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Chemotactic tube-foot responses of the spongivorous sea star *Perknaster fuscus* to organic extracts of sponges from McMurdo Sound, Antarctica

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Abstract: Studies were continued to investigate the ability of secondary metabolites sequestered in Antarctic sponges to cause feeding deterrent responses (tube foot retractions) in a common predator of Antarctic sponges, the sea star *Perknaster fuscus*. Lipophilic (dichloromethane/methanol) and hydrophilic (methanol/water) extracts of 15 new species of Antarctic marine sponges were tested for their ability to induce sustained tube-foot retraction. One additional species, *Cinchyra antarctica*, was re-tested from a previous study because we discovered a colour morph that was of comparative interest. Employing established protocols, sponge extracts were imbedded in silicone and presented to an extended tube-foot on the tip of a glass rod. Extracts of ten of the 15 new species of sponges (67%) caused significantly longer tube-foot retractions than controls. Among all sponges tested, significant tube-foot retraction activity was primarily associated with dichloromethane/methanol extracts (eleven sponge species or colour morphs), while significant tube-foot retraction activity was less common in response to methanol/water extracts (three sponges species or colour morphs). Both lipophilic and hydrophilic extracts from the sponges *C. antarctica* (yellow morph) and *Scolymastia joubini* elicited significant tube-foot retraction activity, suggesting that more than one compound from these species might elicit tube-foot retractions in *P. fuscus*. Overall these findings lend considerable support to the hypothesis that there has been significant evolutionary selection for chemical defences among Antarctic marine sponges in McMurdo Sound, in contrast to earlier biogeographic selection models that predicted low levels of chemical defences in polar marine invertebrates.

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Introduction

Marine sponges, particularly temperate and tropical species, are well known for their ability to produce secondary metabolites (reviewed by Faulkner 1978, 1998). While literally thousands of sponge secondary metabolites have been identified, comparatively little is known about their functional significance (Bakus *et al.* 1986, Paul 1992, Pawlik 1993, McClintock & Baker 1997a). There is now compelling evidence that sponge metabolites are employed to prevent fouling and predation, and may also be utilized as allelochemics to mediate competition for space (Bakus *et al.* 1986, Paul 1992, Pawlik 1993, McClintock *et al.* 1994, Pawlik *et al.* 1995, McClintock & Baker 1997a).

The Antarctic marine benthos has a rich and diverse sponge fauna (Koltun 1970, Dayton *et al.* 1974, Dayton 1979). This system has been environmentally stable over the past 22 million years (Dayton *et al.* 1994). Biotic factors such as predation and competition appear most important in structuring the benthos, including the ecologically dominant sponge communities (Dayton *et al.* 1974). Early biogeographic models, based on latitudinal patterns of fish predation, predicted an inverse correlation between latitude and chemical defences in marine invertebrates (Bakus & Green 1974). While spongivorous fishes are rare in Antarctic waters (Eastman 1993), predation by spongivorous sea stars is high, even compared to temperate and tropical marine systems (McClintock 1994). Moreover, the long lifespans that characterize many Antarctic marine invertebrates (Clarke 1983), create conditions where predation intensity may average out over lifespan to be similar to temperate or even tropical species (McClintock & Baker 1997a). Dramatic plankton blooms contribute substantial seasonal fouling pressure to sponges (Stoecker *et al.* 1995, Moeller 1998), while dense populations of sponges ensure ongoing competition for space and food resources (Dayton *et al.* 1974). Collectively, these conditions are likely to favour species that have evolved chemical defences.

