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Bryozoan colonization of the marine isopod *Glyptonotus antarcticus* at Signy Island, Antarctica

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Abstract Sixty specimens of the giant marine isopod *Glyptonotus antarcticus* Eights, collected from Borge Bay, Signy Island, Antarctica were examined for epizoids. Ten species of cheilostomatid bryozoans were found on the isopods. The purpose of the study was to quantify the prevalence, intensity, abundance, and spatial distribution of the bryozoans on the isopods. The proportion of isopods colonized was 42%. The larger isopods had both significantly more epizoic bryozoan colonies and species. The greatest density of bryozoans was on the fused pleon and telson. There was no significant difference between the dorsal and ventral abundance of bryozoan colonies. The diversity of epizoic bryozoans on the isopods is higher than on other host organisms from more stable environments. This may be because of active selection by settling larvae. The frequency of local substrata being scoured by ice is high around Signy Island, so there may be a selective advantage in colonizing a motile host.

Introduction

It has been well documented that in benthic communities, substratum space is often a limiting resource and competition is considered intense (e.g., Connell and Keough 1985). The recruitment and growth of colonizers on the external surfaces of other organisms (i.e., epibiosis) is a viable alternative in such environments. Epibiosis is particularly common on sessile host organ-

isms with permanent (not molted) external surfaces (e.g., brachiopods, molluscs, and corals), but may also occur on motile hosts with ephemeral external surfaces (e.g., vertebrates, merostomatans, and crustaceans).

This study begins to address the question of whether epibiosis on motile ephemeral substrata is selectively more advantageous in benthic environments where the conventional abiotic substratum is frequently disturbed. This question is approached using bryozoans living on the giant Antarctic marine isopod, *Glyptonotus antarcticus* Eights, in an environment where ice scour is frequent.

This paper uses terminology as follows. The prevalence of colonizing refers to the proportion of infested host individuals. Abundance is the number of symbionts per host individual, and intensity is the number of symbionts per infested host individual.

The particular aims of this study are: (1) to quantify the incidence of bryozoan colonization of an ephemeral motile host in an environment where the abiotic substratum is frequently disturbed by ice scour; (2) to determine the taxonomic composition of the epizoic bryozoan community on *Glyptonotus antarcticus* at Signy Island; (3) to determine how the size and diversity of the epizoic bryozoan community vary with host size; and (4) to quantify the spatial distribution of bryozoan colonies on the cuticle of the isopods.

Ice has been described as influencing the nearshore Antarctic benthic environment and inhibiting benthos in several distinct ways. The ecology of the intertidal and immediate subtidal zones may be most influenced by the seasonal formation of an ice foot (Barnes 1995a,b). Scour by floating ice is a major cause of local faunal denudation, zonation, and arguably diversity (Hedgpeth 1971). Anchor ice and ice shelves may influence higher latitude communities (Dayton et al. 1970). Generally, the frequency and degree of ice influence decrease with depth (Arntz et al. 1994; Barnes 1995a). Observations and other studies (e.g., Barnes 1996) at the present study site and its depth (12 m) suggest that the frequency of ice-induced catastrophic benthic disturbance may be as often as biennial.

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At the study site there is a zone from mean low-water neap tide level to 1.5 m depth that is essentially devoid of organisms because of the seasonal formation of an ice foot (Barnes 1995b). Below this, ice scour limits community development such that sessile animals first occur at 2 m depth and are generally scarce above 3 m (Barnes 1995b). Disturbance by ice processes is the major factor in controlling the spatial distribution, abundance, and diversity of bryozoans (and other benthos) below 3 m in the area (Barnes 1995a).

The giant Antarctic marine isopod, *Glyptonotus antarcticus* Eights, was selected as the host organism for the present study because its abundance and large size make it easily collectible. *G. antarcticus* is a highly motile (White 1970) eurybathic species (Chaigneau et al. 1991), and it commonly occurs in the intertidal and subtidal zones.

Materials and methods

The study was carried out in Factory Cove, which is a small inlet off Borge Bay next to the British Antarctic Survey base. The base is located on the east side of Signy Island in the South Orkney Islands off the Antarctic Peninsula at 60°43'S, 45°36'W (Fig. 1).

The water depth in Borge Bay ranges from 0 to 30 m with a mean of 10 m (Clarke et al. 1988). The collection site was at 12 m depth in an area where the substratum consists of loose pebble to boulder-sized rocks in a sand/mud matrix.

The isopods were collected using SCUBA in February 1992. After collection, the isopods were held in flow-through aquaria. First, the size of each isopod was measured using Vernier calipers. Length was measured as the distance from the anterior tip of the cephalothorax to the posterior tip of the telson, and width was measured as the maximum dimension perpendicular to the length (Fig. 2) (i.e., at the fourth free thoracic segment (White 1970)).

