NOTE

Predator classification by the sea pen *Ptilosarcus gurneyi* (Cnidaria): role of waterborne chemical cues and physical contact with predatory sea stars

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Abstract: Using laboratory and field experiments we examined the defensive behaviour of the sea pen *Ptilosarcus gurneyi* (Gray) towards three species of sea stars representing three levels of predatory threat. In the laboratory we first quantified the behaviour of *P. gurneyi* following physical contact with the sea stars *Dermasterias imbricata* (specialist predator), *Pycnopodia helianthoides* (generalist predator), and *Pisaster ochraceus* (nonpredator). Whereas the majority (73%) of the sea pens rapidly burrowed into the sediment following contact with *D. imbricata*, their response to *P. helianthoides* was highly variable and only 23% exhibited burrowing. In contrast, the response of *P. gurneyi* to *P. ochraceus* was weak and similar to that elicited by contact with a glass rod (control). Also, whereas the majority of sea pens displayed colony-wide bioluminescent flashes towards *D. imbricata* and *P. helianthoides*, their responses to *P. ochraceus* and the control were weaker and more localized. We subsequently examined whether waterborne predator chemical cues alone could trigger the defensive responses of *P. gurneyi* to *D. imbricata* and *P. helianthoides*, using laboratory bioassays of varying stimulus intensity. Interestingly, although exposure to chemical cues from predatory sea stars did not elicit any defensive response in *P. gurneyi*, subsequent physical contact with these predators triggered complete burrowing. Field bioassays using SCUBA yielded similar results, as *P. gurneyi* did not respond to the proximity of predators but rather delayed its response until physical contact occurred. Our study thus provides the first experimental evidence of predator-classification abilities in cnidarians and suggests that physical contact with predatory sea stars is required to trigger defensive behaviours in *P. gurneyi*.

Résumé : Des expériences en laboratoire et en nature nous ont permis d'étudier le comportement de défense de la plume de mer *Ptilosarcus gurneyi* (Gray) face à trois espèces d'étoiles de mer représentant trois niveaux de menace. En laboratoire, nous avons d'abord quantifié le comportement de *P. gurneyi* à la suite d'un contact physique avec les étoiles de mer, *Dermasterias imbricata* (prédateur spécialiste), *Pycnopodia helianthoides* (prédateur généraliste) et *Pisaster ochraceus* (non prédateur). Alors que la majorité des plumes de mer (73 %) se sont rapidement enfouies dans les sédiments après contact avec *D. imbricata*, leur réaction en présence de *P. helianthoides* s'est avérée très variable et seulement 23 % ont eu un comportement d'enfouissement. La réaction de *P. gurneyi* face à *P. ochraceus* était faible et semblable à celle obtenue au contact de tiges de verre (témoins). De plus, alors que la majorité des plumes de mer ont émis des éclairs bioluminescents à l'échelle de la colonie en présence de *D. imbricata* et de *P. helianthoides*, leurs réactions étaient moins intenses et plus localisées en présence de *P. ochraceus* et des témoins. Nous avons par la suite vérifié si des stimulus chimiques transportés dans l'eau pouvaient à eux seuls déclencher les réactions de défense de *P. gurneyi* en présence de *D. imbricata* et de *P. helianthoides* au cours de tests en laboratoire avec des stimulus d'intensité variable. Étonnamment, bien que l'exposition à des stimulus chimiques n'ait pas déclenché de réaction de défense chez *P. gurneyi*, un contact physique subséquent avec ces prédateurs a provoqué l'enfouissement complet. Des expériences de plongée sous-marine en nature ont donné des résultats semblables et *P. gurneyi* n' a pas réagi à la proximité des prédateurs tant qu'il n'y a pas eu de contact physique. C'est la première fois que la capacité des cnidaires de « classifier » leurs prédateurs est démontrée expérimentalement; nos résultats indiquent aussi qu'il faut un contact physique avec les étoiles de mer prédatrices pour qu'il y ait une réaction de défense chez *P. gurneyi*.

