



Palatability and chemical defenses of sponges from the western Antarctic Peninsula

Kevin J. Peters^{1,*}, Charles D. Amsler¹, James B. McClintock¹,
Rob W. M. van Soest², Bill J. Baker³

¹Department of Biology, University of Alabama at Birmingham, 1300 University Blvd., Birmingham, Alabama 35294-1170, USA

²Zoological Museum of the University of Amsterdam, PO Box 94766, 1090 GT Amsterdam, The Netherlands

³Department of Chemistry, University of South Florida, 4202 East Fowler Ave., Tampa, Florida 33620-5240, USA

ABSTRACT: The present study surveyed the palatability of all sponge species that could be collected in sufficient quantities in a shallow-water area along the western Antarctic Peninsula. Of 27 species assayed, 78% had outermost tissues that were significantly unpalatable to the sympatric, omnivorous sea star *Odontaster validus*. Of those species with unpalatable outer tissues, 62% had inner tissues that were also unpalatable to the sea stars. Sea stars have often been considered as the primary predators of sponges in other regions of Antarctica, and their extra-oral mode of feeding threatens only the outermost sponge tissues. The observation that many of the sponges allocate defenses to inner tissues suggests the possibility that biting predators such as mesograzers, which could access inner sponge layers, may also be important in communities along the Antarctic Peninsula. In feeding bioassays with extracts from 12 of the unpalatable species in artificial foods, either lipophilic or hydrophilic extracts were deterrent in each species. These data indicate an overall level of chemical defenses in these Antarctic sponges that is comparable to, and slightly greater than, that found in a previous survey of tropical species.

KEY WORDS: Chemical defenses · Sponge · Antarctica · Predation · Optimal defense theory

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Sponges are abundant and ecologically dominant members of the Antarctic benthos that occur across a broad range of depths and are often characterized by circumpolar distributions (McClintock et al. 2005). Being sessile, sponges are at a distinct disadvantage when compared to motile organisms in terms of their ability to seek refuge or move away from threats that can include spatial competition (Engel & Pawlik 2000), fouling (Tsoukatou et al. 2007), or predation. Consequently, sponges and other groups of sessile marine invertebrates have evolved alternate modes of defense, including the incorporation of physical defenses (Chanas & Pawlik 1995, Huang et al. 2008) and/or the production of defensive secondary metabolites (Pawlik et al. 1995, Assmann et al. 2000, Kubanek et al. 2000, McClintock & Baker 2001, Furrow et al. 2003).

Marine predator–prey relationships have been interpreted within the context of several ecological theories (Cronin 2001, Amsler & Fairhead 2006). One of these is the optimal defense theory (ODT). The ODT considers variations in defenses within organisms and, assuming these defenses invoke some fitness cost to the organism, predicts when and where defenses will be allocated in lieu of internal competition for resources for growth and defense (Rhoades 1979). In an environment in which the predation risk is absent or low, the ODT predicts that there would be no benefit to producing defenses; however, in an environment in which predation risk is high, the cost of the defense could be outweighed by the benefit of being protected. If the probability of attack is high, the ODT predicts that defenses will be under strong positive selection. Conversely, if the cost of producing the defense is greater than the benefit obtained, then the ODT predicts that

*Email: kpeters@uab.edu

selection will favor the production of fewer defenses. At the level of the individual, ODT predicts that defenses will be allocated in higher concentrations to the most vulnerable and/or valuable tissues. This will vary between prey, depending on the type of predators influencing the evolution of defenses in the prey.

The shallow, nearshore waters of the Antarctic Peninsula are characterized by a rich and diverse benthos (Brand 1974, Barnes & Brockington 2003, Barnes 2005). The predominant predators of benthic marine sponges in this and other regions of Antarctica are sea stars (Dayton et al. 1974, McClintock et al. 2005), with an abundance of omnivorous sea star species that include sponges among a broad array of prey, as well as strictly spongivorous species (Dearborn 1977, McClintock 1994).

As sea stars are the dominant predators of Antarctic sponges they are likely the primary driving force in the evolution of anti-predator defenses. Accordingly, sponge defenses would be predicted to be differentially allocated within sponges such that they most effectively deter sea stars from feeding upon them. The mode of feeding of sea stars is unique in that each arm is equipped with rows of chemosensory tube feet that, upon contact, facilitate an evaluation of prey palatability (Sloan 1980). If a potential prey is subsequently deemed acceptable, sea stars then extrude their cardiac stomach directly against the surface of the prey to initiate extra-oral digestion. This unique extra-oral mode of feeding results in sea stars encountering only the outer surfaces of prey (Dearborn 1977). As such, the most vulnerable region of sponges attacked by sea stars is the exterior surface. Allocation of defenses to inner sponge tissues would not be an efficient utilization of resources, as sea stars encounter these regions of the sponge only after first digesting outer layers.

There are several different mechanisms by which sponges could be undesirable as food sources to predators. One possibility is found in the structural defenses that preclude predator access to palatable regions. This might be achieved by concentrating large, rigid spicules near the sponge exterior, preventing predators from accessing the softer layers beneath the spicules (van Alstyne & Paul 1992). While this could be an effective mechanism to deter predators, it also would require additional energy and resources to produce large protective spicules, in addition to possibly reducing surface area available to choanocytes that actively filter water and provide nutrition to the sponge. For sponges from the Gulf of Mexico and Caribbean Sea, studies have found little or no evidence of spicules providing significant feeding deterrence (Chanas & Pawlik 1995, Huang et al. 2008). Both of these studies utilized biting fish as predators. However, a study of temperate sponges found that spicules

can significantly deter feeding from a hermit crab predator (Hill et al. 2005). In Antarctica, where sea stars are the primary predators on sponges (Dayton et al. 1974), spicules appear to be an unlikely mechanism of defense. This may be related to the ability of sea stars to extrude their cardiac stomachs and therefore to potentially digest tissue around the spicules (Dearborn 1977).

