

Chapter 10

Epizoic Bryozoans on Predatory Pycnogonids from the South Orkney Islands, Antarctica: “If You Can’t Beat Them, Join Them”

Fouled Pycnogonids from Antarctica

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Abstract Antarctic bryozoans are poor spatial competitors compared to many sessile invertebrates. Antarctic bryozoans are frequently destroyed by ice scouring of the substratum during open water periods, and Antarctic bryozoans are specifically preyed upon by pycnogonids. Based on this, it was hypothesized that Antarctic bryozoans should foul pycnogonids more than other motile hosts and other sessile biotic and abiotic substrata. To test these hypotheses, 115 live pycnogonids were collected in the South Orkney Islands, Antarctica. Their carapaces were examined for epizoic bryozoans, and each colony’s size was measured and its location mapped. Nine species of pycnogonids were identified containing 156 bryozoan colonies belonging to seven cheilostome species. Of the 115 pycnogonids, 26% were fouled by bryozoans. The bryozoan species richness on pycnogonids is similar to that on the adjacent boulders. Compared to other motile host animals, the number of bryozoan species per unit host surface area is an order of magnitude higher on pycnogonids. This may be attributed to carapaces of pycnogonids acting as refugia for the bryozoans from competition for space on hard substrata, ice scour, and predation by their host.

Keywords Ecology • Epibiosis • Bryozoans • Pycnogonids • Antarctica

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Introduction

Epibiosis, or fouling, is a common and well-documented occurrence on sessile hosts. It has also been documented amongst bryozoans on motile marine animals such as crabs (e.g., Key et al. 1997), isopods (Key and Barnes 1999), sea snakes (Key et al. 1995), pycnogonids (Wyer and King 1973), and even on floating gastropods (Taylor and Monks 1997).

Bryozoans are typically poor space competitors (Soule and Soule 1977), but some bryozoans escape from competition for substratum space by erect growth (McKinney and Jackson 1989). However, many bryozoans are extremely effective at rapid colonization of young surfaces including the external surfaces of both sessile and motile hosts (Moore 1973; Soule and Soule 1977; Key et al. 1996a). Such epibiosis, whether it is opportunism through to host specific commensalism, has the potential to be an advantage in the evasion of substratum competition. In most environments the 'lifespan' of abiotic substrata is likely to be greater than those of biotic substrata, but in the polar regions, animals' life spans are long and disturbance of abiotic substrata is frequent (Barnes et al. 1996). Epibiosis, therefore, can be of particular advantage in both the evasion of predators when the host is motile and in the evasion of substratum disturbance in the Antarctic, which is subject to massive and frequent ice scouring (Barnes and Clarke 1995; Key and Barnes 1999).

In the current study we aimed to: (1) quantitatively describe the prevalence of fouling of pycnogonids (sea spiders) by bryozoans in terms of the number, size, and percentage of hosts fouled, the number and size of colonies on fouled hosts, and the number of different bryozoan species on fouled hosts; (2) correlate host size with the prevalence and species richness of epizoic bryozoans (i.e., following the Theory of Island Biogeography); (3) test the hypothesis that bryozoans should foul pycnogonids more than other motile hosts and more than abiotic hard substrata as epibiosis on pycnogonids should remove the bryozoans from competition for space on hard substrata, substratum scouring, as well as predation.

The Hosts

The host pycnogonids are basibionts in Wahl's (1989) terminology. The body of pycnogonids is usually thin, elongate, and segmented, with an elongate proboscis (Fig. 10.1). The trunk is made of four to six segments with the first acting as part of the head, whereas the remaining ones each attach to a pair of walking legs. Most pycnogonids have four pairs of walking legs, but may have as many as six in some species. Other appendages include chelifores, which are small clawed appendages used in feeding, and a pair of ovigerous legs occurring in both sexes in some species, which are used for cleaning appendages of epibionts and, on males, for egg-carrying (Arnaud and Bamber 1987). Ovigerous legs are absent from females of some species. The long and slender walking legs are composed of eight segments, each with a terminal claw (King 1973).