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Introduction

Predation has favoured the development of an astonishing array of defensive morphologies and behaviours in prey over evolutionary time (Edmunds 1974). These defensive traits often entail direct energetic costs as well as indirect costs such as a reduction in feeding opportunities (Lima and Dill 1990). Presumably because of these costs, prey have acquired the ability to adjust the intensity of their defensive responses to changes in predation-risk level (Lima and Dill 1990) or to the relative threat different predators represent (Legault and Himmelman 1993). In aquatic and marine environments, numerous prey animals display defensive behaviours upon detecting waterborne chemical cues from predators (reviewed by Kats and Dill 1998). For example, the gastropod *Olivella biplicata* burrows into the sediment upon detecting chemical cues from predatory asteroids (Phillips 1977). Such chemically mediated defensive behaviours are likely to be most advantageous to prey that have a low probability of surviving predatory attack (e.g., slow-moving or sessile prey), as they allow prey to respond to predatory threat at a distance, before life-threatening encounters with predators take place.

Although chemosensory assessment of predation risk is widespread in prey animals, among marine invertebrates the majority of studies have focused on molluscs, crustaceans, and echinoderms (Kats and Dill 1998). Surprisingly few studies have examined the behavioural responses of other invertebrate phyla, especially those lacking a developed central nervous system, to waterborne chemical cues from predators. In their extensive review, Kats and Dill (1998) report on only two studies examining the response of cnidarians to chemical cues from predators: the swimming escape response of the anemone *Stomphia coccinea* to the sea star *Dermasterias imbricata* (Yentsch and Pierce 1955) and the tentacle withdrawal of the anemone *Anthopleura elegantissima* in response to the nudibranch *Aeolidia papillosa* (Howe and Harris 1978). Although these studies indicate that these cnidarians can detect and respond to chemical cues from predators, whether they can differentiate predators from nonpredators, and how general are their responses, remain uncertain.

The orange sea pen, *Ptilosarcus gurneyi* (Gray), is a sessile colonial anthozoan found in dense aggregations on subtidal sandy bottoms along the coasts of the eastern Pacific Ocean from southern California to Alaska (Gotshall 1994). *Ptilosarcus gurneyi* has a thick peduncle, mostly buried into the substrate, over which is deployed a rachis bearing several paired lateral leaves (pinnea). Sea pens are best known for their spectacular bioluminescent displays, which range in intensity from single polyp flashes to colony-wide flashes characterized by rapidly moving (up to 25 $cm \cdot s^{-1}$) waves along the surface of the rachis (Davenport and Nicol 1955; Morin 1976). The bioluminescent response is controlled by a neural network that connects the individual polyps (Davenport and Nicol 1955; Cormier et al. 1974; Morin 1976). Although the functional significance of bioluminescence in sea pens remains unclear, some believe that it may play a defensive role against visual predators such as fishes (Morin 1976). Like other sea pens, *P. gurneyi* is a passive suspension feeder whose diet consists mainly of phytoplankton captured by the autozooids on the ventral surface of the leaves (Best 1988). Siphonozooids, located along the central axis on the dorsal surface of the rachis, provide ventilation to the colony by conducting water through a series of canals that extend through the animal (Davenport and Nicol 1955; Kozloff 1993). *Ptilosarcus gurneyi* can contract its body and burrow into the sediment by expelling water and mucus from its hydroskeleton through the siphonozooids (Kozloff 1993). Interestingly, *P. gurneyi* alternately expands for feeding and contracts into the sediment at irregular intervals, a behavioural pattern apparently unrelated to environmental factors such as current velocity, turbidity, and light level (Birkeland 1974; Dickinson 1978). Although the ecological significance of this behavioural rhythm is uncertain, burrowing could allow *P. gurneyi* to be less conspicuous to its main predators (nudibranchs and sea stars), which use chemotaxis to locate their prey (Birkeland 1974). That burrowing may be an escape response to predators is indicated by field observations of *P. gurneyi* contracting into the sediment when attacked by the sea star *Hippasteria spinosa* (Mauzey et al. 1968). However, it is not known whether this burrowing response is triggered exclusively by predatory sea stars. Preliminary laboratory observations indicate that *P. gurneyi* displays defensive behaviours, including complete burrowing, following physical contact with predatory sea stars and responds more strongly to predatory than to nonpredatory sea stars (K. Attridge, Bamfield Marine Station Student report, unpublished data). It remains unclear, however, whether the defensive behaviour elicited by predatory sea stars is triggered by physical contact per se or by waterborne chemical cues naturally exuded by sea stars (e.g., saponins; Mackie et al. 1968).

