of a rocky shore gastropod to the effluents of predatory and non-predatory crabs: avoidance and attraction. *Biological Bulletin*, **180**, 363–370.
- Palmer, A. R., Szymanska, J. & Thomas, L.** 1982. Prolonged withdrawal: a possible predator evasion behavior in *Balanus glandula* (Crustacea, Cirripedia). *Marine Biology*, **67**, 51–55.
- Reese, E. S.** 1969. Behavioral adaptations of intertidal hermit crabs. *American Zoologist*, **9**, 343–355.
- Rittschof, D.** 1980. Chemical attraction of hermit crabs and other attendants to simulated gastropod predation sites. *Journal of Chemical Ecology*, **6**, 103–118.
- Rittschof, D. & Hazlett, B. A.** 1997. Behavioural responses of hermit crabs to shell cues, predator haemolymph and body odour. *Journal of the Marine Biological Association of the United Kingdom*, **77**, 737–751.
- Rittschof, D., Tsai, D. W., Massey, P. G., Blanco, L., Kueber, G. L. & Haas, R. J.** 1992. Chemical mediation of behavior in hermit crabs: alarm and aggregation cues. *Journal of Chemical Ecology*, **18**, 959–984.
- Scarratt, A. M. & Godin, J. G. J.** 1992. Foraging and antipredator decisions in the hermit crab *Pagurus acadianus* (Benedict). *Journal of Experimental Marine Biology and Ecology*, **156**, 225–238.
- Schmitt, R. J.** 1981. Contrasting anti-predator defenses of sympatric marine gastropods (family Trochidae). *Journal of Experimental Marine Biology and Ecology*, **54**, 251–263.
- Smee, D. & Weissburg, M.** 2006. Hard clams (*Mercenaria mercenaria*) evaluate predation risk using chemical signals from predators and injured conspecifics. *Journal of Chemical Ecology*, **32**, 605–619.
- Stenzler, D. & Atema, J.** 1977. Alarm response of the marine mud snail, *Nassarius obsoletus*: specificity and behavioral priority. *Journal of Chemical Ecology*, **3**, 159–171.
- Trussell, G. C. & Nicklin, M. O.** 2002. Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology*, **83**, 1635–1647.
- Turner, A. M., Fetterolf, S. A. & Bernot, R. J.** 1999. Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. *Oecologia*, **118**, 242–247.
- Vermeij, G. J.** 1978. *Biogeography and Adaptation. Patterns of Marine Life*. Cambridge, Massachusetts: Harvard University Press.
- Watson, G. J., Hamilton, K. M. & Tuffnail, W. E.** 2005. Chemical alarm signalling in the polychaete *Nereis (Neanthes) virens* (Sars) (Annelida: Polychaeta). *Animal Behaviour*, **70**, 1125–1132.
- Ydenberg, R. C. & Dill, L. M.** 1986. The economics of fleeing from predators. *Advances in the Study of Behavior*, **16**, 229–249.
- Zeil, J. & Hemmi, J.** 2006. The visual ecology of fiddler crabs. *Journal of Comparative Physiology A*, **192**, 1–25.