As outlined above, predation by spongivorous sea stars is important in Antarctic benthic communities (Dayton *et al.* 1974, McClintock 1994). Sea stars often feed by extruding their cardiac stomachs over their prey (Hyman 1955). Because of this unique stomach extension feeding mechanism, feeding assays typically used with other predators are less appropriate for sea stars. This is particularly true in Antarctica where sea star predation events on sponges occur over very long time periods (McClintock & Baker 1997a). Consequently, it was necessary to develop a new bioassay to detect the presence of, and evaluate the importance of, chemical defences against sea star predators in Antarctic sponges. We have previously developed a bioassay that takes advantage of the tube-foot retraction response in *Perknaster fuscus*, a common Antarctic sea star that is a specialist predator on sponges (McClintock *et al.* 1994). It is generally accepted that tube-feet are a primary site for chemical reception in echinoderms (Lawrence 1975, Sloan & Campbell 1982, McClintock *et al.* 1984) and tube-foot chemoreception in sea stars is primarily a defensive response (Sloan 1980a, 1980b). In this assay, sponge extracts suspended in a silicone matrix are coated on to the end of a glass rod. Rods with extracts or controls are placed in contact with an extended tube-foot and the retraction time of the tube-foot measured. McClintock *et al.* (1994) used this assay to determine tube-foot responses towards extracts of 18 Antarctic sponge species, most of which were known to be eaten by or avoided by sea stars in nature (Dayton *et al.* 1974, Dayton 1989). *Mycale acerata*, which is a rapidly growing species and the primary prey of *P. fuscus* (Dayton *et al.* 1974), was the only species that did not elicit a significant tube-foot retraction response. Extracts of *Homaxinella balfourensis*, another rapidly growing sponge which is also preyed upon by *P. fuscus* (Dayton *et al.* 1974, Dayton 1989), elicited only a very weak tube-foot retraction response. The other 16 sponge species are all relatively slow growing and are not typically consumed by *P. fuscus* (Dayton *et al.* 1974, Dayton 1979). Consequently, there is a strong correlation between tube-foot retraction activity and apparent unpalatability in nature.

The purpose of the present study was to expand this database on chemical feeding deterrent properties of Antarctic marine sponges, and therefore to provide a more robust sample size for biogeographic comparisons. We report on the incidence of bioactivity in an additional 15 sponge species, bringing the collective total number examined to 33 species (McClintock *et al.* 1994).

Materials and methods

Collections of sponges were conducted using SCUBA between depths of 20 and 35 m. The sponges were collected at sites on both the east and west sides of McMurdo Sound (see McClintock *et al.* 1994 for map). *Cinachyra antarctica* (Carter, 1872) (yellow and white morph), *Myxodoryx hanitschi* (Kirkpatrick, 1908) and *Scolymastra joubini* (Topsent, 1910) were collected directly in front of McMurdo Station near the seawater intake jetty. *Clathria nidificata* (Kirkpatrick, 1907), *Hemigellius fimbriatus* (Kirkpatrick, 1907) and *Microxina charcoti* (Topsent, 1910) were collected at New Harbor. *Isodictya spingerosa* (Kirkpatrick, 1907) and *Xestspongia* sp. were collected at Arrival Heights just 0.5 km north of McMurdo Station. *Ectyodoryx ramilobosa* (Topsent, 1916) was collected at Little Razorback Island, *c.* 25 km north of McMurdo Station. *Phorbus areolata* (Thiele, 1905) was collected at Marble Point and *Haliclona scotti* (Kirkpatrick, 1907) *c.* 20 km north-west of Marble Point at Granite Harbor. The locations and depths of collections of five unidentified sponges are given in Table I along with pertinent descriptive information. Voucher specimens were donated to the collection of Dr. Robert van Soest (University of Amsterdam). Specimens of the spongivorous sea star *Perknaster fuscus* were collected from Arrival Heights at depths ranging from 20–35 m.

Organic extracts were prepared using a modification of the methods of McClintock *et al.* (1994). Sponges were freeze-dried and then approximately 10 g dry wt broken into small pieces, weighed, and then extracted twice with 25 ml dichloromethane/methanol (1:1) for 12 h. The resulting extracts were mixed and the solvents removed by evaporation under reduced pressure to yield a lipophilic extract. The freeze-dried material was then subsequently extracted with methanol/water (1:1) in a similar manner to yield a hydrophilic extract.

Tube-foot retractions bioassays were conducted using the methods described in McClintock *et al.* (1994). Briefly, extended sensory tube-feet were presented to both hydrophilic and lipophilic sponge extracts imbedded in a silicone matrix (1:1) on the tip of a glass rod and retraction response recorded (time of sustained tube-foot retraction) if they occurred. Experimental treatments consisted of conducting ten tube-foot trials for each extract or control. After each five randomized trials, the sea star being tested was replaced with a new individual. A total of 14 sea stars were rotated through the bioassays. This ensured that multiple individuals were assayed with each extract or control. However, because the tube-foot response within an individual animal is localized to an individual tube-foot (Sloan 1980a, 1980b), individual

Table I. Unidentified sponge species. Collection sites, collection depth, and gross morphology of the five unidentified sponge species included in the present study.