In the present study, laboratory and field experiments were used to examine the defensive behaviours exhibited by *P. gurneyi* towards selected predatory and nonpredatory sea stars. Specifically, we examined the behavioural response of *P. gurneyi* to tactile stimulation by the predatory sea stars *D. imbricata* and *Pycnopodia helianthoides*, as well as the nonpredatory sea star *Pisaster ochraceus*. We further examined whether exposure to waterborne chemical cues exuded by *D. imbricata* and *P. helianthoides* can trigger defensive responses in *P. gurneyi*.

Materials and methods

Collection site and study animals

Using SCUBA, we collected sea pens (*P. gurneyi*; $n = 32$, 3–13 cm in length) from 6–12 m depth at Scott's Bay in Barkley Sound, British Columbia, Canada (48°50′6″N, 125°8′42″W). We also collected the sea stars *D. imbricata* ($n = 10$, 7–10 cm in diameter), *P. helianthoides* ($n = 10$, 7–13 cm in diameter), and *P. ochraceus* ($n = 10$, 10–14 cm in diameter) from the same location. *Dermasterias imbricata* is a specialist predator that feeds mainly on anthozoans such as anemones and sea pens (Birkeland 1974). Conversely, *P. helianthoides* is a generalist predator that feeds on a wide array of prey, including sea urchins, bivalves, and sea cucumbers (Mauzey et al. 1968). However, whether *P. helianthoides* preys upon sea pens is not known. Finally, the intertidal sea star *P. ochraceus* is unlikely to be a predator of *P. gurneyi* because their habitats do not overlap. The sea pens and sea

stars were brought to the Bamfield Marine Station and maintained in tanks continuously supplied with seawater (11°C) under natural photoperiod. The sea pens used for the physical-contact experiment (n = 22) were individually placed in 75-L tanks (60 × 31 × 40 cm), whereas those used for the chemical-cue experiments (n = 10) were individually placed in 2.5-L tanks (13 × 13 × 15 cm). To allow the sea pens to burrow into the sediments, as they would under natural conditions, the bottom of each tank was covered with 4–5 cm of sandy substrate collected within the sea pen bed at Scott's Bay. The sea pens were allowed to acclimate to laboratory conditions for 24 h before being subjected to the bioassays. The sea stars were maintained continuously submerged in seawater tables in individual plastic containers (21 × 14 × 10 cm, with 2 mm plastic mesh sides and covers). Every 2 d, *P. ochraceus* and *P. helianthoides* were fed mussels (*Mytilus trossulus*), whereas *D. imbricata* were fed anemones (*A. elegantissima*). The sea stars were starved for 4 d before being used in the bioassays.

Behavioural responses to physical contact

The bioassay involved gently touching each sea pen on a leaf, halfway along the rachis, for 5 s with the tip of a sea star arm (either *D. imbricata*, *P. helianthoides*, or *P. ochraceus*) or a glass rod as a control for physical contact. The degree of contraction of the sea pens was recorded on an ordinal scale using the following categories: (*i*) no response, (*ii*) localized contraction of the rachis, (*iii*) partial burrowing, and (*iv*) complete burrowing. We also recorded bioluminescent responses of the sea pens using the following categories: (*i*) no response, (*ii*) a single polyp flash, (*iii*) a leaf flash, or (*iv*) a colony-wide flash. Each sea pen was subjected to all 4 treatments (3 sea stars and control) in a random order at 24-h intervals. The contraction and bioluminescent responses of the sea pens were compared among treatments using Friedman's non-parametric ANOVAs with individual sea pens as blocks, followed by Tukey-type multiple comparisons (Zar 1999).