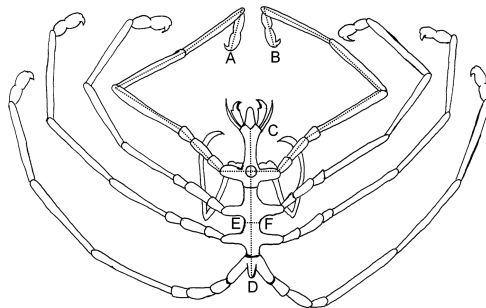


Fig. 10.1 Template of a generic pycnogonid showing characters measured and segments onto which bryozoan colonies were mapped. AB = span of the first pair of walking legs (measured when the legs are both extended perpendicular to the body). CD = trunk length (measured from the base of the proboscis to the terminal end of the anus). EF = trunk width (measured directly behind the second walking legs)

Most pycnogonids are benthic, although some are able to swim. Pycnogonids are fairly slow-moving carnivorous grazers and thus feed on either sessile or slow-moving prey. Pycnogonids prey upon a variety of animals including sponges, cnidarians, molluscs (esp. nudibranchs), echinoderms, and polychaetes, but their main food sources are hydroids and bryozoans (King 1973; Wyer and King 1973; Ryland 1976; Arnaud and Bamber 1987; Bain 1991; Piel 1991; Mercier and Hamel 1994).

Molting frequency in pycnogonids decreases through ontogeny with increasing size, until sexual maturity at adulthood when it generally stops (Tomaschko et al. 1997). From the larval stage to sexually mature adult, male pycnogonids typically undergo 8 molts, whereas females undergo 9–11 molts, depending on the species. Males do not molt while carrying eggs (King 1973; Arnaud and Bamber 1987).

Known shallow water epibionts of pycnogonids include protozoans, algae, hydroids, postveliger bivalves, and bryozoans, whereas in deeper water they include foraminifera, sponges, hydroids, serpulids, cirripeds, brachiopods, and bryozoans (Wyer and King 1973; Arnaud and Bamber 1987; Sherwood et al. 1998).

The Epibionts

Applying the nomenclature for marine organism-hard substratum relationships proposed by Taylor and Wilson (2002), the epibiotic bryozoans fouling the living pycnogonid hosts are termed sclerobionts in general and epizoozoans in particular. Bryozoans are preyed on by a variety of animals including platyhelminths, nematodes, arthropods, mollusks, echinoderms, chordates, and pycnogonids (Ryland 1970; McKinney and Jackson 1989; McKinney et al. 2003). Pycnogonids occurring on bryozoan colonies are well known from the literature (King 1973), but actual documented examples of pycnogonid predation of bryozoans are fewer (Table 10.1).

Table 10.1 Documented examples from the literature of pycnogonid predation of bryozoans

Pycnogonid	Bryozoan	Reference
<i>Ascorhynchus</i> sp.	<i>Serialaria</i> spp.	Döhrn (1881)
<i>Phoxichilidium femoratum</i>	<i>Crisia</i> sp.	Prell (1910)
<i>Anoplodactylus</i> sp.	<i>Bowerbankia</i> sp.	Lebour (1945)
<i>Austrodecus glaciale</i>	<i>Cellarinella foveolata</i>	Fry (1965)
<i>Pycnogonum littorale</i>	<i>Flustra foliacea</i>	Wyer and King (1973)
<i>Achelia echinata</i>	<i>Flustra foliacea</i>	Wyer and King (1973, 1974)
<i>Nymphon gracile</i>	<i>Bowerbankia imbricata</i>	King (1973); Wyer and King (1973, 1974)
<i>Tanystylum isabellae</i>	<i>Amathia distans</i>	Varoli (1994)
<i>Anoplodactylus stictus</i>	<i>Amathia distans</i>	Varoli (1994)
<i>Stylopallene longicauda</i>	<i>Amathia wilsoni</i>	Sherwood et al. (1998)
<i>Pseudopallene watsonae</i>	<i>Orthoscuticella</i> cf. <i>ventricosa</i>	Staples (2004)
<i>Pseudopallene reflexa</i>	<i>Orthoscuticella</i> cf. <i>ventricosa</i>	Staples (2004)

Pycnogonids are zooid-level predators of bryozoans (McKinney et al. 2003), so the predation is generally not lethal at the colony level, as the entire colony is not consumed (Berning 2008). Four different methods of predation of bryozoans by pycnogonids have been documented. (1) Access through the frontal pores of the bryozoan. Fry (1965) reported how the pycnogonid *Austrodecus glaciale* uses its proboscis to penetrate through the frontal pores of *Cellarinella foveolata* zooids. (2) Access through the operculum of the bryozoan. Wyer and King (1973) reported how the pycnogonid *Achelia echinata* uses its proboscis to penetrate through the operculum of *Flustra foliacea* zooids. Staples (2004) reported that the digitiform process of the chela of the larval form of the pycnogonid *Pseudopallene watsonae* is used to manipulate the operculum covering the orifice of each *Orthoscuticella* cf. *ventricosa* zooid facilitating insertion of the proboscis. As a result of predation, many of the zooids are empty with the operculum displaced to a vertical position (Staples 2004). (3) Using acute spines at tips of the palps to bore into zooecia before inserting proboscis. Arnaud and Bamber (1987) reported the pycnogonid genera *Austrodecus* and *Rhynchothorax* using this method. (4) Access through the crushed zooecium of the bryozoan. The chela of the adult form of the pycnogonid *Pseudopallene watsonae* is used to crush the zooids before insertion of the proboscis (Staples 2004). As pycnogonids are suctorial, carnivorous, grazing predators (Arnaud and Bamber 1987), predation ends with the pycnogonid sucking out the internal organs of the bryozoan with its muscular pharynx located inside its long thin proboscis, shredding them with its chelae, and transferring them to the setal “oyster basket” mouth at the anterior end of the proboscis for ingestion (Wyer and King 1973, 1974). King (1973) reported the chelae of *Nymphon gracile* being used to macerate the bryozoan *Bowerbankia* and hold it against the mouth for ingestion. Those methods involving the proboscis depend on the predator having the right size and shape proboscis for the prey’s morphology (e.g., operculum size and shape) (King 1973).