Species number	Collection site	Depth (m)	Morphology
6	Little Razorback Island	24	small white staghorn-shape, multiple oscula running along long axis
20	Little Razorback Island	24	low profile, yellow, slimy
21	Marble Point	30	short siliceous spicules emerging, tubular shaped with multiple tubes unified at base, white with tan base
23	Marble Point	38	(not recorded)
24	McMurdo station jetty	39	round, dense, multiple small oscula, white, spicules clumped

tube-foot responses were treated as independent samples. We chose to conduct two controls ($n = 30$ trials for each control). One consisted of presenting silicone alone on the glass rod, and a second that consisted of presenting only the glass rod to the extended tube-foot. We chose not to conduct an attractant control, as we had previously demonstrated the lipophilic extract of fish muscle (*Trematomus bernacchii*) did not cause significant tube foot retractions in *Perknaster fuscus* ($n = 510$ trials across 51 sea stars) (McClintock *et al.* 1994).

We compared the two control treatments (silicone and glass rod) using a Mann-Whitney *U*-test in order to determine if they could be combined for comparisons with experimental treatments. A Kruskal-Wallis One-Way Analysis of Variance was employed to determine whether there were any significant differences between control and experimental treatments. When we found significant differences, pairwise comparisons were conducted using a Mann-Whitney *U*-test.

Results

Tube-foot retraction times following exposure to glass rods alone or glass rods with silicone were very low (< 5 sec) and no significant ($P > 0.05$) difference was found between tube-foot response times of either control group. Therefore, we combined the two control data sets for comparison with tube-foot retraction times for sponge extracts imbedded in silicone.

The spongivorous sea star *Perknaster fuscus* displayed significantly ($P < 0.05$) longer sensory tube-foot retractions when exposed to the organic extracts of 12 of the 16 species of tested sponges (Fig. 1). No significant ($P > 0.05$) tube foot retraction responses were detected in the extracts from the sponges *Haliclona scotti, Hemigellius fimbriatus, Microxina charcoti, Myxodoryx hanitschi* and one unidentified sponge (#21).

The strongest and most consistent tube-foot retraction responses were noted in lipophilic extracts (11 of the species or morphs and nine of these caused retractions lasting 30 s or longer), while significant ($P < 0.05$) and strong tube-foot retractions (> 30 s) occurred in response to hydrophilic extracts of three sponges including the yellow morph of *Cinachyra antarctica, Clathria nidificata* and *Scolymastra joubini.* Both the lipophilic and hydrophilic extracts of *S. joubini* and the yellow morph of *C. antarctica* elicited significant ($P < 0.05$) tube-foot retractions. However, no significant ($P > 0.05$) tube foot retraction activity was detected in the hydrophilic extract of the white morph of *C. antarctica.*

