

An antarctic feeding triangle: defensive interactions between macroalgae, sea urchins, and sea anemones

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ABSTRACT: A relationship between macroalgae (*Phyllophora antarctica* and *Iridaea cordata*), the sea urchin *Sterechinus neumayeri*, and the sea anemone *Isotealia antarctica* in Antarctica is described. Both macroalgal species are chemically defended against herbivory by *S. neumayeri*. Where macroalgae and urchins co-occur in the field, over 95% of the urchins use macroalgae as cover and the vast majority of available drift is held by them. Urchins collected from sites without macroalgae prefer macroalgae over other cover materials in the laboratory, suggesting that they make an active behavioral choice to cover with macroalgae when available. Macroalgal cover acts as a defense against the major sea urchin predator, *I. antarctica*. Algal cover significantly increases the likelihood that urchins will escape from *I. antarctica* because the anemones' tentacles attach to the algae, which are subsequently released by the anemone or by both the urchin and the anemone. This defense is physical as thalli from which defensive chemicals have been extracted are equally protective. Macroalgae appear to derive benefit from this relationship because fertile drift plants are retained in the photic zone where they can continue to contribute to the gene pool. The urchins also extend the effective horizontal and vertical distributions of the macroalgae, which may help sustain the range of these algal populations in periods of reduced light availability. Hence, even though the macroalgae are chemically defended from urchin herbivory, this relationship is apparently mutualistic. It benefits the sea urchins by providing a defense against their primary predator and benefits the macroalgae by helping to sustain a reproductive population.

KEY WORDS: Chemical defense · Physical defense · Mutualism · Macroalgae · Sea urchins · Sea anemones · Antarctica

INTRODUCTION

Plants and animals utilize a diverse array of chemical and physical mechanisms to prevent herbivory or predation. Chemical defenses typically involve production of secondary metabolites that are toxic, distasteful, or both to potential consumers (cf. Paul 1992, Roitberg & Isman 1992, Pawlik 1993, Eisner & Meinwald 1995, Hay 1996, McClintock & Baker 1997a, Faulkner 1998). Physical defenses can include the production of armor or an otherwise tough external coating, the production

of thorns or other physical barriers, or the production or incorporation of detachable structures (cf. Steneck & Watling 1982, Vitt 1983, Harvell 1984, Endler 1986, Myers & Brazely 1991). Chemical and physical defenses are not mutually exclusive and a variety of organisms utilize them in combination (e.g. Hay et al. 1994, Schupp & Paul 1994, Mauricio & Rausher 1997).

We have previously shown that the antarctic marine red macroalgae *Iridaea cordata* and *Phyllophora antarctica* are chemically defended against herbivory by the sea urchin *Sterechinus neumayeri* (Amsler et al. 1998). These macroalgal species dominate shallow benthic communities in Terra Nova Bay (74° 42' S) with standing wet biomass sometimes exceeding 2 kg m⁻²

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(Gambi et al. 1994). They can also be the dominant macroorganisms in shallow waters at some sites near the southern limit of their distribution above 77° S (Zaneveld 1968) and are the only 2 non-crustose macroalgae throughout most of the year in our study area at McMurdo Sound (77° S; Miller & Pearse 1991).

Sterechinus neumayeri is the most abundant sea urchin in shallow antarctic waters and is a major consumer in the benthic trophic web of the study area (Brey et al. 1995). This species is an omnivore that has been documented to consume microalgae, macroalgae, seal feces, carrion, and a wide variety of invertebrates (reviewed by McClintock 1994). *S. neumayeri* individuals cover their tests with both *Iridaea cordata* and *Phyllophora antarctica* but rarely eat them (Pearse & Giese 1966, Miller & Pearse 1991, McClintock 1994, Amsler et al. 1998). Many species of sea urchins are known to cover themselves with macroalgae, shells, rocks, or a variety of other objects and many explanations for this behavior have been proposed in the past (reviewed by Lawrence 1976). Dayton et al. (1970) reported on covering behavior in *S. neumayeri* from antarctic sites without macroalgae. They described field observations showing that urchins covered by branching hydroid colonies were less susceptible to capture by their major predator, a large sea anemone now called *Isotealia antarctica*. *S. neumayeri* are attacked by *I. antarctica* when a foraging urchin strays into the tentacles of an anemone. Cover materials facilitate escape by forming a detachable shield to which the anemone's tentacles first adhere and that the urchins then release (Dayton et al. 1970).

Interactions between sympatric populations are typically defined as mutualistic if both interacting species derive benefit (Boucher et al. 1982, Ricklefs 1990, Bronstein 1994). These benefits can involve: (1) protection from a predator or from the environment; (2) dispersal of spores, gametes, larvae, seeds, or other propagules; (3) transport away from unsuitable habitats; and (4) provision of energy, nutrients, or other substances necessary for growth (Boucher et al. 1982). Although a wide range of such interactions has been examined, interactions of plants and animals with the plant species deriving a reproductive benefit are particularly well documented (Bronstein 1994).