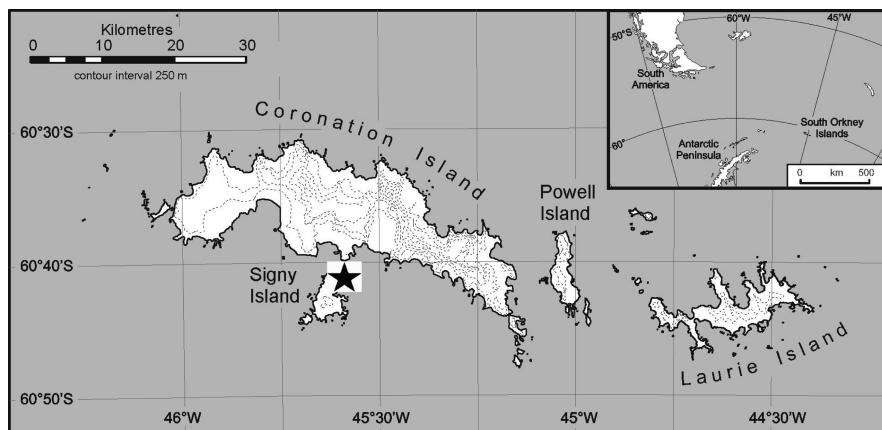


Fig. 10.2 Map showing location of the study site (star) in the South Orkney Islands, Antarctica. Modified from http://www.antarctica.ac.uk/living_and_working/research_stations/signy/index.php

Materials and Methods

A total of 115 living pycnogonids were collected for this study. They are housed in the British Antarctic Survey. They were collected in Outer Borge Bay, between Signy Island and Coronation Island in the South Orkney Islands, Scotia Arc, Southern Ocean, maritime Antarctic (Latitude $60^{\circ} 42' S$, $45^{\circ} 37' W$) (Fig. 10.2). Collection occurred during the austral summer from December 1991 to February 1992. Specimens were collected and sorted from Agassiz benthic trawls ranging from 50 to 150 m water depth towed for bottom durations of 15 min at each location. A combination of echo sounder and hydrographic charts was used to ensure that each sample came from a narrow range of depths (within 10 m of the nominal depth). The environment where these specimens were collected is classified as a South Atlantic coastal boulder community and is the site of frequent ice scouring of the substratum (Barnes 1999).

The size of each pycnogonid was determined using the following three standard morphometric proxies for age: span of the first pair of walking legs (measured when both legs are extended perpendicular to the long axis of the trunk, AB in Fig. 10.1), trunk length (measured from the base of the proboscis to the terminal end of the anus, CD in Fig. 10.1), and trunk width (measured directly behind the second walking legs, EF in Fig. 10.1). Missing limbs and any non-bryozoan epizoozoans were also noted.

The location of each bryozoan colony was mapped onto a generic template (Fig. 10.1), showing dorsal and ventral surfaces for each individual host. The number of individual colonies per host was counted, and the surface area of each individual colony was measured in dorsal and ventral view. As the host's body and leg segments are cylindrical, the entire colony could not always be measured digitally from just the dorsal and ventral views. In these cases, the area of individual

colonies was determined by measuring the diameter and length of the colony. This was used to calculate the maximum surface area of the colony assuming a perfect cylinder, which pycnogonid legs approximate. Finally, any of the colony's surface area from this cylinder that was missing was subtracted. Total bryozoan colony surface area for a given host was determined by adding up individual surface area measurements of all colonies on a host. Repeatability experiments indicate the PC-based image analysis system using digitized video images of the pycnogonids and bryozoans has a maximum measurement error of 3.2%.