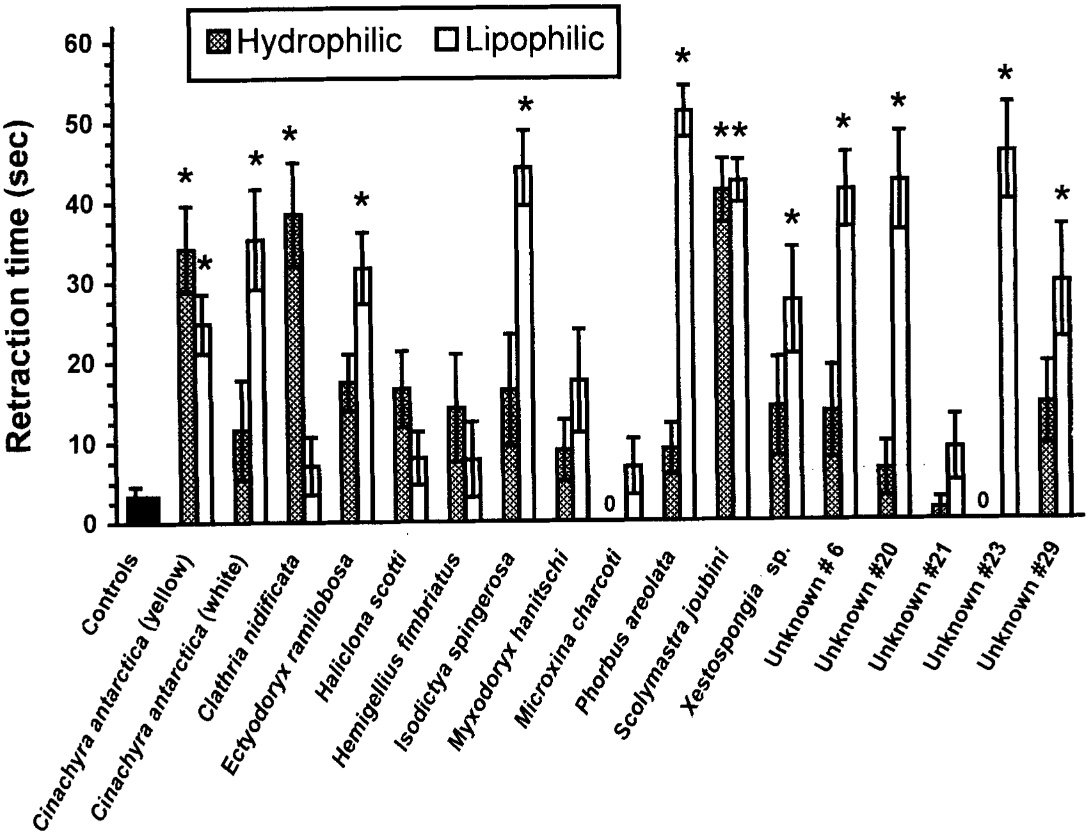

Fig. 1. Chemotactic tube-foot responses of the Antarctic sea star *Perknaster fuscus* to hydrophilic and lipophilic extracts of Antarctic sponges. Each bar shows the mean tube-foot retraction time (sec) for 10 trials, except the control where $n = 60$ trials. Asterisks indicate statistical significance ($P < 0.05$; Kruskal-Wallis One-Way Analysis of variance ranks followed by pairwise comparison with a Mann-Whitney *U*-test) when compared with the control. "0" indicates that assays were performed but with mean retraction times = 0 s.

Discussion

Previous examinations of tube-foot retraction responses in the spongivorous sea star *Perknaster fuscus* indicate that sensory tube-foot contact with mechanical or feeding stimulants may cause short term retractions (5–10 s), similarly observed in other sea stars (Sloan 1980a, McClintock *et al.* 1994). However, these are considered to be innate defensive responses that occur when sea stars detect gross sensory changes in their environment (Sloan 1980a, 1980b). More sustained retraction responses, such as those observed in the present study following chemotactic exposure to some organic sponge extracts, reflect the presence of compounds that are irritants and may cause sea stars to pull their tube-feet away from sponges following contact. As noted above, our previous study (McClintock *et al.* 1994) demonstrated a strong correlation between tube foot retraction in the Antarctic spongivorous sea star *Perknaster fuscus* and earlier, *in situ* observations of *P. fuscus* feeding preferences in McMurdo Sound (Dayton *et al.* 1974). The present study extends this database to additional, common sponge species in McMurdo Sound for which feeding deterrence information is critical for drawing community-wide conclusions. However, for most of these species, no field data on their susceptibility to predation are available. Based on the strong correlation observed previously, we predict that those species eliciting significant tube foot retraction responses are chemically defended from sea star predation.

The Antarctic sea stars *Perknaster fuscus* and *Odontaster validus* (Koehler) use their sensory tube-feet to sense water-borne metabolites released from the Antarctic soft coral *Alcyonium paessleri* (allomones), triggering an avoidance response even before physical contact with potential sessile prey (Slattery *et al.* 1998). It is not known whether some Antarctic sponges may also leach defensive metabolites into sea water. However, the presence of significant sea star tube-foot retraction responses associated with hydrophilic extracts (McClintock *et al.* 1994, present study) indicates that some sponge feeding deterrents are probably diffusible in sea water. That many sponge extracts causing tube-foot retractions are lipophilic, and therefore not water soluble, would suggest that sponges also rely on chemotactile interactions with potential predators.

Considerable variation was detected in both quantitative and qualitative aspects of the tube-foot retraction responses of *Perknaster fuscus* to sponge extracts. In the present study, significant tube-foot retraction responses following exposure to lipophilic extracts were most commonly observed. However, this may not reflect a uniform pattern across Antarctic sponges, as McClintock *et al.* (1994) detected only 39% of 18 Antarctic sponges had activity in their hexane extract, the most lipophilic extract tested. This difference may be attributable in part to the three solvent systems employed in that study (hexane, chloroform, methanol). In contrast to hexane extracts, a high degree of tube-foot bioactivity was detected in response to the chloroform extracts of Antarctic sponges (73% of the species tested; McClintock *et al.* 1994), a solvent that is moderately lipophilic. Collectively it appears that Antarctic sponge metabolites responsible for tube-foot retraction responses in spongivorous sea stars may be hydrophilic as well as lipophilic in nature.