In the present report we document that, even though they are chemically defended from being consumed by the urchins, macroalgae are the actively preferred form of cover for *Sterechinus neumayeri* and that this covering behavior is apparently part of a mutualistic interaction between the macroalgae and urchins. It benefits the macroalgae by retaining plants in the photic zone where they continue to contribute to the gene pool and by extending their spatial distribution. It benefits the sea urchins by providing a detachable

algal barrier that physically defends them from their primary predator, the sea anemone *Isotealia antarctica*.

MATERIALS AND METHODS

Collection sites and organisms. All organisms were collected by scuba diving from McMurdo Sound, Antarctica, in October and November, 1997. Primary collection sites in eastern McMurdo Sound included: the north and south sides of Cape Evans (77° 38' S, 164° 24' E), Little Razorback Is. (77° 40' S, 164° 31' E), Arrival Heights (77° 49' S, 164° 39' E), and McMurdo Station (77° 51' S, 164° 40' E). In western McMurdo Sound, 2 distinct collection sites in the Granite Harbor area (77° 01' S, 162° 51' E and 77° 01' S, 162° 49' E) were utilized. The experimental organisms were maintained in and all laboratory work was conducted in flowing seawater aquaria at McMurdo Station with a temperature of -1.5°C ($\pm 0.5^{\circ}\text{C}$) and with constant illumination (natural summer photoperiod in the study area). Illumination was provided by a combination of overhead lights and indirect sunlight at a photon flux density ranging from 3 to 25 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. *Isotealia antarctica* were fed freeze-dried antarctic krill *Euphausia superba* once per week but not less than 4 d before use in an experiment. Each aquarium contained a well-developed benthic microflora which the *Sterechinus neumayeri* appeared to consume. Under such conditions *S. neumayeri* is able to live for long periods and to develop or maintain mature gonads with viable gametes (McClintock pers. obs.).

Urchin cover transects. All urchins in 1 m wide transects which were oriented vertically along the sloping bottom were counted by a swimming diver. The depth range sampled varied with site topography. Estimated urchin cover was scored in 4 categories: (1) >90% of cover material being *Phyllophora antarctica*; (2) <10% of cover material being *P. antarctica*; (3) between 10 and 90% of cover material being *P. antarctica*; and (4) urchins not covered by any object. Sample transects were: 5 to 15 m depth at the north side of Cape Evans, N = 145 urchins, bottom slope moderately steep (cf. Miller & Pearse 1991); 3 to 30 m depth at Little Razorback Is., N = 310 urchins, bottom slope very steep (>45°) up to 5 m, with a more gradual slope above (nearly vertical cliffs were common below 25 m but did not begin until >33 m at the spot the transect was done); and 7 to 30 m depth at the easternmost Granite Harbor site, N = 1144 urchins, bottom slope very steep (>45°) up to 7 m (at which point the bottom dipped before rising again with a gradual slope). One transect was performed at each site. The percentage of urchins in each cover group was arcsine (square root) transformed to satisfy assumptions of equal variance and

compared statistically by analysis of variance (GLM) and by a Ryan-Einot-Gabriel-Welsch (REGWQ) post hoc test (equivalent to a Ryan's *Q*-test) using SPSS software (SPSS Inc., Chicago, IL).

Cover choice experiments. We collected 41 urchins with their cover from Arrival Heights, a site where macroalgae do not occur, and 60 urchins covered only with *Phyllophora antarctica* from the north side of Cape Evans. All cover items were removed, sorted, and weighed wet. Volumes were determined by water displacement. A cover material mixture was prepared with the combined material from all 41 Arrival Heights urchins and a biomass equivalent to the *P. antarctica* from 41 of the 60 Cape Evans urchins. This mixture contained 44.2 g of *P. antarctica* which displaced 26 ml of water. The mixture also contained 423.6 g of non-algal cover which displaced 349 ml of water and was comprised of 111.7 g of branching hydroid colonies, 30.2 g of sponge fragments (mostly from *Homaxinella balfourensis*), 94.2 g of invertebrate shells or shell fragments, 120.9 g of small rocks, and 66.6 g of other non-macroalgal material (including live bivalves and sea cucumbers, fish bone, worm tubes, and unidentifiable material).

The urchins collected at Arrival Heights were divided into 4 groups of 10 for use in 4 separate choice experiments. This method that combined 10 urchins in a tank was chosen over a single animal design because of the difficulty of individually replicating the complex mixture of the non-algal cover material. Each group was placed in 2 rows down the center a flowing seawater aquarium (1.4 × 0.9 × 0.15 m) and the cover mixture was poured around but not over them. A constant irradiance of 3 to 8 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ was provided by overhead cool white fluorescent lights. After 12 h, the urchins had selected cover materials. Urchins with their cover were removed and the cover material from each urchin was sorted and weighed wet. For analysis, the mass of each cover item (or group) was combined for the 10 urchins in each experiment (sample size for statistical analyses = 4). The percent of tank total for each cover group was calculated. These data were arcsine (square root) transformed to satisfy assumptions of equal variance and cover by algal versus non-algal materials compared statistically by *t*-test using SPSS software.