Results and Discussion

The following nine species of pycnogonids were identified: *Nymphon australe* Hodgson (63% of individuals), *Decolopoda australis* Eights (9%), *Ammothea clausi* Pfeffer (7%), *Ammothea meridionalis* Hodgson (7%), *Pentanympyon antarcticum* Hodgson (7%), *Colossendeis megalonyx* Fry and Hedgpeth (3%), *Ammothea striata* (Möbius) (1%), *Pallenopsis pilosa* (Hoek) (1%), and *Pycnogonum gaini* Bouvier (1%). For *A. clausi*, *A. meridionalis*, *A. striata*, and *P. gaini* this is the first record for the South Orkney Islands (for a list of the known fauna of the South Orkney Islands, see Barnes et al. 2009, Appendix S1).

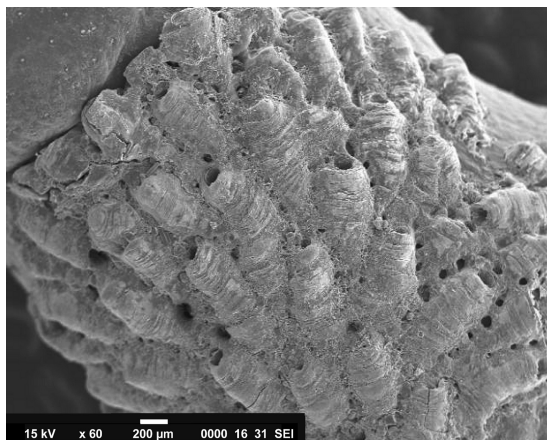
Of the 16 pycnogonids for which gender could be confidently determined, 56% were females, 44% were males, and 29% of the males were carrying eggs. As so few pycnogonids could be sexed, inter-gender comparisons were not tested.

Among the 115 pycnogonids, trunk length varied from 2.16 to 23.00 mm (mean = 7.52 mm, standard deviation = 4.19 mm). Trunk width ranged from 0.51 to 5.14 mm (mean = 1.58 mm, standard deviation = 1.12 mm). The span of the first walking legs ranged from 15.36 to 320 mm (mean = 65.89 mm, standard deviation = 59.15 mm).

Host surface area was not measured directly due to logistical constraints. Instead it was calculated assuming the trunk was a rectangular prism and each pair of legs was a cylinder as wide as the diameter of the encrusting bryozoan colonies (e.g., Fig. 10.3), which was measured, and as long as the span of the first pair of walking legs which was measured. Using Fig. 10.1, the host surface area was calculated as $2*CD*EF + 4*(2*\pi*diameter/2*(AB-EF))$. This resulted in a mean surface area of the hosts of 727 mm² (range = 170–3,500 mm², standard deviation = 656 mm²).

Though sponges and algae were also found living on the host pycnogonids, this study concerns itself only with bryozoans, as they were the most diverse and prevalent of the epizoozoans encountered. Seven cheilostome bryozoan species were identified: *Antarctothoa antarctica* Moyano and Gordon, *Antarctothoa dictyota* (Hayward) (Fig. 10.3), *Antarctothoa discreta* (Busk), *Crassimarginatella perlucida* (Kluge), *Osthimosia* sp. Jullien, *Thrypticocirrus phylactelloides* (Calvet), and *Xylochothridens rangifer* Hayward and Thorpe. The record of *C. discreta* is the first record for the South Orkney Islands. Two of the bryozoan species (*C. antarctica* and *C. dictyota*) found on the pycnogonids have also been reported from adjacent sites encrusting rocks (Barnes et al. 1996) and isopods (Key and

Fig. 10.3 SEM image of *Antarctothoa dictyota* (Hayward) encrusting a cylindrical pycnogonid leg



Barnes 1999). *C. antarctica* and *Osthimosia* sp. have been reported as epizoozoans on Antarctic echinoids (Linse et al. 2008). *C. antarctica* and *X. rangifer* have been reported as epizoozoans on Antarctic brachiopods (Barnes and Clarke 1995). The most commonly occurring species (*C. antarctica*) has been reported on a total of 13 different types of biotic and abiotic substrata (Barnes and Clarke 1995; Key and Barnes 1999). *C. antarctica* and *X. rangifer* are considered low specificity epibiotic species as they occur widely on various host organisms, but rarely on rocks (Barnes and Clarke 1995).

Pycnogonids are fouled by a variety of organisms in addition to the bryozoans reported here. These include foraminiferans, sponges, hydroids, anemones, brachiopods, barnacles, tunicates, serpulids, and molluscs (Hedgpeth 1964; King 1973; Pipe 1982; Barnes et al. 2004). Epizoic bryozoans on pycnogonids are rarely reported in the literature. King (1973) reported the pycnogonid *Nymphon gracile* fouled by the bryozoan *Electra pilosa*. Key and Barnes (1999) reported two species of bryozoans (*Celleporella antarctica* and *C. bougainvillea*) as epibionts on pycnogonids. This study increases the reported number of bryozoan species fouling pycnogonids from three to nine.