Chemically mediated behavioural responses

To examine whether waterborne chemical cues alone could trigger defensive behaviours in *P. gurneyi*, we used laboratory bioassays in which two groups of 5 sea pens were exposed to various stimuli from either *D. imbricata* or *P. helianthoides*. Each sea pen was subjected to 4 bioassays in a random order and its response was recorded using the behavioural categories described above. After each bioassay the sea pens were left undisturbed for at least 24 h. As these bioassays were performed during the daytime, we did not record bioluminescent responses. The first bioassay examined the response of sea pens to the close proximity of predators. To physically isolate the sea pen from the sea stars, the experimental tanks were divided into two compartments using 2-mm plastic mesh. One sea star was placed in the compartment opposite to that of the sea pen and unscented seawater was allowed to flow through a polyethylene tube into the compartment containing the sea star so that the inflowing water circulated over the sea star before coming in contact with the sea pen. We observed each sea pen for 45 min and recorded its most intense behaviour. Finally, to determine if exposure to chemical cues from the sea stars would increase the tendency of sea pens to exhibit defensive behaviours in response to physical contact, we gently touched the sea pen on a leaf with a glass rod. As a control, the sea pens were tested in the absence of sea stars. The second bioassay involved slowly expelling from a Pasteur pipette either 5 mL of water collected from the ambulacral/oral regions of the sea stars or unscented seawater 5 mm from one of the sea pen's leaves. The behaviour of the sea pen was then recorded in the next 60 s. The third bioassay involved quantifying the behaviour of sea pens when exposed to concentrated sea star-scented water. For each trial we placed 4 sea stars in a 20-L overhead tank and interrupted the water flow for 45 min to allow chemical cues from the sea stars to accumulate. The sea star-scented water was then allowed to flow into the tank containing the sea pen through a polyethylene tube at a rate of ≈5 $L \cdot min^{-1}$. We observed the sea pen throughout the addition of the sea star-scented water (≈4 min) and recorded its most intense response. As a control, the same manipulations were performed, except that no sea stars were placed in the overhead tank. Finally, to assess the responsiveness of the sea pens, we subjected each sea pen to physical contact with *D. imbricata*, *P. helianthoides*, and a glass rod. Although the observation periods varied among bioassays, the most intense behavioural response displayed by the sea pens always occurred within the first 60 s of each bioassay. Hence, to make the bioassays more directly comparable, we used the data recorded during the first 60 s of each bioassay in the statistical analysis. The degrees of contraction of the sea pens were compared among bioassays using Friedman's non-parametric ANOVA followed by Tukey-type multiple comparisons (Zar 1999).

Field observations of sea pen defensive behaviours

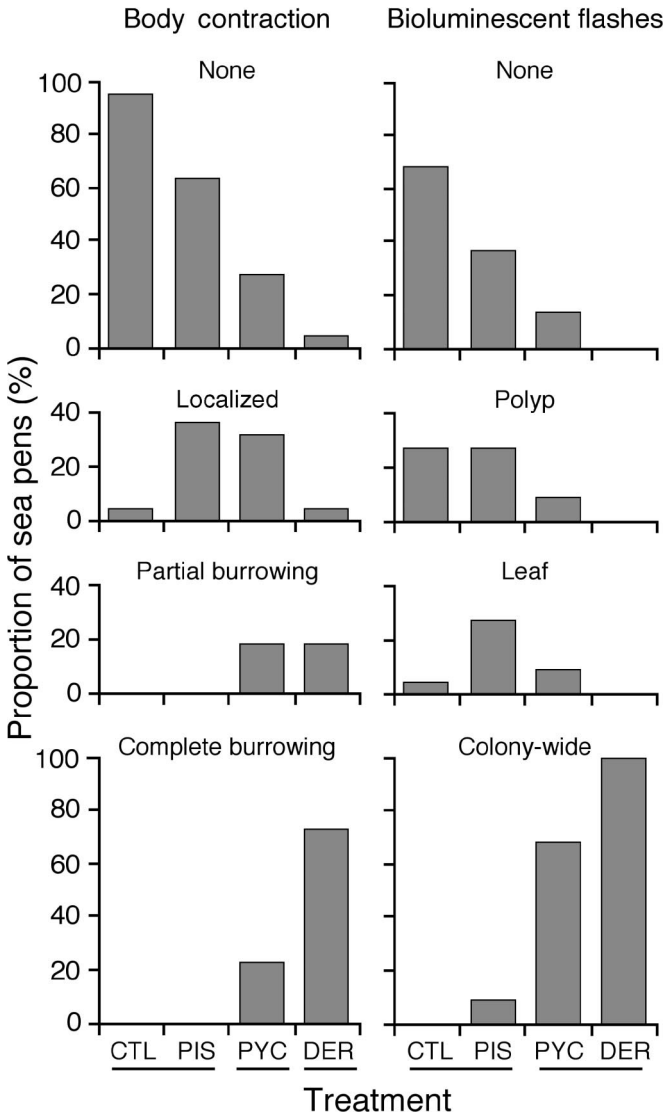
To examine how the results obtained in the laboratory could be extrapolated to natural conditions, we performed an in situ bioassay using SCUBA at 12 m depth at Scott's Bay. For this bioassay we used the same sea stars as in our laboratory experiments, after the latter had been starved for 3–4 d. Each trial involved haphazardly selecting a sea pen (1–26 cm in length) from the natural population, slowly approaching a sea star (*D. imbricata*, *P. helianthoides*, or *P. ochraceus*) to within 1 cm of the sea pen and then touching the latter on a leaf with one of the sea star's arms for 5 s. We then recorded the degree of contraction of the sea pens in the next 60 s using the same categories as in the laboratory. Because these observations were made during the daytime, we could not quantify the bioluminescent response. A total of 11 sea pens were tested with *D. imbricata*, 10 with *P. helianthoides*, and 10 with *P. ochraceus*. The responses of the sea pens to the different sea stars were compared using a Kruskal–Wallis test followed by Tukey-type multiple comparisons (Zar 1999).