Urchin escape assays. *Iridaea cordata* was collected from the south side of Cape Evans, *Phyllophora antarctica* from Little Razorback Is., and *Isotealia antarctica* from Arrival Heights. *Sterechinus neumayeri* was collected from several locations in eastern McMurdo Sound between Cape Evans and McMurdo Station. *I. antarctica* individuals were attached to small rocks. Half of the *S. neumayeri* individuals were allowed to cover themselves with macroalgae. Subjectively, the

amount of covering algae per urchin was roughly equivalent to that observed for *P. antarctica* cover in nature and slightly less than that observed for *I. cordata* cover in nature. Urchins with or without cover were then placed next to an anemone and allowed to grip the substrate with their oral tube feet as they would during normal foraging in nature. The rock to which the anemone was attached was then gently slid toward the urchin until the edge of the urchin was directly beneath the oral disk of the anemone and, therefore, the urchin was in contact with several of the anemone's tentacles. The urchin-anemone pair was separated from the rest of the aquarium with a plexiglass partition and their interaction followed until the urchin was either free of the anemone's tentacles or had been captured and consumed. A total sample size of 20 urchins was utilized for each treatment (algal type or no-algae control) in each experiment. Anemones were offered $\frac{1}{2}$ of a freeze-dried antarctic krill (mean dry weight = 131 mg) 1 to 2 h before the experiment. If an anemone did not consume the krill, which happened very rarely, it was not used in the experiment. Anemones which consumed an urchin were not utilized again for at least 7 d and no anemones were used in more than 1 replicate trial for any algal type. The number of captured versus escaped urchins in each experiment was statistically compared using a Fisher's exact test (Zar 1984).

Urchin test diameters ranged from 3.0 to 4.7 cm. Anemone oral disk diameters ranged from 6 to 11 cm. The mean ratio of urchin test diameter to anemone oral disk diameter was the same for each treatment (cover or no cover) in each experiment (*t*-test, $p > 0.05$) and 0.52 over all experiments. Within the small range of diameter ratios used (0.33 to 0.66), there was no significant relationship between diameter ratio and the outcome of a trial (*t*-test, $p > 0.05$). Ratio data were arcsine (square root) transformed for statistical analyses, which were performed using SPSS software.

To determine if the secondary metabolites responsible for macroalgal defense against urchins were responsible for protecting the urchins against anemones, macroalgal thalli were extracted in 1:1 CH_2Cl_2 :methanol followed by 1:1 methanol:water. Although the volume of solvents used per unit algal biomass in the previous study (Amsler et al. 1998) should have quantitatively removed the defensive compounds, the solvents were used at even higher volumes per unit biomass in the present study to ensure complete extraction. After extraction the algae were passed through multiple changes of filtered seawater for 24 h and then held in flowing seawater before use in urchin escape assays. Subjectively, compared to urchins that covered with live macroalgae, the amount of extracted algae per urchin was roughly equivalent to that

observed for *Iridaea cordata* and slightly less than that observed for *Phyllophora antarctica*.

Algal fertility survey. *Phyllophora antarctica* growing attached to rock and also being used as cover by urchins was collected between 7 and 10 m depth at Little Razorback Is. and at both locations in Granite Harbor. Plants being used as cover by urchins were also collected along the 15 m depth contour at each site. For each plant group at each site, 31 randomly selected plants were examined visually for the presence of cystocarps. These represent a sporophytic generation which develops directly on lateral protrusions of female gametophytes and releases spores. Cystocarps are visible because they cause the proliferations to become swollen. *Iridaea cordata* was found only at Cape Evans. At the time these collections were made, only 11 attached plants at 6 m depth and 54 drift plants being used as cover by urchins between 9 and 12 m depth could be located on the north side of the cape and all were examined for the presence of cystocarps, which in *I. cordata* are visible as dark, thickened regions on the blades. Percent fertility data were arcsine (square root) transformed and statistically compared using SPSS software GLM and REGWQ tests.

RESULTS

We have observed *Sterechinus neumayeri* in nature using a wide variety of objects as cover but at sites where macroalgae co-occur with *S. neumayeri* the vast majority of urchins are covered with drift algae. In vertically oriented transects at 3 such sites, 96.5% of the urchins were using *Phyllophora antarctica* for 90% or more of their cover (Fig. 1). The 90% threshold was used to expedite sampling but the vast majority of these urchins appeared to be completely covered with *P. antarctica*. *Iridaea cordata* was also present at 1 of the transect sites (Cape Evans) but was unusually rare compared to previous seasons based on observations by ourselves and others (Miller & Pearse 1991). Urchins covered with *I. cordata* were present there but did not occur in the transect.