Of the 115 host specimens, 30 (26%) were fouled by bryozoans. The total number of bryozoan colonies found was 156. The number of bryozoan colonies per pycnogonid ranged from zero (for unfouled hosts) to 25 (mean = 1.36, standard deviation = 4.09). For the 30 fouled hosts, the number of bryozoan colonies ranged from one to 25 (mean = 5.20, standard deviation = 6.71).

The 156 bryozoan colonies occurred on a total of 310 host trunk/leg segments. Of the 156 bryozoan colonies, 101 (65%) occurred on only one segment. For example, of the 25 bryozoan colonies fouling the pycnogonid in Fig. 10.4, 23 occur on single segments, and only two spanned two segments. The maximum number of segments covered by a single colony was eight, and the mean was 1.99 segments (standard deviation = 1.86 segments). The larger colonies covered significantly more segments (linear regression, $R^2 = 0.534$, $p < 0.001$). The restriction of most colonies to a single segment of their host may reflect the movement of

Fig. 10.4 Pycnogonid *Decolopoda australis* Eights fouled by 25 bryozoan colonies indicated by lighter color on darker carapace of host. Specimen is 9 cm across



the host's exoskeleton at articulated segment joints (Manton 1978), which may restrict lateral growth of the bryozoan colony. This pattern has been documented on other arthropod hosts fouled by bryozoans (Key and Barnes 1999; Key et al. 1996b, 1999, 2000).

Most (95%) bryozoan colonies were found growing on the ovigerous and walking legs. Only 5% were on the central trunk region. This most likely is simply a function of the fact that the legs represent a much larger proportion (82%) of the surface area of the pycnogonids compared to the trunk (18%), based on the relative sizes of the segments in Fig. 10.1. As also reported by Barnes and Clarke (1995), the number of bryozoan colonies per leg segment was proportional to the length of the leg segment.

The exoskeleton of the pycnogonid is made of a hard cuticle, which in some species is covered by hair-like setae (King 1973). We noticed that those species with more setae, tended to have fewer and more fragmented colonies, so perhaps an additional function of the setae is to reduce fouling. In addition, the ovigerous legs are used for cleaning the walking legs, especially in the females, which don't carry eggs (King 1973). King (1973) reported the egg carrying males of the pycnogonid *Nymphon gracile* were more fouled by the bryozoan *Electra pilosa*. This was interpreted to be because the ovigerous legs were unavailable for cleaning, and the males not molting while carrying eggs. Thus, we could expect the number and size of bryozoan colonies to be greater on those hosts with eggs compared to those without, but no significant difference was found (t-tests, $p > 0.05$). However the sample size was small (only 11 of the 115 pycnogonids (10%) had eggs). Otherwise, our results support Arnaud and Bamber's (1987) suggestions that the ovigerous legs are not effective at removing encrusting bryozoans from appendages.

The surface area of individual colonies ranged from 0.19 to 171.53 mm², (mean = 18.84 mm², standard deviation = 27.92 mm²). The combined total surface area of bryozoan colonies on individual pycnogonids ranged from zero (for unfouled hosts) to 1,039.32 mm² (mean = 25.45 mm², standard deviation = 119.88 mm²). For the 30 fouled hosts, the combined total surface area of bryozoan colonies on individual pycnogonids ranged from 1.24 to 1,039.32 mm² (mean = 97.54 mm², standard deviation = 221.85 mm²). Based on the fouled host areas calculated, the

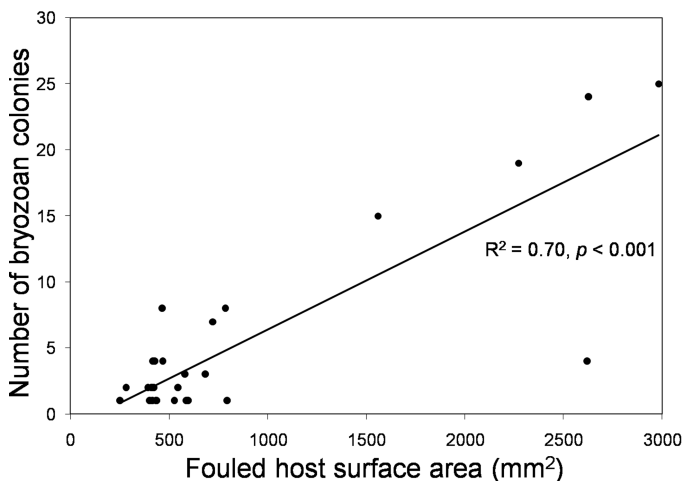


Fig. 10.5 Plot of number of bryozoan colonies versus surface area of fouled host pycnogonids

percentage of host surface area covered by bryozoans ranged from 0.1% to 72% (mean = 10%, standard deviation = 17%).