Low nutritional benefit to predators (Duffy & Paul 1992, Bullard & Hay 2002) and/or the presence of chemical compounds (Assmann et al. 2000, Becerro et al. 2001, Mahon et al. 2003, Amsler et al. 2005) may also influence predatory preferences for particular prey. As sea stars have to invest time and energy reserves in order to digest their prey, it is possible that poor-quality prey may not compensate for the investment in digestion. This may drive selection for the exploitation of high-quality prey. However, it is unlikely that this is the case in the Antarctic benthos where sponges have relatively high nutritional levels (particularly soluble protein; McClintock 1987).

Defensive secondary metabolites in marine sponges contribute to prey being unpalatable or may potentially inhibit digestive processes post-ingestion (Becerro et al. 1998). Chemical defenses are common in sessile marine organisms lacking external protective shells, including algae (Steinberg 1985, Amsler 2008) and invertebrates (Pawlik et al. 1995, Kubanek et al. 2000, Iken et al. 2002, Becerro et al. 2003, Mahon et al. 2003), and sponges are perhaps one of the most well-known examples of invertebrate phyla known to exploit such defenses (Wilson et al. 1999, Assmann et al. 2000, McClintock & Baker 2001, Burns et al. 2003). As sponges qualitatively and quantitatively dominate Antarctic benthic communities below the algal zone (Barnes & Brockington 2003, Barnes 2005), an understanding of the factors that contribute to their defenses is particularly important for understanding the dynamics of these communities.

The goals of the present study were to test 3 general predictions concerning the relationship between sponges and their sea star predators in shallow, Antarctic coastal waters. These include: (1) most sponges will have outer tissues that are unpalatable to sympatric sea stars because these tissues are continuously exposed to predation and (2) the inner tissues of sponges with unpalatable outer tissues will be palatable to sea stars. This is because sea stars have an extra-oral mode of predation that should restrict their predation on sponges through the outer tissues alone and remove selection of allocation of defenses to internal tissues. (3) Secondary metabolite chemistry should have a substantial role in the provision of defenses in sponges subjected primarily to sea star spongivory.

MATERIALS AND METHODS

Collections. Multiple individuals of each sponge species were collected by hand using SCUBA from subtidal waters from numerous locations within 3.5 km of Palmer Station, Anvers Island, Antarctica (64°46.5'S, 64°03.3'W; cf. Amsler et al. [1995] for map) during 2 successive field seasons (January to May 2003 and February to June 2004). Sponges ranging in mass from 10s of grams to several kilograms were collected from hard-bottom substrates at depths of 5 to 39 m. Macroalgae dominated many of the sponge collecting sites, although some had vertical cliffs and overhangs where macroalgae covered <100% of the benthos. In these areas the majority of the sponges were found. In order to assess the percentage of palatable versus unpalatable species with an unbiased experimental design, every demosponge species that was encountered was collected for analysis. Sponges were returned immediately to the laboratory and sorted into distinct species. Voucher photographs and specimens are maintained at the University of South Florida.

Outer versus inner fresh tissue bioassays. In order to test the palatability of the fresh outer sponge layers, a small (approximately 0.5 cm³) piece of sponge was excised using a single-edge razor from the outer surface of each individual. Each sponge was then dissected to expose its approximate center (for mounding species), and a similarly sized piece of tissue was excised from this central region. Each individual sponge was used as the source of only a single piece each of internal and external tissue for feeding assays. Encrusting species and tubular species had internal tissue taken from areas furthest from the exterior, where predators would encounter them, although some species were not amenable to separation of outer tissue from inner tissue due to the close proximity of both tissues. These sponge pieces were then presented to the sympatric omnivorous (including sponge prey) sea star *Odontaster validus* following the methods described in McClintock & Baker (1997).

Prior to feeding assays, *Odontaster validus* were placed in ambient flow-through seawater tanks for no less than 24 h before being used in any feeding assay. The maintenance diet consisted of control artificial food pellets. When held in aquaria, *O. validus* move up the interior wall until they reach the surface and extend 1 or more arms along the air–water interface. This provided access to the oral side of arms, the chemosensory tube feet of which line the ambulacral groove. Excised sponge pieces from the exterior surface of sponges were presented to *O. validus* equidistant between the oral opening and the arm tip such that the outer surface of the sponge cube (pinacoderm) was in direct contact with the chemosensory tube feet. The behavioral feed-

ing response of the sea star was then noted as an acceptance when the potential food item was carried to the oral opening and held there for extra-oral digestion. A rejection response was considered any response other than this acceptance behavior. The most common rejection behaviors observed included moving the potential food item out of the ambulacral groove and off the side of the arm, retracting the tube feet and letting the potential food item drift away, or moving the potential food item away from the mouth towards the arm tip and then releasing it. Responses occurred within the first minute of presentation the majority of the time; however, items were left on the ambulacral groove for 5 min before a rejection was noted.

Once a sea star either accepted or rejected the fresh sponge tissue, an artificial food pellet was presented to the sea star as a control. The control food consisted of a 2% alginate matrix infused with 5% (dry wt) lyophilized, powdered krill in sea water (McClintock et al. 2003, 2004). The alginate and krill combination was gelatinized using 1 M cold CaCl₂, and pellets similar in size to the excised sponge pieces were presented to the sea star. Once the outer sponge tissue had been assayed, the tissue excised from the interior of the sponge was assayed in exactly the same manner. Sea star feeding bioassay sample sizes were up to 16 individual sponges of a given species, but the number was lower if fewer individuals of a given sponge species were collected. One species was assayed twice to include 2 morphotypes that were distinct in the field. Responses were similar independent of whether the item being assayed was fresh sponge tissue or artificial food pellet. Each food item was presented to a separate sea star, and no sea star was used multiple times in fresh-tissue or artificial-food assays that would be statistically compared with one another.