Results

Behavioural responses to physical contact

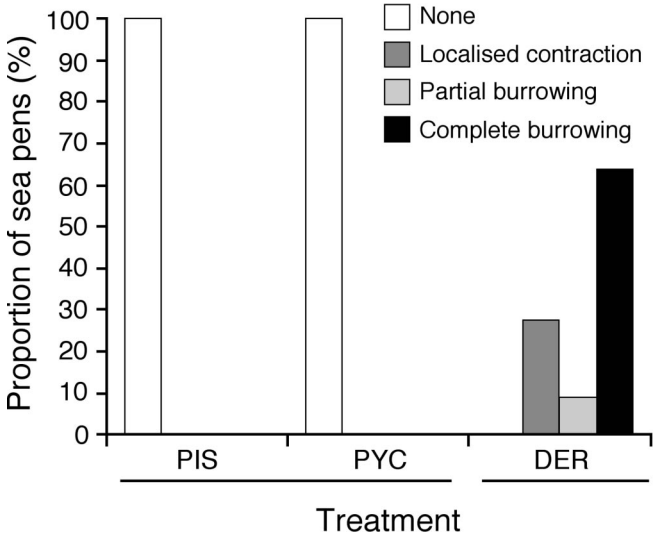
The degree of contraction of *P. gurneyi* triggered by physical contact varied markedly among treatments (Friedman's ANOVA, χ_r^2 = 49.5, $P < 0.001$; Fig. 1). *Dermasterias imbricata* and *P. helianthoides* elicited much stronger responses

Fig. 1. Behavioural and bioluminescent responses of the sea pen *Ptilosarcus gurneyi* following physical contact with the sea stars *Pisaster ochraceus* (PIS), *Pycnopodia helianthoides* (PYC), and *Dermasterias imbricata* (DER) under laboratory conditions. A glass rod was used as a control (CTL). Horizontal lines below group names depict those that are not significantly different as determined by Tukey-type multiple comparisons following Friedman's tests of overall significance ($\alpha = 0.05$).



in *P. gurneyi* than did *P. ochraceus* and the glass-rod control (Tukey-type multiple comparisons, $P < 0.05$). However, whereas most (73%) of the sea pens rapidly burrowed into the sediments subsequent to contact with *D. imbricata*, their response to *P. helianthoides* was more variable and only 23% exhibited burrowing (Fig. 1). In contrast, the responses of *P. gurneyi* to *P. ochraceus* were weak and similar to those elicited by contact with the glass rod ($P > 0.05$), none of which involved burrowing (Fig. 1). The bioluminescent responses of the sea pens also varied significantly among treatments (Friedman's ANOVA, $\chi_r^2 = 46.6$, $P < 0.001$; Fig. 1). *Dermasterias imbricata* and *P. helianthoides* triggered markedly more intense responses in the sea pens than did *P. ochraceus* and the control ($P < 0.05$). Whereas the majority of sea pens displayed colony-wide bioluminescent flashes towards *D. imbricata* and *P. helianthoides*, their responses to *P. ochraceus* and the control were weaker and more localized (Fig. 1).

Fig. 2. Behavioural responses of the sea pen *P. gurneyi* following physical contact with the sea stars *P. ochraceus* (PIS), *P. helianthoides* (PYC), and *D. imbricata* (DER) in a field bioassay performed using SCUBA at 12 m depth at Scott's Bay, Barkley Sound, British Columbia. Horizontal lines below group names depict those that are not significantly different as determined by Tukey-type multiple comparisons following a Kruskal–Wallis test of overall significance ($\alpha = 0.05$).