The Target Area Effect Hypothesis of MacArthur and Wilson's (1967) Theory of Island Biogeography predicts that larger islands should have higher species richness (Lomolino 1990). This is because larger islands have (amongst other things) higher immigration rates simply because they are a bigger target for 'propagules' (Stracey and Pimm 2009). If one considers the host pycnogonids as hard substratum 'islands' in a 'sea' of soft substratum muds, then it is predicted that there should be more bryozoans colonies on larger hosts as they provide a larger target for bryozoan larval settlement. As predicted by the Target Area Effect Hypothesis, the number of bryozoan colonies across species increases significantly with increasing host surface area when considering all hosts (linear regression, $R^2 = 0.202$, $p < 0.001$) or only fouled hosts (linear regression, $R^2 = 0.705$, $p < 0.001$; Fig. 10.5). As expected with more room to grow and more colonies, the larger hosts have a significantly larger total surface area of bryozoan colonies (linear regression, $R^2 = 0.062$, $p = 0.008$), but the correlation between host surface area and the percent of host surface area covered by bryozoans is not significant (linear regression, $R^2 = 0.021$, $p = 0.453$). The Target Area Effect has been documented on a variety of motile hosts fouled by bryozoans (Key and Barnes 1999; Key et al. 1996a, 2000).

Comparison with Other Substrata

How does the bryozoan species richness on the pycnogonids (i.e., seven species) compare with that on abiotic hard substrata from adjacent sites? In trawl samples in

Table 10.2 Comparison of fouling prevalence and epizoic bryozoan species richness among motile ephemeral hosts of varying size and latitude

Host	Host surface area (cm ²)	# of hosts	% of hosts fouled	# of bryozoan species	% of hosts fouled per cm ²	# of bryozoan species per cm ²	Latitude	Source
Pycnogonids	7	115	26	7	3.71	1.00	61°S	This study
Isopods	73	60	42	10	0.58	0.14	61°S	Key and Barnes (1999)
Brachyuran crabs	104	168	16	3	0.15	0.03	35°N	Key et al. (1999)
Horseshoe crabs	504	56	77	2	0.15	0.00	1°N	Key et al. (2000)
Trilobites	10	14,958	0.1	3	0.01	0.30	20°S ^a	Key et al. (2010)
Sea snakes	398	1,364	1	1	0.00	0.00	2°N	Key et al. (1995)

^aUpper Ordovician paleolatitude

the same region and at similar depths, eight species of encrusting bryozoans were found on other substrata, with only one species (*Thrypticocirrus phylactelloides*) in common (Barnes 1995). Likewise, 20 encrusting cheilostome bryozoan species were reported on rocks from 42 m depth (Barnes et al. 1996) and seven species from five recent trawls at 150–250 m (Barnes et al. 2009). Thus, bryozoan species richness on pycnogonids is of similar magnitude to that on adjacent abiotic substrata on the shallow shelf. Strict comparisons of richness per unit area between pycnogonids and abiotic substrata would be complex to interpret, as they would require measurements of substratum stability, surface rugosity, biofilms, etc.

In the shallow subtidal (5 m water depth) in the same area as in this study, 84% of the pycnogonids were fouled by bryozoans (Barnes and Clarke 1995). This is higher than the 26% reported here from 50 to 150 m water depth (but by fewer species). In contrast, settlement panels at 25 m in the same area as this study revealed only 2% cover after 21 months (Barnes 1996), but 90% of rocks at 42 m at this site had bryozoans on them (Barnes et al. 1996). Smaller and shallower rocks are more frequently disturbed (i.e., turned over by scouring) (Barnes et al. 1996) which may be similar in some respects to the disturbance caused by molting of the pycnogonids.

How does this 26% fouling prevalence of pycnogonids by epizoic bryozoans compare to other motile ephemeral hosts from different environments? Table 10.2 shows the results from published studies using the same methodologies as this study on the prevalence and epizoic bryozoan species richness among host organisms of varying sizes and from varying latitudes. All are motile, and all are ephemeral due to molting of their carapace (i.e., horseshoe crabs, brachyuran crabs, isopods, trilobites, and pycnogonids) or shedding of their skin (i.e., sea snakes). They range in size from a mean surface area of 7 cm² (i.e., the pycnogonids of this study) to 504 cm² (i.e., horseshoe crabs). The general trend, as expected from the

Target Area Effect Hypothesis of the Theory of Island Biogeography, is that larger hosts in Table 10.2 should have a higher prevalence of fouling, but it was not significant (linear regression, $R^2 = 0.217$, $p = 0.352$). The one outlier is the one non-arthropod host (i.e., the sea snake). Sea snakes are air breathers and spend part of their life out of water, which is detrimental to the bryozoans resulting in a lower prevalence of fouling (Key et al. 1995). Removing this outlier, the correlation is more significant (linear regression, $R^2 = 0.759$, $p = 0.054$).