Extract bioassays. Twelve of the sponge species that were found to be unpalatable as fresh tissue were used in extract bioassays following methods previously described in McClintock et al. (2003, 2004). Once the sponges had been dissected as described above, both inner and outer tissues were combined, weighed, frozen and lyophilized, and then re-weighed in preparation for chemical extraction. A lipophilic crude extract was prepared using 3 changes of 1:1 dichloromethane:methanol. Immediately following the lipophilic extraction, a hydrophilic crude extract was prepared from the previously extracted tissue using 3 changes of 1:1 methanol:water. Crude extracts were then dried under reduced pressure and weighed, providing the yield of extract per mass of dry sponge.

The dried extracts were added to the control food noted in the previous section (5% dried krill in 2% alginate marine solution) in the following manner. The extracts were solubilized in a minimal amount of solvent

before being added to the dried krill such that the extract concentration on the final krill pellet equaled the extract concentration naturally found in the sponge on a wet weight basis. The krill coated with extract was dried under reduced pressure, added to a 2% alginate solution, and thoroughly mixed. To gelatinize the mixture, 1 M cold CaCl_2 was added. Solvent controls treated with the same volume of solvents used to solubilize the extract, as well as the 5% krill and 2% alginate, were also prepared. Artificial food pellets were cut into blocks (approximately 0.5 cm^3) using a single-edge razor.

Experimental and solvent control pellets were presented to sea stars as given above for fresh tissue feeding assays. Non-solvent-treated control food pellets were prepared as above and used as satiation controls. Only feeding assays in which the satiation control was accepted were included in statistical analysis. Once 12 replicates were successfully completed, the acceptance rate of the extract-containing pellets was compared to the acceptance rate of the solvent control pellets. For any given sponge, pellets containing lipophilic extracts were always tested in sequence first, and, only if accepted, were the pellets containing hydrophilic extract tested.

Statistical analysis. Fisher's exact tests were performed using Vassar Stats (<http://faculty.vassar.edu/lowry/VassarStats.html>) to determine which outer and/or inner layers of sponges were rejected signifi-

cantly more often than controls, as well as which of those unpalatable sponges contained crude organic extracts that were unpalatable.

RESULTS

Twenty-seven sponge species were collected in sufficient numbers ($n \geq 3$) for statistical analysis with 1 additional species having only 1 individual collected. The majority (18 species) were of the order Poecilosclerida, with species of the orders Hadromerida, Halichondrida (2 species), Haplosclerida (4 species) and Dendroceratida also being present (Table 1). Individuals representing 1 unknown sponge species were also included. Taxonomic identification was not possible for this species due to the loss of voucher material.

Outer versus inner fresh tissue bioassays

Of the 27 sponge species that had fresh outer tissue presented to *Odontaster validus* in feeding bioassays, 21 (78%) were significantly rejected ($p \leq 0.05$; Fig. 1). In 13 of these 21 (62%), the result was highly significant ($p \leq 0.01$). Two additional species (7%) displayed apparent trends towards being unpalatable, but the sample sizes were too small for these to be statistically signifi-

Table 1. Taxonomy of identified sponges

Species	Order	Suborder	Family	Subfamily
<i>Artemisina plumosa lipochele</i> Hentschel, 1914	Poecilosclerida	Microcionina	Microcionidae	Ophlitaspongiinae
<i>Artemisina</i> sp. Vosmaer, 1885	Poecilosclerida	Microcionina	Microcionidae	Ophlitaspongiinae
<i>Cladocroce gaussiana</i> (Hentschel, 1914)	Haplosclerida	Haplosclerina	Chalinidae	
<i>Clathria (Axosuberites) flabellata</i> (Topsent, 1916)	Poecilosclerida	Microcionina	Microcionidae	Microcioninae
<i>Clathria (Axosuberites) nidificata</i> (Kirkpatrick, 1907)	Poecilosclerida	Microcionina	Microcionidae	Microcioninae
<i>Crella</i> sp. Gray, 1867	Poecilosclerida	Myxillina	Crellidae	
<i>Dendrilla membranosa</i> (Pallas, 1766)	Dendroceratida		Darwinellidae	
<i>Haliclona (Gellius) rudis</i> (Topsent, 1901)	Haplosclerida	Haplosclerina	Chalinidae	
<i>Haliclona</i> sp. Grant, 1836	Haplosclerida	Haplosclerina	Chalinidae	
<i>Haliclonissa verrucosa</i> Burton, 1932	Haplosclerida	Haplosclerina	Niphatidae	
<i>Homaxinella balfourensis</i> (Ridley & Dendy, 1887)	Hadromerida		Suberitidae	
<i>Hymeniacidon fernandesi</i> Thiele, 1905	Halichondrida		Halichondriidae	
<i>Hymeniacidon torquata</i> Topsent, 1916	Halichondrida		Halichondriidae	
<i>Iophon unicorne</i> Topsent, 1907	Poecilosclerida	Microcionina	Acarinidae	
<i>Isodictya</i> aff. <i>cactoides</i> (Kirkpatrick, 1908)	Poecilosclerida	Mycalina	Isodictyidae	
<i>Isodictya antarctica</i> (Kirkpatrick, 1908)	Poecilosclerida	Mycalina	Isodictyidae	
<i>Isodictya erinacea</i> (Topsent, 1916)	Poecilosclerida	Mycalina	Isodictyidae	
<i>Isodictya kerguelenensis</i> (Ridley & Dendy, 1886)	Poecilosclerida	Mycalina	Isodictyidae	
<i>Isodictya lankesteri</i> (Kirkpatrick, 1907)	Poecilosclerida	Mycalina	Isodictyidae	
<i>Kirkpatrickia variolosa</i> (Kirkpatrick, 1907)	Poecilosclerida	Myxillina	Hymedesmiidae	
<i>Latrunculia (Latrunculia) apicalis</i> Ridley & Dendy, 1886	Poecilosclerida	Latrunculina	Latrunculiidae	
<i>Lissodendoryx (Ectydoryx) ramilobosa</i> (Topsent, 1916)	Poecilosclerida	Myxillina	Coelsphaeridae	
<i>Mycale (Oxymycale) acerata</i> Kirkpatrick, 1907	Poecilosclerida	Mycalina	Mycalidae	
<i>Myxodoryx hanitschi</i> (Kirkpatrick, 1907)	Poecilosclerida	Myxillina	Hymedesmiidae	
<i>Phorbas areolatus</i> (Thiele, 1905)	Poecilosclerida	Myxillina	Hymedesmiidae	
<i>Tedania (Tedaniopsis) charcoti</i> Topsent, 1913	Poecilosclerida	Myxillina	Tedaniidae	