To determine if the apparent preference for macroalgal cover by *Sterechinus neumayeri* in nature represents an active choice by the urchins or merely an abundance of drift macroalgae available for cover, we determined preferences for cover in the laboratory using *S. neumayeri* individuals collected from a site where attached macroalgae do not occur and where drift macroalgae are quite rare. We allowed the cover on urchins in nature to determine the relative amounts of algal and non-algal cover to be used in the experiments and, as noted above, this resulted in a much smaller total mass and volume of *Phyllophora antarctica*

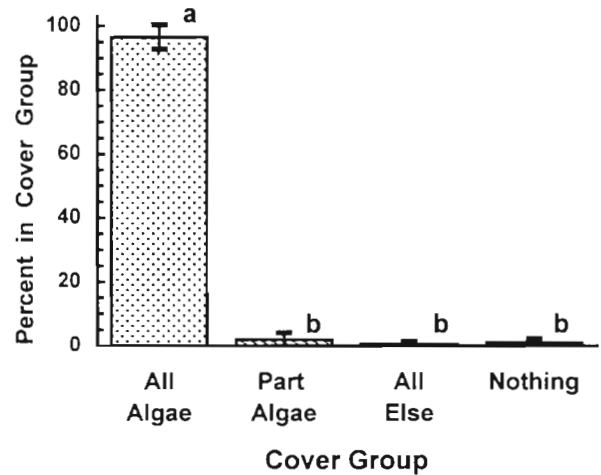


Fig. 1. Percentage of urchin *Sterechinus neumayeri* in nature covered with macroalgae *Phyllophora antarctica* versus other objects. Means \pm 1 standard deviation. See text for group definitions. Analysis of variance indicated significant differences between groups ($F_{3,11} = 136.9$, $p = 0.0001$). REGWQ post hoc test indicated that significantly more urchins were in the All Algae group than in any other ($p < 0.0001$), as indicated in the figure by letters a and b

tica relative to non-algal material (44.2 g *P. antarctica* vs 423.6 g non-algal, water displacement 26 ml for *P. antarctica* vs 349 ml for non-algal). After 12 h, the urchins had covered themselves with significantly more ($p < 0.001$) of the total available *P. antarctica* than of the total available non-algal cover (Fig. 2). All urchins had at least some *P. antarctica* as part of their cover. Although we did record choices of individual groups of non-algal cover, it was very rare for urchins in nature to be covered by any single non-algal cover item so no per-urchin equivalent could be established for anything but total macroalgal and total non-algal cover. Also, because the only equivalent groupings in the experiment were total macroalgal versus total non-algal cover, the relative proportion of individual types of non-algal cover are not directly comparable with each other or with the macroalgal cover. However, percentages of tank totals of individual types of non-algal cover being held by urchins ranged only from 4.7 to 13.2% (Fig. 2), suggesting that no individual non-algal cover item was as highly preferred as the macroalgae.

In order to experimentally assess whether macroalgal cover provides protection to *Sterechinus neumayeri* during predation by *Isotealia antarctica*, we presented urchins with and without macroalgal cover to *I. antarctica* in an aquarium. In control treatments without macroalgal cover, 14 to 16 of the 20 urchins in each experiment were captured and consumed by *I. antarctica* (Fig. 3). These interactions were something of a 'tug-of-war' since an urchin would be held in place or pulled toward the anemone while the

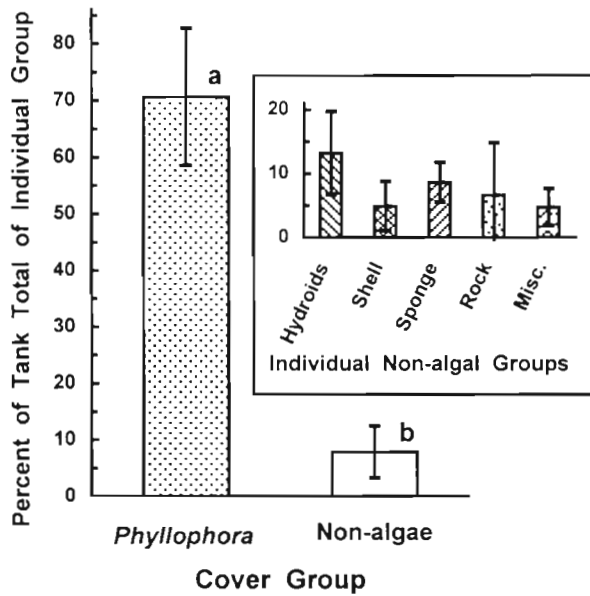


Fig. 2. *Sterechinus neumayeri* cover choice experiments comparing *Phyllophora antarctica* to non-algal cover items in the laboratory. Data expressed as means \pm 1 standard deviation of tank total of each cover group picked up by urchins in 12 h. The 2 groups are significantly different (*t*-test, $p < 0.001$), as indicated on the figure by letters a and b. Inset indicates data from individual non-algal cover groups. These data are not directly comparable with each other or with the *P. antarctica* data (see text)