Chemically mediated behavioural responses

The degree of contraction of the sea pens varied significantly among bioassays (Friedman's ANOVAs, $\chi_r^2 = 15.0$, 3 df, $P = 0.0018$ for both *P. helianthoides* and *D. imbricata*). The response of the sea pens did not differ significantly among bioassays involving chemical cues from predatory sea stars alone (Tukey-type multiple comparisons, $P > 0.05$), none of the sea pens displaying defensive behaviours. In contrast, their responses to physical contact with *D. imbricata* and *P. helianthoides* were significantly stronger ($P < 0.05$) than those displayed in the other bioassays, all of the sea pens completely burrowing into the sediment. Finally, none of the sea pens displayed defensive behaviours in the control trials for each bioassay.

Field observations of sea pen defensive behaviours

As in our laboratory experiments, the sea pens tested in the field did not respond to the close proximity of sea stars but did so following physical contact with the latter. The degree of contraction of *P. gurneyi* triggered by physical contact varied markedly among sea stars (Kruskal–Wallis test, $H = 28.6$, 2 df, $P < 0.0001$; Fig. 2). *Dermasterias imbricata* triggered significantly more intense behaviours in *P. gurneyi* than in *P. helianthoides* or *P. ochraceus* (Tukey-type multiple comparisons, $P < 0.05$). The sea pens responded similarly to *P. helianthoides* and *P. ochraceus* ($P > 0.05$). Whereas the majority (64%) of the sea pens completely burrowed into the sediment when touched by *D. imbricata*, none did so when touched by *P. helianthoides* or *P. ochraceus*.

Discussion

Both our laboratory and field bioassays indicate that the sea pen *P. gurneyi* can differentiate between predatory and non-predatory sea stars and adjust the intensity of its defensive behaviour to the relative threat different sea stars represent. Whereas physical contact with the predatory sea star *D. imbricata* triggered complete burrowing in the majority of sea pens, contact with *P. helianthoides* and *P. ochraceus* elicited significantly weaker responses (Fig. 1). Although the responses of the sea pens to *D. imbricata* and *P. ochraceus* were similar in our laboratory and field bioassays, their response to *P. helianthoides* was slightly weaker in the field than in the laboratory (Figs. 1, 2). The cause of this discrepancy is unclear, although variations in the activity level of the sea stars and the feeding status of the sea pens in the field are possibilities. That *P. gurneyi* generally did not respond strongly to *P. helianthoides* suggests that this sea star may not be a common predator of sea pens. The bioluminescent response of *P. gurneyi* elicited by physical contact in our laboratory experiment also varied markedly among sea stars (Fig. 1). The sea pens displayed similar bioluminescent responses to *P. ochraceus* and the control, the majority of which were weak and localized. However, although the degree of contraction of *P. gurneyi* triggered by contact with *D. imbricata* was greater than that elicited by *P. helianthoides*, the sea pens displayed similar bioluminescent responses to these sea stars, suggesting that these responses may be uncoupled. This is also indicated by laboratory observations of the interaction between the sea pansy *Renilla koellikeri* and the predatory nudibranch *Armina californica* (Bertsch 1968) in which *R. koellikeri* contracted its rachis extensively when *A. californica* was crawling over its body but did not display bioluminescent responses until *A. californica* initiated active feeding. In contrast to body contractions, bioluminescence in sea pens and sea pansies is likely not a defensive mechanism against nonvisual predators such as sea stars and nudibranchs. Rather, bioluminescence could be an epiphenomenon of internal reactions such as those associated with communication between polyps in the colony through the neural network.