cant. The Fisher's exact test has little power when there are a small number of replicates. Two of the sponges were not amenable to separation of inner and outer layers. Of the remaining 25 sponge species that had inner

tissues presented to *O. validus*, 14 of these (56%) had their inner tissue significantly rejected.

Of the 21 sponge species that were significantly rejected on the basis of outer tissue, 8 (38%) had inner

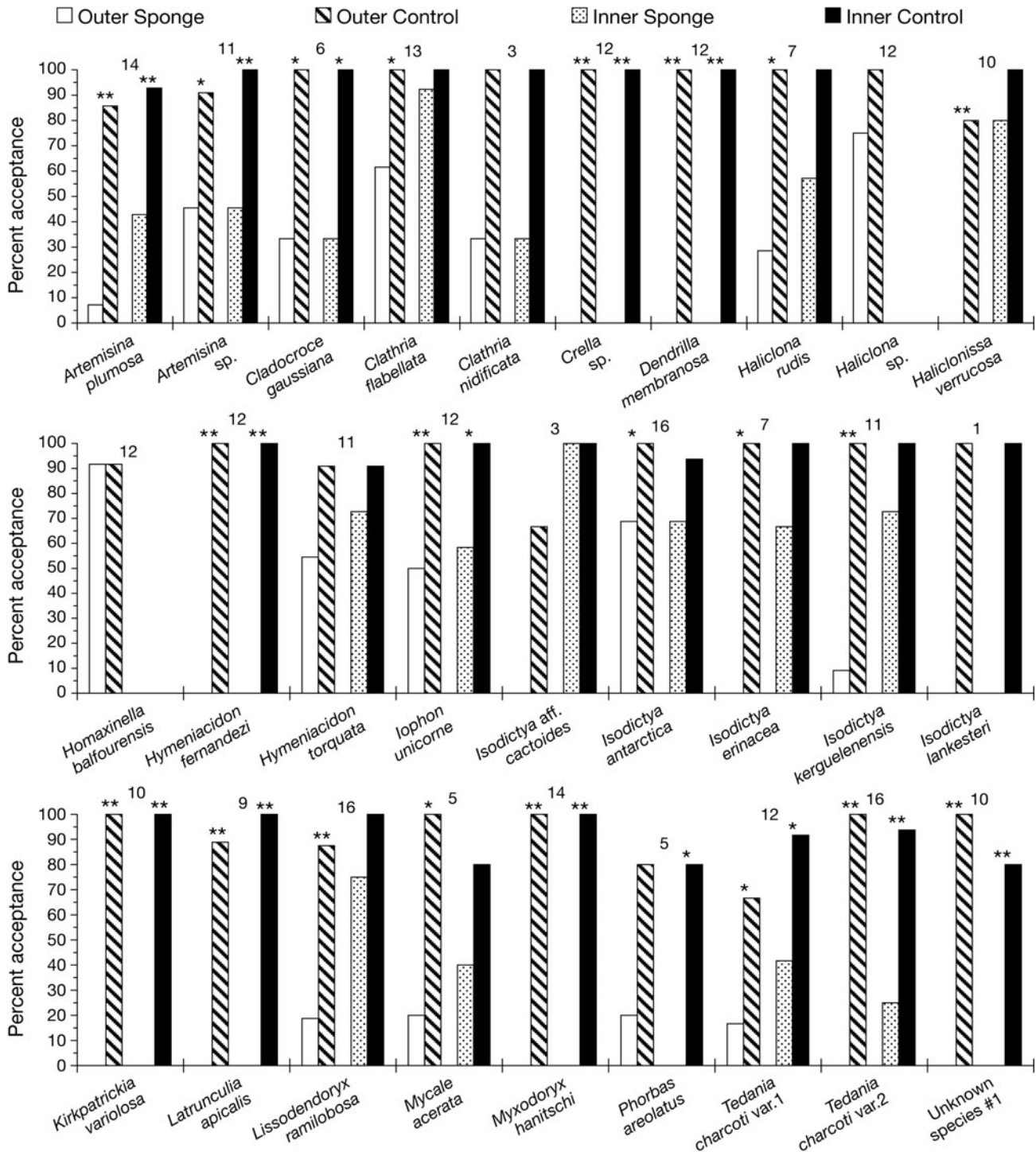


Fig. 1. *Odontaster validus*. Bioassays offering outer and inner sponge tissues to sea stars. Numbers above each set of columns, with each species having equal outer and inner tissue replicates. *Haliclona sp.* and *Homaxinella balfourensis* only had outer tissue presented to sea stars. All species with 3 or more replicates were analyzed for statistical differences between acceptance of sponge tissue and control (Fisher's exact test); * $p \leq 0.05$, ** $p \leq 0.01$