anemone extended its body column to engulf the urchin (Fig. 4). To escape, an urchin needed to be able either to pull itself away from the tentacles completely or to pull itself far enough away so that the anemone could not extend its body column to engulf it. In the latter cases, the anemones eventually released their grip on the urchins although this sometimes took over an hour to occur. Cover with either live *Phyllophora antarctica* or live *Iridaea cordata*, however, allowed the vast majority of urchins to escape capture (only 1 of 20 urchins with each cover type were consumed; Fig. 3) and to do so quickly. The macroalgae being carried by urchins facilitated escape through 1 or both of 2 mechanisms. The anemone would first grip the macroalgae with its tentacles while initiating an attack on the urchin. Often, the urchin would release the macroalgae being gripped by the anemone and move away. The anemones never consumed the macroalgae and subsequently released their grip, allowing the algae to drift off. Alternately, the anemone would release the macroalgae before the urchin, allowing the urchin to move away with its

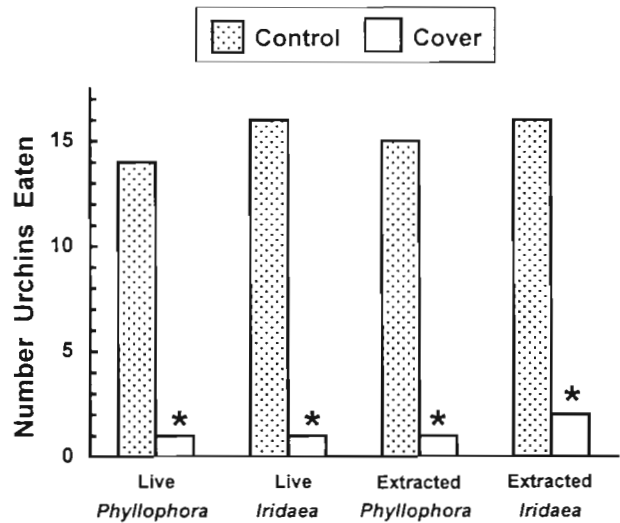


Fig. 3. Number of *Sterechinus neumayeri* consumed by *Isotealia antarctica* (of 20 total per experiment) with live and extracted macroalgae as cover versus no-cover controls. Fisher exact tests (2-tail) indicated significant differences between controls and experimental treatments in all experiments ($p < 0.00004$), as indicated by asterisks

cover intact. *I. antarctica* is typically observed to initially grip any living or inert object that comes into contact with its tentacles and to subsequently release those items it does not prefer to consume (McClintock & Baker 1997b). In the most rapid escapes, particularly where the anemone released the macroalgae before the urchin did, it is possible that the anemone did not recognize the urchin prey but the urchins were always



Fig. 4. *Isotealia antarctica* consuming *Sterechinus neumayeri* in nature. Extended anemone length is approximately 15 to 20 cm

observed to move away from the anemone after contact. In cases where covered urchins were consumed by the anemones, it appeared that several tentacles were able to get around the algal cover and attach to the urchin directly. Most if not all macroalgae consumed by an anemone along with an urchin was subsequently regurgitated in an undigested and apparently healthy state.

To determine if the defensive compounds that prevent *Sterechnus neumayeri* from consuming *Phyllophora antarctica* and *Iridaea cordata* (Amsler et al. 1998) play a role in defending *S. neumayeri* covered by these macroalgae from predation by *Isotealia antarctica*, we extracted the compounds from both macroalgal species and allowed urchins to cover themselves with the extracted thalli. These extracted thalli provided the same level of protection from urchin predation as the intact thalli (Fig. 3), indicating that the defensive compounds do not serve a necessary role in allowing *S. neumayeri* to escape from *I. antarctica*.

At all sites we have observed in McMurdo Sound where attached macroalgae occur, drift macroalgae are typically much more abundant than attached plants and virtually all drift algae are used as cover by *Sterechnus neumayeri*. Very few, if any, drift macroalgae that were not being used as cover by urchins were observed. Since the bottom topography at most of these sites is a very steep slope, plants not retained by urchins would likely be washed out of the photic zone quickly. The plants held by *S. neumayeri* remain normally pigmented and apparently healthy (also noted by Miller & Pearse 1991). Of much greater significance, they retain their ability to produce spores while being carried by the urchins. We sampled 3 sites where attached *Phyllophora antarctica* was restricted to a depth range of only 7 to 10 m but where drift plants on urchins were abundant over the entire depth range observed (3 to 40 m). Of the attached plants, 76.3% were fertile (cystocarpic) compared to 63.4% of the drift plants collected in the 7 to 10 m depth zone (Fig. 5). At 15 m, which was below the depth range of attached plants at these 3 sites (at least when we sampled them) but which is within the range reported for *P. antarctica* in other years and elsewhere (Miller & Pearse 1991, Gambi et al. 1994), 44.0% of the drift plants held by urchins were fertile. We also sampled *I. cordata* at the single site we were able to collect it. A few attached plants were collected at 6 m depth and of these, 90.9% were cystocarpic (Fig. 5). We were only able to collect drift plants, all on urchins, between 9 and 12 m depth. Of these, 75.9% were fertile (Fig. 5). Plants of either species scored as non-fertile could have been male but Miller & Pearse (1991) suggested that males are quite rare in both species in McMurdo Sound.