The results from our laboratory experiments indicate that exposure to waterborne chemical cues naturally exuded by predatory sea stars does not trigger defensive behaviours in *P. gurneyi*. This is further indicated by our field observations that *P. gurneyi* did not respond to the proximity of predators and only exhibited defensive behaviours following physical contact with predators. This contrasts with numerous studies showing that predator chemical cues alone trigger defensive responses in a variety of prey taxa, including cnidarians, subjected to bioassays similar to our study (reviewed by Kats and Dill 1998). However, the fact that exposure to a homogenate of the nudibranch *A. californica* also does not trigger defensive responses in the sea pansy *R. koellikeri* (Bertsch 1968) suggests that exposure to predator chemical cues alone may not trigger defensive responses in colonial cnidarians, unlike the solitary anemones (Yentsch and Pierce 1955). Conversely, other studies have shown that defensive responses in prey are only triggered upon detection of chemical cues from predators that are actively feeding on conspecific prey (e.g., Crowl and Covich 1990; Mathis and Smith 1993). For instance, the snail *Physella virgata* exhibits an avoidance response when exposed to water containing crayfish feeding on conspecific snails but not water containing crayfish alone or water containing crushed conspecific snails (Crowl and Covich 1990). Similarly, the anemone *A. elegantissima* only responds to chemical cues from the predatory nudibranch *Aeolidia cerata* if the latter has previously fed on conspecific anemones, presumably because the predator becomes chemically labeled with anemone chemical cues from its diet (Howe and Harris 1978). Conversely, the sculpin *Cottus cognatus* exhibits similar responses to predatory trout when the latter are fed different diets (Bryer et al. 2001). Hence, although chemically mediated defensive responses in prey are widespread, the cues that trigger these responses can vary markedly among prey, likely because of differences in their natural histories. Since this is the first study to examine the role of chemical cues from predatory sea stars in the defensive response of *P. gurneyi*, we focused our bioassays on predator chemical cues alone and thus did not feed sea pens to the predators before the bioassay. Hence, it remains unclear whether predators labeled with chemical cues from sea pens would trigger defensive responses in the latter. Interestingly, the results from our laboratory experiment suggest that exposure to predator chemical cues alone potentially enhances the intensity of the sea pens' response to subsequent physical contact with these predators. This is indicated by the greater frequency of complete burrowing responses elicited by physical contact with predatory sea stars in sea pens subjected to our chemical-cue bioassays than in those in our bioassay involving physical contact alone. Whether this pattern is real or due to chance, because of the smaller sample size in our chemical-cue bioassay, is unknown. That physical contact with predatory sea stars is required to trigger defensive responses in *P. gurneyi* raises questions as to what cues are used to differentiate between predators and non-predators. One possibility is that sea pens rely on differences in microtopography or the movement rate of sea stars' tube feet. Alternatively, sea pens may be responding to nondiffusable chemicals present on the surface of sea stars as periwinkles (*Littoraria irrorata*) do to mucus from predatory snails (Dix and Hamilton 1993). Finally, perhaps *P. gurneyi* can detect the chemical presence of predators at a distance but delays its burrowing response until attacked by predators. Further studies are needed to elucidate what cues trigger defensive behaviours in *P. gurneyi* and other pennatulaceans.

The ability to differentiate between predators and non-predators can have an important impact on the lifetime fitness of prey animals, as it allows them to alleviate the costs associated with unnecessary escape. By burrowing into the sediment, sea pens likely incur costs, as this (*i*) reduces feeding opportunities and (*ii*) re-expansion of the colony requires energy for the active pumping of water by the siphonozooids to fill the coelenteric spaces (Dickinson 1978). The predator-classification ability documented herein likely allows *P. gurneyi* to alleviate these costs by restricting its burrowing response to life-threatening encounters with predatory sea stars. Given that *P. gurneyi* is sessile, responding at a distance to the scent of approaching predators would seem advantageous, as burrowing into the sediment likely decreases its conspicuousness to predators. However, our results indicate that *P. gurneyi* does not initiate burrowing until physical contact with predatory sea stars occurs. Because the burrowing response of sea

pens is quite rapid (generally within 60 s; personal observation) and *D. imbricata* rarely digs into the sediment to capture burrowed sea pens (Birkeland 1974), delaying burrowing until physical contact occurs could nonetheless be adaptive. As *P. gurneyi* are generally found in dense aggregations (Birkeland 1974; personal observation), burrowing upon detection of the scent of approaching predators without acquiring information on whether or not they are the target of the predatory attack could lead to inappropriate responses and unnecessary costs. Further studies are needed to determine whether *P. gurneyi* similarly delay their escape response until physical contact occurs with predatory sea stars that excavate burrowed sea pens (e.g., *Hippasteria spinosa* and *Mediaster aequalis*; Mauzey et al. 1968).

Although predator-classification abilities are documented in several invertebrate and vertebrate taxa (Kats and Dill 1998), our study provides the first experimental evidence of such abilities in cnidarians, one of the most ancient metazoan phyla in the animal kingdom. Whether the ability to distinguish between predators and non-predators has been selected for in ancestral invertebrates or has evolved independently multiple times remains unclear. Further studies on *P. gurneyi* and other cnidarians would provide valuable insight into the evolution of predator-classification abilities and chemosensory assessment of predation risk in prey animals.

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