tissues not significantly rejected by *Odontaster validus* (Table 1). One sponge (*Phorbas areolatus*) had its inner tissue significantly rejected ($p = 0.0238$), while its outer tissue was not significantly rejected ($p = 0.1032$). Only 5 replicates of this species were tested, and, out of these 5 outer samples, 4 of them were rejected, but with the small sample size, this was an insignificant result. Four species, including *P. areolatus*, had p -values close to being significant, with the inner layer almost being significant in 3 other cases (*Haliclona rudis*, *Isodictya antarctica* and *Lissodendoryx ramilobosa*), although the small number of replicates did not appear to be as great a factor in these 3 other cases ($n \geq 7$ in all cases). These species had individuals with defenses present in inner or outer tissues, but when the individuals are grouped together, the tissues were not found to be significantly defended.

Extract bioassays

Given the time constraints in the field, only 12 of the 21 sponge species that had fresh tissue rejected could be included in extract bioassays. The extracts for these 12 species were the first available, and no selection was involved in determining in which order to analyze the extracts. These 12 sponges consisted of 7 species that had both outer and inner tissues rejected; 4 that had outer, but not inner, tissues rejected; and 1 species (*Phorbas areolatus*) that had inner, but not outer, tissue rejected. Either lipophilic or hydrophilic extracts of all 12 species were rejected in sea star feeding bioassays when compared to solvent controls (Fig. 2). Lipophilic extracts were significantly rejected ($p \leq 0.05$) for 10 of the 12 species (83%). Lipophilic extracts from the re-

maining 2 species (*P. areolatus* and *Isodictya antarctica*) were not significantly rejected ($p = 0.0775$ for both). Both of these species had their hydrophilic extracts subsequently assayed and both of these demonstrated highly significant ($p \leq 0.01$) levels of pellet rejection.

DISCUSSION

This survey examined the incidence of unpalatability among a broad suite of demosponges from the western Antarctic Peninsula to the ubiquitous, sympatric, omnivorous sea star *Odontaster validus*. Although the present study included only approximately 8% (30 of 352 species; McClintock et al. 2005) of the total demosponge fauna of Antarctica, it encompassed all of the shallow-water demosponges that could be collected in sufficient quantities for bioassays in the vicinity of Anvers Island along the central western Antarctic Peninsula.

In Antarctica, sea stars are the dominant predators of sponges and other benthic macroinvertebrates (Dayton et al. 1974, Dearborn 1977). *Odontaster validus* is one of the most abundant sea stars along the western Antarctic Peninsula (Stanwell-Smith & Clarke 1998, Peck et al. 2008), including the region immediately surrounding Palmer Station (K. Peters, C. Amsler, J. McClintock pers. obs.). The vast majority (78%) of the sponges assayed in the present study had outer tissues that were unpalatable to *O. validus*, and additional species that could only be assayed with relatively small sample sizes displayed strong trends toward being unpalatable. One mechanism by which sponges may render themselves unpalatable is through the production of physical defenses such as spicules. However, this prospective defense mechanism has been

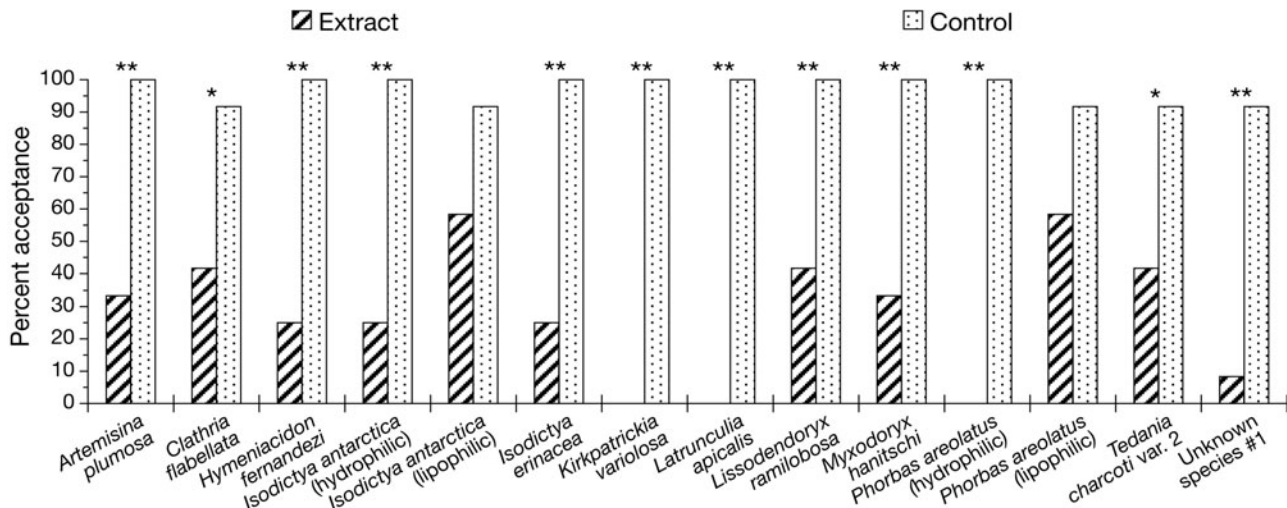


Fig. 2. *Odontaster validus*. Bioassays offering artificial foods containing lipophilic or hydrophilic sponge extracts to sea stars ($n = 12$ for all species). Lipophilic extracts were always offered first and only if they were not significantly rejected were hydrophilic extracts offered. Asterisks indicate significant difference between extract and control (Fisher's exact test); * $p \leq 0.05$, ** $p \leq 0.01$