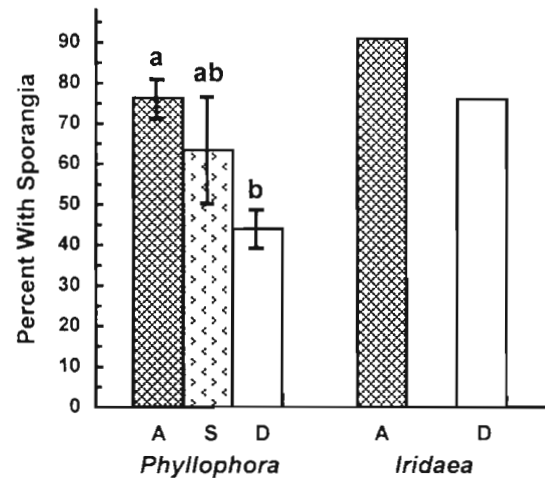


Fig. 5. Percent fertile macroalgae attached directly to the bottom and being used as cover by urchins. Means \pm 1 standard deviation for *Phyllophora antarctica* (N = 3 sites). Values at a single site for *Iridaea cordata*. A = attached directly to bottom. Depth range 7 to 10 m for *P. antarctica* and 6 m for *I. cordata*. S = shallow macroalgae being used as cover by urchins. Depth range 7 to 10 m for *P. antarctica*. No shallow *I. cordata* on urchins was present. D = deep macroalgae being used for cover by urchins. Depth was 15 m for *P. antarctica* and 9 to 12 m for *I. cordata*. GLM indicated a significant difference between *P. antarctica* sample groups ($F_{2,8} = 7.235$, $p = 0.025$). REGWQ ($\alpha < 0.05$) showed that there was no significant difference between fertility of *P. antarctica* on urchins at 7 to 10 m and either attached plants or plants on urchins at 15 m but that attached plants and plants on urchins at 15 m had significantly different fertility percentages, as indicated on the figure by letters a and b

DISCUSSION

To our knowledge, this relationship between the macroalgae *Phyllophora antarctica* and *Iridaea cordata* and the sea urchin *Sterechnus neumayeri* represents the first report of marine plants sustaining their reproductive output and spatial distribution through the active behavioral choice of a sympatric animal. Because this animal is also a herbivore that the plants chemically defend themselves against and because the animal benefits by being protected from its major predator, we believe this relationship represents a form of mutualism facilitated through chemical and physical defenses.

Ecological relationships between macroalgae, sea urchins, and predators of sea urchins are commonly reported and are often regarded as having major roles in the determination of benthic community structure (reviewed by Lawrence 1975, Mann 1982, Dayton 1985, Elnor & Vadas 1990, Lobban & Harrison 1994, Estes & Duggins 1995). In such interactions, the sea urchins are viewed as major potential or actual consumers of macroalgae. When urchins become abundant they can dev-

astate macroalgal communities via overgrazing, but urchins are prevented from becoming abundant by predators such as sea otters or lobsters (or by other biotic or abiotic factors; Elner & Vadas 1990, Lobban & Harrison 1994). Although *Sterechinus neumayeri* can be abundant (Pearse & Giese 1966, Brey et al. 1995), is a major benthic consumer in McMurdo Sound (Brey et al. 1995), and does consume some macroalgae (Pearse & Giese 1966, McClintock 1994), it is prevented from overgrazing *Phyllophora antarctica* and *Iridaea cordata* by chemical defenses (Amsler et al. 1998). Furthermore, not only are the macroalgae ungrazed, but the urchin covering behavior directly benefits the macroalgae because large numbers of fertile plants are retained in the photic zone. Although some macroalgal species may benefit indirectly from sea urchin feeding behaviors when their macroalgal competitors are preferentially grazed (e.g. Leighton 1971, Vadas 1977, Estes & Duggins 1995), we are not aware of any other examples of a macroalgal species deriving direct benefit from sea urchin behavior.

The very high ratio of urchin-cover macroalgae to attached macroalgae we observed at all sites with attached plants has also been reported for *Phyllophora antarctica* and another red macroalga elsewhere in Antarctica (Nakajima et al. 1982). Even though we observed somewhat lower percentages of fertility in plants used as cover relative to attached plants, the larger numbers of cover plants suggest it is virtually a certainty that, in total, they make a much greater contribution to the spore cloud than do those attached directly to the substrate. Although multiple factors influence the ultimate success of macroalgal recruitment (cf. Santelices 1990, Vadas et al. 1992), such an increase in the total number of spores available would be, at the very least, a potential advantage for successful recruitment even if other factors were predominant at particular individual sites. Relative to other macroalgae, the presence of a large local spore source is most likely to be important for maintenance of red macroalgal populations in general because of their non-motile propagules, particularly in the relatively low turbulence water columns under antarctic sea ice (cf. Amsler & Searles 1980, Santelices 1990, Amsler et al. 1992, Norton 1992).