Due to the Target Area Effect, the data must be corrected for the different sizes of the host substrata. This was done by dividing the percentage of hosts fouled and the number of bryozoan species by the surface area of the host. For both the percentage of hosts fouled per cm^2 and the number of bryozoan species per cm^2 , the pycnogonid hosts are an order of magnitude higher (Table 10.2). This may be attributed to one or more of the following factors. The carapaces of pycnogonids may be acting as refugia for the bryozoans from selective pressures of predation by their host, from ice scour, or from space competition on abiotic hard substrata.

The selective pressure for epibiosis on pycnogonid hosts may come from predation of bryozoans by the pycnogonids themselves. As discussed previously, some pycnogonids eat bryozoans (Table 10.1). As is true for most pycnogonids, it is not known if any of these species prey on the epizoic bryozoan species found in this study. Five of the nine pycnogonid species come from genera (i.e., *Ammothea*, *Colossendeis*, and *Pycnogonum*) known for having a well developed proboscis used to thrust into the tissue of their prey for feeding (King 1973). It is possible that by residing on an inaccessible part of their predator, such as on the trunk or the proximal segments of the legs, the bryozoans could avoid being consumed. Soule and Soule (1977) suggested that epibiotic bryozoans should in general experience reduced predation compared to those on abiotic hard substrata.

The selective pressure for epibiosis on pycnogonid hosts may come from the destruction of the benthic community by scouring from drifting, floating ice (Peck and Bullough 1993; Arntz et al. 1994; Conlan et al. 1998; Barnes 1999; Gutt 2000, 2001; Gutt and Piepenburg 2003; Barnes and Conlan 2007). This is especially true of bryozoans (Barnes 1999; Brown et al. 2004; Bader and Schäfer 2005). The sessile organisms cannot move out of the way to avoid the scouring (Gutt et al. 1996; Peck et al. 1999; Gutt 2001). In Antarctica, ice scour occurs down to 500 m (Barnes and Lien 1988; Lien et al. 1989; Gutt et al. 1996), well below the depths of this study (i.e., 50–150 m). Ice scour has been occurring over geological and evolutionary time scales, so the Antarctic shelf species are ice scour-adapted (Barnes and Conlan 2007). Motile animals, which are the first to recolonize scoured areas (Conlan et al. 1998; Peck et al. 1999; Lee et al. 2001), may also be the most adept at avoiding being killed by scours (Brown et al. 2004).

In polar environments, ice scour, not predation, is often the main structuring element of nearshore communities as almost all of the macrofauna is removed by the gouging and trampling effects of grounding of floating ice during the summer (Dayton 1990; Dayton et al. 1994; Gutt et al. 1996; Peck et al. 1999; Brown et al. 2004). This has been shown for bryozoans in particular (Barnes and Bullough 1996). Therefore epibiosis on motile hosts that eliminates competition for space

on hard substrata as well as avoids ice scour should be selectively advantageous. Pycnogonids could avoid icebergs by walking or swimming, but as they do both so slowly (King 1973), they would most likely just be pushed out of the way due to their almost neutral buoyancy (Morgan 1977; Schram and Hedgpeth 1978).

This physically controlled (i.e., high frequency of substratum disturbance by ice) view of the Antarctic benthos (Barnes 1999; Barnes and Conlan 2007), especially of epibiosis on motile hosts, is in contrast to the biologically accommodated view of Gutt and Schickan (1998). The latter interpret Antarctic epibiosis as a result of evolution in a physically stable environment leading to a biologically accommodated community. Unfortunately, their study excluded encrusting forms, such as bryozoans, which are the most common epizoozoans.

Just as the actions of gouging, scraping, and crushing predators impacted the evolution of growth form in bryozoans (McKinney et al. 2003), the actions of gouging, scraping, and crushing icebergs may have impacted the evolution of epibiosis in polar bryozoans. If this is true, then the bryozoan diversity on motile hosts should be higher in polar regions. Table 10.2 shows this exact pattern. The number of epizooic bryozoans species per host is usually three or less, but there are two outliers (i.e., the isopods with ten species and pycnogonids with seven species, both of which are from high latitudes, in this case the Antarctic).