demonstrated to have variable results (Chanas & Pawlik 1995, Hill et al. 2005, Huang et al. 2008) and does not appear to be a likely method in an environment where sea stars are the dominant predators and should be able to bridge such physical defenses during predation. Another mechanism that could discourage predation is that sponges are poor-quality prey that lack sufficient nutrients to make them worth consuming (Duffy & Paul 1992, Bullard & Hay 2002). While no nutritional value measurements of the sponges were made in our study, nutritional compositions of sponges from McMurdo Sound, Antarctica (77° 51' S, 164° 40' E) have been gathered previously (McClintock 1987). Five species examined in this previous study from McMurdo Sound are also represented among the sponges in the present study. All 5 had outer tissues rejected by *O. validus* and had total protein levels ranging from 28 to 56% dry weight. With such a wide range of protein values, a small sample size of sponges, and distinct geographic differences between the 2 study regions, it is not possible to rigorously evaluate whether there is a relationship between nutritional content and palatability in these sponges. The protein levels reported in McClintock (1987) are in the same range as those reported by Chanas & Pawlik (1995) for Caribbean sponges, although the data were reported differently (gravimetric vs. volumetric), because the ecologically relevant predators have different feeding methods. A similar analysis examining the chemical defenses of a broad suite of marine macroalgae on the western Antarctic Peninsula found no correlation between algal nutritional value (Peters et al. 2005) and palatability (Amsler et al. 2005).

Differences in methodologies between the present study and previous studies make direct comparisons problematic. Previous studies of defenses in multiple sponge species have tested sponge spicules and extracts imbedded in food pellets (Chanas & Pawlik 1995, Pawlik et al. 1995). As we employed fresh sponge tissues, this makes it difficult to make direct comparisons with these earlier studies. However, despite our subsampling extracts from only 12 of the 21 sponge species that were unpalatable, the fact that all 12 species displayed sea star deterrence in at least 1 extract (lipophilic or hydrophilic) supports our hypothesis that chemical defenses play a major role in determining patterns of sponge predation in Antarctica. With this information, we are able to compare the fresh outer tissue data to data reported from previous studies in which only the chemical aspect of defense was analyzed.

Previous studies have proposed a latitudinal gradient of chemical defenses in marine invertebrates, with these defenses being more prevalent in low latitude, tropical environments, as opposed to higher latitudes where the incidence of fish predators preying upon

their tissues is certainly diminished (Bakus & Green 1974, Ruzicka & Gleason 2008). If this were the case, then it would be expected that a smaller percentage of marine invertebrates in Antarctica would invest in chemical defenses, or secondary metabolite defenses might be expected to be weak. However, the percentage of Antarctic peninsular sponges in our survey that were defended against sea stars (outer tissues: 78%) is slightly higher than a sponge survey conducted in the Caribbean Sea where 69% of the species were found to be chemically defended against fish (Pawlik et al. 1995). We are aware of no comparable surveys conducted at temperate latitudes or in other locations. However, the fact that there are similar levels of defenses in sponges from Antarctica and from tropical waters indicates that at present there is no evidence of a latitudinal gradient for sponge chemical defenses. Becerro et al. (2003) came to the same conclusion using different methodologies comparing congeners from temperate and tropical waters.

We know of no other studies at temperate, tropical, or polar latitudes that have examined differing levels of palatability between fresh tissues taken from the outer versus the inner central tissues of sponges; however, one previous study conducted with the sponge *Latrunculia apicalis* from McMurdo Sound, Antarctica, did detect a strong gradient of chemical defenses, with greater levels in the outermost tissue and then a sharp decline moving deeper into the sponge (Furrow et al. 2003). Extracts prepared from different layers of benthic macroinvertebrates from warmer waters have yielded conflicting results. In one study, differences between tissue layers in their palatability were not detected (Burns et al. 2003), while in other studies body tissues first encountered by predators were found to be regions of increased defenses (Avila & Paul 1997, Schupp et al. 1999). In all of these studies, the predominant predators on the sponges were fish, which are capable of biting through outer tissues and thus feeding on both inner and outer tissues.

Our analysis of the patterns of palatability between outer and inner sponge tissues facilitates a test of the predictions of the ODT. As sea stars feed via extra-oral digestion on the surfaces of their prey, this limits their encounter to the outer surfaces of sponges. Thus, defenses in sponges with sea star predators would be predicted (in accordance with the ODT) to be strongest in association with outer surfaces. We found that inner sponge tissues were palatable, while outer tissues were unpalatable in 8 of the 21 species examined. Therefore, 38% of the species examined met the predictions of the ODT. However, the other 13 sponge species (62%) did not adhere to the predictions of the ODT, and have inner tissues that are defended even though they appear to be at little risk of attack by sea star predators. While

38 % of species following the ODT prediction is not trivial, that the other 62 % is not following the ODT predictions suggests that there might be a problem with the theory or with its underlying assumptions as applied to this predator–prey system.

A possible explanation for the lack of some sponge species meeting the predictions of the ODT is that, unlike previous studies of sponge assemblages in McMurdo Sound (Dayton et al. 1969, 1974, Dayton & Oliver 1977), the marine communities that characterize the western Antarctic Peninsula are exposed to considerable densities of biting and/or burrowing sponge predators that are able to penetrate external defenses by burrowing or biting through defended outer tissues or exploiting oscula or ostia for access to feed on internal palatable tissues. One possibility is mesograzers, particularly amphipods, feeding on the sponges. Amphipods are a remarkably abundant component of shallow water communities on the Antarctic Peninsula, including Anvers Island and its environs (Iken et al. 1997, Graeve et al. 2001, Huang et al. 2007). In preliminary quantitative observations, we found that amphipods are common sponge associates and sometimes have sponge spicules in their guts (M. Amsler unpubl. obs.). The majority of these amphipod–sponge associations appear to occur within internal tissues, but it remains unknown how they gain access to internal regions. One possibility is that amphipods enter the large oscula some of the sponges possess, thereby bypassing the defenses in the external tissues. Conversely, if the amphipods are not driving the production of the internal defenses, these might be evolutionary relics from ancestral sponges that existed in seas where larger, biting predators that would have been able to access internal tissues were more common. Sponge tissues often include large and diverse microbial communities (Wilkinson 1978), and the presence of secondary metabolites might be produced by these microbes for purposes other than predation deterrence. It has recently been documented that the sponge-associated secondary metabolites do not inhibit bacterial growth of sympatric bacteria, but they do cause significant mortality in settling diatoms collected from the same environment (Peters et al. unpubl. data).