The macroalgae benefit not only by having large numbers of plants maintained in the photic zone but also because the urchins extend the effective depth range of the plants. In the year the present study was conducted, attached *Phyllophora antarctica* was abundant between 7 and 10 m depth but was not observed deeper at any site even though attached plants have previously been observed in abundance down to 18 m at Cape Evans and Granite Harbor (Miller & Pearse 1991). The presence of large numbers of fertile plants

on urchins at these depths in years when attached plants do not occur there may facilitate recolonization in years when conditions allow growth of attached plants at greater depths. Similarly, small amounts of drift macroalgae are occasionally observed at locations in McMurdo Sound where attached plants do not occur, and, when so, the drift plants are always being used as part of the cover of *Sterechinus neumayeri* (authors' pers. obs.). Macroalgal dispersal via drift plants, either fertile when detached or becoming fertile in the drift, is not uncommon (Santelices 1990, Amsler et al. 1992, Norton 1992). Should environmental conditions at such sites change so that they could support attached macroalgal populations (most likely due to changes in annual and interannual sea ice cover), the cover plants being held in the photic zone by *S. neumayeri* could increase the likelihood or rate of macroalgal recruitment into these areas.

We have previously described another symbiotic relationship involving chemical defense in antarctic organisms. The pelagic antarctic pteropod *Clione antarctica* is chemically defended from predation by fish (McClintock & Janssen 1990, Bryan et al. 1995, Yoshida et al. 1995, McClintock & Baker 1998). The antarctic hyperiid amphipod *Hyperiella dilatata* captures *C. antarctica*, and individual amphipods hold individual pteropods on their backs. The chemical defenses of the captured pteropods then also defend the amphipods from predation by fish (McClintock & Janssen 1990, McClintock & Baker 1998). However, in this relationship the captured pteropod ceases feeding and, presumably, this negatively impacts its nutritional state. Moreover, the amphipod is not a potential pteropod predator and physical defenses are not involved, so this symbiotic relationship is distinct from the macroalgae-urchin mutualism we describe in the present study.

Another macroalga-herbivore-carnivore relationship has recently been described between the chemically defended alga *Dictyota menstrualis*, the decorator crab *Libinia dubia*, and omnivorous fishes (Stachowicz & Hay 1999). The decorator crabs camouflage themselves with *D. menstrualis* although they treat *D. menstrualis* as a low-priority food item. The chemically defended macroalgal camouflage in turn reduces the susceptibility of the crabs to fish predation. Although similar in many respects to the antarctic macroalga-urchin relationship, this differs most importantly in being of no apparent benefit to the macroalgae. Even though *D. menstrualis* might well remain or become fertile when used as camouflage, these plants do not appear to constitute a large percentage of the total population as we have observed with the antarctic macroalgae and, in addition, there is no evidence that the decorator crabs might help maintain the

spatial distribution of the population over time. The macroalga-crab-fish interaction also differs from the antarctic macroalga-urchin-anemone interaction in the ways in which defenses are involved. The macroalga-crab-fish interaction does not involve physical defenses. Furthermore, *D. menstrualis* defends the crabs from the fish because of chemical defenses that also protect the macroalgae from being eaten by the omnivorous fish. In addition to the fact that the chemical defenses that protect the antarctic macroalgae from urchin herbivory play no apparent role in protecting the urchins from *Isotealia antarctica*, there is no reason to suspect that this anemone is a herbivore that the macroalgae would defend themselves against by any mechanism. In this respect, the protection that macroalgae afford *Sterechnus neumayeri* can be described as passive since it involves neither physiological, biochemical, nor behavioral defenses.

A similar mutualism which involves the passive defense of an invertebrate by macroalgae (and other sessile epibionts) has been described by Vance (1978). Predation by the sea star *Pisaster giganteus* on the clam *Chama pallucida* is reduced by the presence of algal and other epibionts on the clams' shells. The epibionts, which also grow on a wide variety of other substrata, reportedly derive benefit from the rough surface provided by the clams as well as because the clams live in habitats with generally lower numbers of epibiont-grazing sea urchins (Vance 1978). The epibionts appear to protect the clams by making it less likely that a sea star will recognize them as a food item (Vance 1978). Although the macroalgae used as cover by *Sterechnus neumayeri* probably play a similar role sometimes in preventing *Isotealia antarctica* from recognizing the urchins as food, the macroalgae also clearly aid in the escape of urchins that are actively being attacked by anemones, as described above. Most mutualistic interactions that involve defense differ from both the epibiont-clam-sea star and macroalga-urchin-anemone interactions in that they involve active behavioral defenses of an animal rather than passive effects of plant cover (cf. Boucher et al. 1982, Glynn 1987, Ricklefs 1990).