Comparisons of the tube-foot retraction responses of *Perknasterus fuscus* presented with extracts of either white or yellow morphs of the sponge *Cinachyra antarctica* revealed significant differences. The white sponge morph had potent bioactivity in only the lipophilic extract, while the yellow morph of the sponge had significant tube-foot bioactivity in both lipophilic and hydrophilic extracts. While we did not differentiate which colour morph was examined in our earlier study (McClintock *et al.* 1994), hexane, chloroform and methanol extracts all caused significant tube-foot retractions in *P. fuscus*. Nonetheless, activity was twice as high in the chloroform and methanol extracts. Our observations suggest that there may be chemomorphs of this species (Bergquist 1978). Moreover, it is possible that the pigment responsible for coloration of the yellow morph is itself responsible for the tube-foot activity. Pigments from both the Antarctic sponges *Latrunculia apicalis* and *Kirkpatrickia variolosa* cause tube-foot retractions responses in the sea star *Perknaster fuscus* (McClintock & Baker 1997a).

The specific compounds responsible for tube-foot retraction responses in this suite of Antarctic sponges remains to be determined. Importantly, the bioactivity data presented for crude extracts can be used to guide the isolation and structural elucidation of specific deterrent compounds. A variety of bioactive compounds, some of which cause tube-foot retractions in sea stars, have been identified using standard chemical means from previously examined Antarctic sponges. These include diterpene metabolites from *Dendrilla membranosa* (Molinski & Faulkner 1987, 1988, Baker *et al.* 1993, 1994, 1995), variolins from *Kirkpatrickia variolosa* (Perry *et al.* 1994, Trimurtulu *et al.* 1994), discorhabdin pigments from *Latrunculia apicalis* (Yang *et al.* 1995, Baker *et al.* 1993, 1994), eribusenone from *Isodictya erinacea* (Moon *et al.* 1998), rhapsamine from *Isodictya setifera* (Jayatilake *et al.* 1997), and suberitoenones from *Suberites* sp. (Baker *et al.* 1997). A series of diketopiperizines and phenazine alkaloids from the bacterium *Pseudomonas aeruginosa* associated with the Antarctic sponge *I. setifera* have been identified indicating that bioactive compounds in Antarctic sponges may also be derived from bacterial symbionts (Jayatilake *et al.* 1996).

In contrast to the sponges examined in our previous study, the ecology of the Antarctic sponges examined in the present study is poorly known (i.e., only one of these sponges was studied by Dayton *et al.* (1974)). Nonetheless, these sponges are relatively common species that are conspicuous members of the benthic community (author's personal observations). Information on their chemical deterrent properties against sea star predators is critical for a more complete evaluation of the importance of such defences in these benthic communities. The ecology of only one of the sponges included in the present study has been examined in any detail. The volcano sponge *Scolymastra joubini* is a very large vase sponge that occurs at 33 m and deeper in McMurdo Sound and we observed strong tube-foot responses to both hydrophilic and lipophilic extracts of this species. Dayton *et al.* (1974) found that *S. joubini* was rarely attacked and eaten by *P. fuscus*, accounting for only 2.4% of total feeding observations by this spongivorous sea star.

Some studies have demonstrated predator-specificity in terms of the efficacy of chemical defences (Hay 1996, McClintock & Baker 1997b). Some Antarctic sponges, such as *M. acerata*, lack chemical defences against *P. fuscus* (McClintock *et al.* 1994) and appear to offset intense predation by this sea star through rapid growth (Dayton *et al.* 1974). Since sponge skeletal elements (spicules) do not deter fish predators (Chanas & Pawlik 1995), nor are they likely to defend against sea stars which extrude their cardiac stomach against the sponge pinacoderm (Dayton *et al.* 1974, McClintock 1994), chemical defences are likely to provide the main lines of defence in marine sponges.

The results of the present study extend the number of Antarctic marine sponges examined for sea star feeding deterrent properties to 33 species of which 82% cause tube-foot retractions. While much remains to be done to determine the specific chemical nature of the compounds responsible for feeding deterrence, the tube-foot responses observed in the present study when combined with our previous work (McClintock *et al.* 1994), clearly suggest that chemical defences are not uncommon among Antarctic sponges. This appears to also be the case for other groups of sessile or sluggish benthic marine invertebrates in Antarctica. Chemical defences against predators or fouling organisms have now been detected in representatives of the bryozoa, brachiopoda, ascidacea, nemertea, mollusca, and echinodermata (reviewed by McClintock & Baker 1997a, 1998). While earlier predictions suggested global patterns of chemical defences among marine sessile and sluggish marine invertebrate fauna (Bakus & Green 1974, Vermeij 1978) we feel it is more likely that patterns of chemical defences are likely to reflect mesoscale variability in predation, fouling or competition.

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