Our present study has demonstrated that many sponges (48 % of 27 species examined) have evolved both external and internal defenses that may deter burrowing mesograzer predators such as amphipods. In summary, if sponges and other sessile invertebrates in benthic communities along the Antarctic Peninsula are subject to a mesograzer-dominated environment that includes sponge predators, then there may be selection to allocate chemical defenses to both external and internal tissues.

Acknowledgements. We are grateful to the numerous members of the Antarctic field teams for assistance with collections. This work would not have been possible without logistical support in Antarctica provided by the employees and subcontractors of Raytheon Polar Services Company. This research was facilitated by National Science Foundation awards to C.D.A. and J.B.M. (OPP-0125181) and to B.J.B. (OPP-0125152).

LITERATURE CITED

- Amsler CD (ed) (2008) Algal chemical ecology. Springer, Berlin
- Amsler CD, Fairhead VA (2006) Defensive and sensory chemical ecology of brown algae. *Adv Bot Res* 43:1–91
- Amsler CD, Rowley RJ, Laur DA, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition. *Phycologia* 34: 424–430
- Amsler CD, Iken K, McClintock JB, Amsler MO and others (2005) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. *Mar Ecol Prog Ser* 294:141–159
- Assmann M, Lichte E, Pawlik JR, Köck M (2000) Chemical defenses of the Caribbean sponges *Agelas wiedenmayeri* and *Agelas conifera*. *Mar Ecol Prog Ser* 207:255–262
- Avila C, Paul VJ (1997) Chemical ecology of the nudibranch *Glossodoris pallida*: Is the location of diet-derived metabolites important for defense? *Mar Ecol Prog Ser* 150: 171–180
- Bakus GJ, Green G (1974) Toxicity in sponges and holothurians: a geographic pattern. *Science* 185:951–953
- Barnes DKA (2005) Changing chain: past, present and future of the Scotia Arc's and Antarctica's shallow benthic communities. *Sci Mar* 69:65–89
- Barnes DKA, Brockington S (2003) Zoobenthic biodiversity, biomass and abundance at Adelaide Island, Antarctica. *Mar Ecol Prog Ser* 249:145–155
- Becerro MA, Paul VJ, Starmer J (1998) Intracolony variation in chemical defenses of the sponge *Cacospongia* sp. and its consequences on generalist fish predators and the specialist nudibranch predator *Glossodoris pallida*. *Mar Ecol Prog Ser* 168:187–196
- Becerro MA, Goetz G, Paul VJ, Scheuer PJ (2001) Chemical defenses of the sacoglossan mollusk *Elysia rufescens* and its host alga *Bryopsis* sp. *J Chem Ecol* 27:2287–2299
- Becerro MA, Thacker RW, Turon X, Uriz MJ, Paul VJ (2003) Biogeography of sponge chemical ecology: comparisons of tropical and temperate defenses. *Oecologia* 135:91–101
- Brand TE (1974) Trophic interactions and community ecology of the shallow-water marine benthos along the Antarctic Peninsula. PhD thesis, University of California, Davis
- Bullard SB, Hay ME (2002) Palatability of marine macro-holoplankton: nematocysts, nutritional quality, and chemistry as defenses against consumers. *Limnol Oceanogr* 47: 1456–1467
- Burns E, Ifrach I, Carmeli S, Pawlik JR, Ilan M (2003) Comparison of anti-predatory defenses of Red Sea and Caribbean sponges. I. Chemical defense. *Mar Ecol Prog Ser* 252: 105–114
- Chanas B, Pawlik JR (1995) Defenses of Caribbean sponges against predatory reef fish. II. Spicules, tissue toughness, and nutritional quality. *Mar Ecol Prog Ser* 127:195–211
- Cronin G (2001) Resource allocation in seaweeds and marine invertebrates: chemical defense patterns in relation to defense theories. In: McClintock JB, Baker BJ (eds) *Marine*