The selective pressure for epibiosis on pycnogonid hosts may come from space competition on abiotic hard substrata. In sessile communities, space is often a limiting resource (Dayton 1971; Paine 1974; Jackson 1977), and this is especially true for Antarctic bryozoans (Barnes and De Grave 2002; Barnes 2005). A more restricted but important substratum for sessile organisms in the Antarctic is motile animal substrata (Barnes et al. 2004) which may be a more stable substratum than easily overturned rocks (Gutt 2000), even despite the instability caused by molting. Epibiosis is a frequent solution to the problem of limited conventional (i.e., hard, abiotic) substratum space (Wahl 1989, 2009) as epibionts may benefit from improved survivorship (Lohse 1993) and/or feeding (Laihonen and Furman 1986) compared to those on abiotic hard substrata. Bryozoans are a common, and often the most abundant, faunal component of epibiota on a variety of host substrata, and most recently Wahl (2009: Fig. 4.2) reported that there are more epizooic bryozoan species than any other group of metazoans.

Costs and Benefits of Epibiosis

Epibiosis creates a variety of costs and benefits to both the epizoozoan and the basibiont (Wahl 2009). Possible detrimental effects to the bryozoans include: (1) unstable substratum (e.g., due to movement of articulated joints and molting; molting is especially a problem if the host molts before the bryozoan reaches a size large enough for sexual reproduction), (2) risky habitat change (e.g., host movement to water of different pressure, temperature, and/or salinity not conducive to bryozoan growth), and (3) shared doom (e.g., predation of host resulting in

accidental predation of its epizoid bryozoans, but see discussion below of minimal predation on pycnogonids).

Possible beneficial effects for the bryozoans include: (1) increased substratum area (e.g., reduced competition for space among bryozoans compared to abiotic hard substrata), (2) favorable hydrodynamics (e.g., host movement may improve filter feeding of bryozoans by lifting them out of the bottom boundary layer), and (3) free transport (e.g., avoiding ice scour by being on a motile host as compared to a abiotic hard substratum as well as improved gamete dispersal and increased geographic range).

Possible detrimental effects to the pycnogonids include: (1) increased weight; probably not a major problem due to the almost neutral buoyancy of the epizoids, (2) increased drag; probably not a major problem due to the encrusting nature of the epizoids and the slow walking movement of the hosts, (3) decreased flexibility; possibly a problem as 35% of the bryozoan colonies extended over at least two body segments, (4) shared doom (e.g., predation of bryozoans probably not a major problem as the epizoid bryozoan lifestyle probably reduces their susceptibility to predation via camouflage), and (5) increased susceptibility to predation (e.g., if the bryozoan colonies increase the host's weight and drag, decrease its flexibility, and attract predators of the bryozoans which may also eat the host). There were a few hosts where bryozoans had grown over the eyes of the pycnogonid, suggesting that the epibionts were impairing the host's sensory perception, which could increase susceptibility to predation.

The possible beneficial effect for the pycnogonids is camouflage. For example, Vance (1978) documented a decrease in predation by starfish on clams, which were covered by bryozoans. By camouflage we include Wahl's (2009) concept of insulation (i.e., hiding of the host from optical, tactile, and chemical detection by its prey). As only 10% of the host pycnogonids are covered on average by bryozoans, this benefit may not apply to many of the pycnogonids. The only other reported percent epibiont cover of pycnogonids was 1% from the North Sea (Pipe 1982). In addition, as pycnogonids have such little tissue and such a high proportion of cuticle to tissue, they are not a common prey item of predators which include anemones, isopods, crabs, shrimp, and fishes (King 1973; Arnaud and Bamber 1987).

Conclusions

In this study of epizoid bryozoans fouling pycnogonids from Antarctica, nine species of pycnogonids were identified containing 156 bryozoan colonies belonging to seven cheilostome species. The percentage of host surface area covered by bryozoans averaged 10%. As predicted by the Target Area Effect Hypothesis of Island Biogeography Theory, the number of bryozoan colonies increased significantly with increasing host surface area. Of the 115 pycnogonids, 26% were fouled by bryozoans.

The bryozoan species richness on pycnogonids is similar to that on adjacent abiotic hard substrata. Compared to the other motile host animals, the number of bryozoan species per unit host surface area is an order of magnitude higher on

pycnogonids. The carapaces of pycnogonids may be acting as refugia for the bryozoans from hard substratum competition, ice scour, and predation by their host. Living on a motile host, the bryozoans may also benefit from improved feeding and gamete dispersal. The pycnogonids may not accrue any benefits from the bryozoan fouling except possible reduced predation resulting from camouflage created by the patchy nature of the bryozoan colonies on the pycnogonids' carapaces.

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