Although the macroalgae appear to benefit by being the preferred form of urchin cover, this benefit is only relative to a situation in which the drift plants would wash into much deeper water or onto shore. Even though the plants on urchins retain the ability to become fertile, plants collected from urchins at the same depths (7 to 10 m) where attached plants occur are slightly less fertile than attached plants and, compared to the attached plants, there is a significant decrease in percent fertility when plants are collected from urchins at 15 m. Therefore, drift plants on urchins probably do not make as great a contribution to the

gene pool as attached plants and if the urchins were responsible for dislodging the macroalgae from the substrate, this clearly would not represent a mutualistic relationship. However, it is very unlikely that urchins are responsible for removing the macroalgae from their rock substrate. In the relatively shallow waters where the plants occur they are dislodged by anchor ice when the sea surface is covered by land-fast ice (Dayton et al. 1969, 1970) and are dislodged by iceberg scour and wave action during periods of open water (Neushul 1965, Kauffman 1974, Dayton 1990). As noted, the macroalgae are chemically defended from being consumed by the urchins (Amsler et al. 1998). When disks cut from the live thallus of either macroalga were placed over the mouth of an urchin, the urchins rejected them very rapidly (Amsler et al. 1998), which indicates that the urchins would not dislodge plant material with their mouths as is reported for urchins and macroalgae in other systems (e.g. Leighton 1971, Mann 1973). An alternate mechanism by which an urchin might dislodge a macroalga is by tearing it from the substrate using tube feet. Although we have not made biophysical measurements of either the strength of macroalgal attachment or of the strength of urchin tube feet, our experiences with both suggest that this scenario is extremely unlikely.

Sea urchin covering behaviors are observed in a wide range of species throughout the world (cf. Lawrence 1976) and there is no reason to suspect that the behavior, in and of itself, evolved independently in *Sterechnus neumayeri* as a predator defense mechanism. However, it is clear that this behavior is adaptive as a defense in *S. neumayeri* and, as such, that natural selection should have favored maintenance of the behavior in populations that co-occur with *Isotealia antarctica*. Since the defensive compounds from macroalgae do not play a necessary role in allowing *S. neumayeri* to escape from *I. antarctica* and since hydroid colonies used as cover have previously been reported to also facilitate escape (Dayton et al. 1970), we can only speculate on why *S. neumayeri* prefers macroalgae over other forms of cover. Population densities of *I. antarctica* can commonly be quite high (authors' pers. obs.) so an urchin that escaped one anemone could quickly encounter another. Since *I. antarctica* sometimes releases the macroalgae before *S. neumayeri*, allowing the urchins to both escape and retain their cover, macroalgal cover would clearly be preferable to a cover of something that the anemone would recognize as a prey item and not release. Our experience in removing finely branching hydroid colonies from urchins in laboratory preference experiments indicated that they often become entangled in an urchin's spines and, therefore, may not be as quickly or completely released as macroalgae. Finally, the flexible

and relatively light macroalgae may have hydrodynamic or weight benefits relative to rocks, shells, or other abiotic materials which, like macroalgae, would be released by *I. antarctica*.

Phyllophora antarctica, *Iridaea cordata*, and *Sterechnus neumayeri* all have circumpolar distributions in Antarctica (Neushul 1968, Moe & DeLaca 1976, Brey et al. 1995, and references therein). Consequently, the mutualistic relationship between them is unlikely to be restricted to McMurdo Sound. *P. antarctica* and *I. cordata* are the only fleshy macroalgae throughout most of the year in McMurdo Sound (77° S) and remain as dominant members of the flora with *S. neumayeri* also abundant at least as far north as 74° S in the Ross Sea (Zaneveld 1966, 1968, Miller & Pearse 1991, Gambi et al. 1994). With the exception of the most northern latitudes in Antarctica along the Antarctic Peninsula where anchor ice does not dislodge organisms in shallow water and where macroalgal species richness and total biomass are often very high (Amsler et al. 1995 and references therein), relatively little is known about the macroalgal flora along most of the rest of the antarctic coast. However, communities dominated by *P. antarctica* and *S. neumayeri* or where they are at least major components of the flora and fauna are reported throughout much of the rest of the continent including the Halswell Islands (66° S, 93° E; Propp 1970), the Vesfold Hills (78° S, 68° E; Dhargalkar et al. 1988, Kirkwood & Burton 1988), and East Ongul Island (69° S, 39° E; Nakajima et al. 1982). Anchor ice has a major impact in the shallow regions where macroalgae occur in McMurdo Sound (Dayton et al. 1969, 1970) as well as along much if not most of the antarctic coast (Kirkwood & Burton 1988, Knox 1994, and references therein). Anchor ice is probably responsible for most of the large amounts of macroalgal drift we observed in McMurdo Sound. It is likely that benthic communities along most of the antarctic coast are more similar to the *P. antarctica*/*I. cordata*-dominated and anchor-ice-disturbed Ross Sea benthos than to the species-rich and less-disturbed Antarctic Peninsula benthos (Knox 1994). Thus the mutualistic interaction between macroalgae and urchins is likely to be important in maintaining macroalgal populations along most of the antarctic coastline.

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