- chemical ecology. CRC Press, Boca Raton, FL, p 325–353
- Dayton PK, Oliver JS (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197: 55–58
- Dayton PK, Robilliard GA, DeVries AL (1969) Anchor ice formation in McMurdo Sound, Antarctica, and its biological impacts. *Science* 163:273–274
- Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol Monogr* 44:105–128
- Dearborn JH (1977) Foods and feeding characteristics of Antarctic asteroids and ophiuroids. In: Llano GA (ed) *Adaptations within Antarctic ecosystems*. Proceedings of the 3rd symposium on Antarctic biology. Smithsonian Institution, Washington, DC, p 293–326
- Duffy JE, Paul VJ (1992) Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes. *Oecologia* 90:333–339
- Engel S, Pawlik JR (2000) Allelopathic activities of sponge extracts. *Mar Ecol Prog Ser* 207:273–281
- Furrow FB, Amsler CD, McClintock JB, Baker BJ (2003) Surface sequestration of chemical feeding deterrents in the Antarctic sponge *Latrunculia apicalis* as an optimal defense against sea star spongivory. *Mar Biol* 143:443–449
- Graeve M, Dauby P, Scailteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. *Polar Biol* 24:853–862
- Hill MS, Lopez NA, Young KA (2005) Anti-predator defenses in western North Atlantic sponges with evidence of enhanced defense through interactions between spicules and chemicals. *Mar Ecol Prog Ser* 291:93–102
- Huang YM, Amsler MO, McClintock JB, Amsler CD, Baker BJ (2007) Patterns of gammaridean amphipod abundance and species composition associated with dominant subtidal macroalgae from the western Antarctic Peninsula. *Polar Biol* 30:1417–1430
- Huang JP, McClintock JB, Amsler CD, Huang YM (2008) Mesofauna associated with the marine sponge *Amphimedon viridis*. Do its physical or chemical attributes provide a prospective refuge from fish predation? *J Exp Mar Biol Ecol* 362:95–100
- Iken K, Barrera-Oro ER, Quartino ML, Casaux RJ, Brey T (1997) Grazing by the Antarctic fish *Notothenia coriiceps*: evidence for selective feeding on macroalgae. *Antarct Sci* 9:386–391
- Iken K, Avila C, Fontana A, Gavagnin M (2002) Chemical ecology and origin of defensive compounds in the Antarctic nudibranch *Austrodoris kerguelensis* (Opisthobranchia: Gastropoda). *Mar Biol* 141:101–109
- Kubanek J, Pawlik JR, Eve TM, Fenical W (2000) Triterpene glycosides defend the Caribbean reef sponge *Erylus formosus* from predatory fishes. *Mar Ecol Prog Ser* 207:69–77
- Mahon AR, Amsler CD, McClintock JB, Amsler MO, Baker BJ (2003) Tissue-specific palatability and chemical defenses against macropredators and pathogens in the common articulate brachiopod *Liothyrella uva* from the Antarctic Peninsula. *J Exp Mar Biol Ecol* 290:197–210
- McClintock JB (1987) Investigation of the relationship between invertebrate predation and biochemical composition, energy content, spicule armament, and toxicity of benthic sponges at McMurdo Sound, Antarctica. *Mar Biol* 94:479–487
- McClintock JB (1994) Trophic biology of Antarctic shallow-water echinoderms. *Mar Ecol Prog Ser* 111:191–202
- McClintock JB, Baker BJ (1997) Palatability and chemical defense of eggs, embryos and larvae of shallow-water Antarctic marine invertebrates. *Mar Ecol Prog Ser* 154:121–131
- McClintock JB, Baker BJ (eds) (2001) *Marine chemical ecology*. CRC Press, Boca Raton, FL
- McClintock JB, Mahon AR, Peters KJ, Amsler CD, Baker BJ (2003) Chemical defences in embryos and juveniles of two common Antarctic sea stars and an isopod. *Antarct Sci* 15:339–344
- McClintock JB, Amsler MO, Amsler CD, Southworth KJ, Petrie C, Baker BJ (2004) Biochemical composition, energy content and chemical antifeedant and antifoulant defenses of the colonial Antarctic ascidian *Distaplia cylindrica*. *Mar Biol* 145:885–894
- McClintock JB, Amsler CD, Baker BJ, van Soest RWM (2005) Ecology of Antarctic marine sponges: an overview. *Integr Comp Biol* 45:359–368
- Pawlik JR, Chanas B, Toonen RJ, Fenical W (1995) Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrence. *Mar Ecol Prog Ser* 127:183–194
- Peck LS, Webb KE, Miller A, Clark MS, Hill T (2008) Temperature limits to activity, feeding and metabolism in the Antarctic starfish *Odontaster validus*. *Mar Ecol Prog Ser* 358:181–189
- Peters KJ, Amsler CD, Amsler MO, McClintock JB, Dunbar RB, Baker BJ (2005) A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarctic Peninsula. *Phycologia* 44:453–463
- Rhoades DF (1979) Evolution of plant chemical defense against herbivores. In: Rosenthal GA, Janzen DH (eds) *Herbivores: their interaction with secondary plant metabolites*. Academic Press, New York, p 3–54
- Ruzicka R, Gleason DF (2008) Latitudinal variation in spongivorous fishes and the effectiveness of sponge chemical defenses. *Oecologia* 154:785–794
- Schupp P, Eder C, Paul V, Proksch P (1999) Distribution of secondary metabolites in the sponge *Oceanapia* sp. and its ecological implications. *Mar Biol* 135:573–580
- Sloan NA (1980) Aspects of the feeding biology of asteroids. *Oceanogr Mar Biol Annu Rev* 18:57–124
- Stanwell-Smith D, Clarke A (1998) Seasonality of reproduction in the cushion star *Odontaster validus* at Signy Island, Antarctica. *Mar Biol* 131:479–487
- Steinberg PD (1985) Feeding preferences of *Tegula funebris* and chemical defenses of marine brown algae. *Ecol Monogr* 55:333–349
- Tsoukatou M, Marechal JP, Hellio C, Novakovic I and others (2007) Evaluation of the activity of the sponge metabolites avarol and avarone and their synthetic derivatives against fouling micro- and macroorganisms. *Molecules* 12: 1022–1034
- van Alstyne KL, Paul VJ (1992) Chemical and structural defenses in the sea fan *Gorgonia ventalina*: effects against generalist and specialist predators. *Coral Reefs* 11: 155–159
- Wilkinson CR (1978) Microbial associations in sponges. II. Numerical analysis of sponge and water bacterial populations. *Mar Biol* 49:169–176
- Wilson DM, Puyana M, Fenical W, Pawlik JR (1999) Chemical defense of the Caribbean reef sponge *Axinella corrugata* against predatory fishes. *J Chem Ecol* 25:2811–2823