Second, the number and spatial distribution of bryozoan colonies were recorded for each isopod. The cuticle of the isopod was treated as several distinct sectors (Fig. 2). The dorsal surface was separated into two sectors: (1) the fused cephalothorax and pereon; and (2) the fused pleon and telson. The ventral surface was separated into three sectors: (1) the fused cephalothorax and pereon; (2) the fused pleon and telson; and (3) the pereopods. The seven pairs of pereopods on each of the isopods were grouped. Results for pereopods were separated into seven segments: coxa, basis, ischium, merus, carpus, propodus, and dactylus (Fig. 2). The relative size of each of these sectors was measured on Fig. 2 with a personal computer-based image analysis system using digitized video images of the dorsal and ventral surfaces of the host. Repeatability experiments indicate a measurement error of less than 3.4%.

Third, the taxonomic assignment of each bryozoan colony was determined. A binocular microscope suspended over a water-bath, at ambient temperature, was used in identification, so specimens were kept alive and then returned to the sea.

Results

The incidence and diversity of epizoans

Sixty *Glyptonotus antarcticus* ranging in length from 12 to 105 mm (mean = 83.2 mm; SD = 19.8 mm) and width from 6 to 51 mm (mean = 40.5 mm; SD = 9.5 mm) were collected. Of these, 25 (42%) were colonized by

bryozoans. In addition to numerous serpulid worms, ten species of cheilostomatid bryozoans were found on the isopods (Table 1).

The number of isopods colonized by any one bryozoan species ranged from 1 for *Hippadenella inerma*, *Lacerna eatoni*, and *Smittina rogickae* to 18 for *Celleporella antarctica* with a mean of 4.6 (Table 2). This represents a prevalence of 1.7–30.0% (mean = 7.7%). A total of 90 bryozoan colonies were found on the isopods. The mean abundance of bryozoan colonies per host was 1.5. The mean intensity of bryozoan colonies per host ranged from 1 to 12 (mean = 3.6) (Table 2). The abundance of bryozoan colonies per host for any one bryozoan species ranged from one (all bryozoan species) to six (*C. antarctica* and *Inversiula nutrix*) (Table 2).

The number of bryozoan species colonizing any one isopod varied from 0 to 4. There was a positive significant correlation between host size (i.e., cuticle length × width) and the number of colonizing bryozoan species (Pearson correlation coefficient; $P = 0.004$). Like most juvenile arthropods, small isopods molt more frequently and thus are less likely to be colonized (Key et al. 1997). An alternative test revealed that the 30 smallest hosts were colonized by significantly fewer bryozoan species (mean = 0.4; SD = 1.0) than the 30 largest hosts (mean = 1.1; SD = 1.2) (t -test; $P = 0.01$).

The number of bryozoan colonies on any one isopod ranged from 0 to 12. There was a positive correlation between host size (i.e., cuticle length × width) and the number of epizoic bryozoan colonies, but it was not significant ($P = 0.073$). A t -test revealed that colonized hosts were significantly ($P < 0.001$) larger than non-colonized hosts (mean = 4,173 mm²; SD = 687 mm² vs mean = 3,100 mm²; SD = 1445 mm², respectively).

Spatial distribution of epizoans

The spatial distribution of epizoans on the host cuticles was not random. The distribution of epizoans is a function of the settlement preferences of their larvae, the relative surface area of the various sectors of the cuticle, and differential post-settlement mortality (e.g., due to abrasion). All sectors of the isopod had at least one epizoan except for the basis, ischium, and merus of the pereopods (Table 3). After compensating for the different relative areas of the various sectors of the host's cuticle, the abundance of epizoic bryozoan colonies was compared among the sectors on the 60 hosts using chi-squared tests. There were significantly ($P = 0.048$) more epizoic bryozoan colonies on the fused pleon and telson than on the fused cephalothorax and pereon. The ventral surface of the fused cephalothorax and pereon was significantly ($P = 0.007$) more colonized by bryozoan colonies than its dorsal surface. There was no significant difference between the number of bryozoan colonies on the dorsal and ventral surfaces of the fused pleon and telson ($P > 0.05$). The isopod's entire dorsal surface was not colonized significantly more or less than the

ventral surface ($P > 0.05$). There were more bryozoan colonies on the pereopods' propodus and dactylus and fewer on the coxa, basis, ischium, and merus.

Discussion

Bryozoans are ubiquitous colonizing organisms that are known to live on a variety of planktonic (Taylor and Monks 1997), nektonic (Key et al. 1995, 1996a), and motile ephemeral benthic (Key et al. 1996a,b, in press a,b) hosts. They have been reported as epizoans on various motile hosts in Antarctica as well, including holothurians and pycnogonids (Moyano 1972a; Barnes

and Clarke 1995a). Bryozoans have previously been found as epizoans on marine isopods (Moyano 1972a, 1986, 1989; Campbell 1992).

In all these cases, the frequency at which a host molts will affect the prevalence of epizoans (Key et al. 1996a, 1997). *G. antarcticus* has a long intermolt period of greater than 100 days and sometimes up to 730 days, and ecdysis frequency decreases with increasing size and presumably age (White 1970). Upon reaching maturity,

Fig. 1 **A** Position of Signy Island in relation to the South Orkney Islands and the Antarctic Peninsula. *Inset* shows position of Borge Bay in relation to Signy Island. **B** Borge Bay showing position of study site (*) in Factory Cove. Modified from Barnes and Clarke (1995b, Fig. 1)

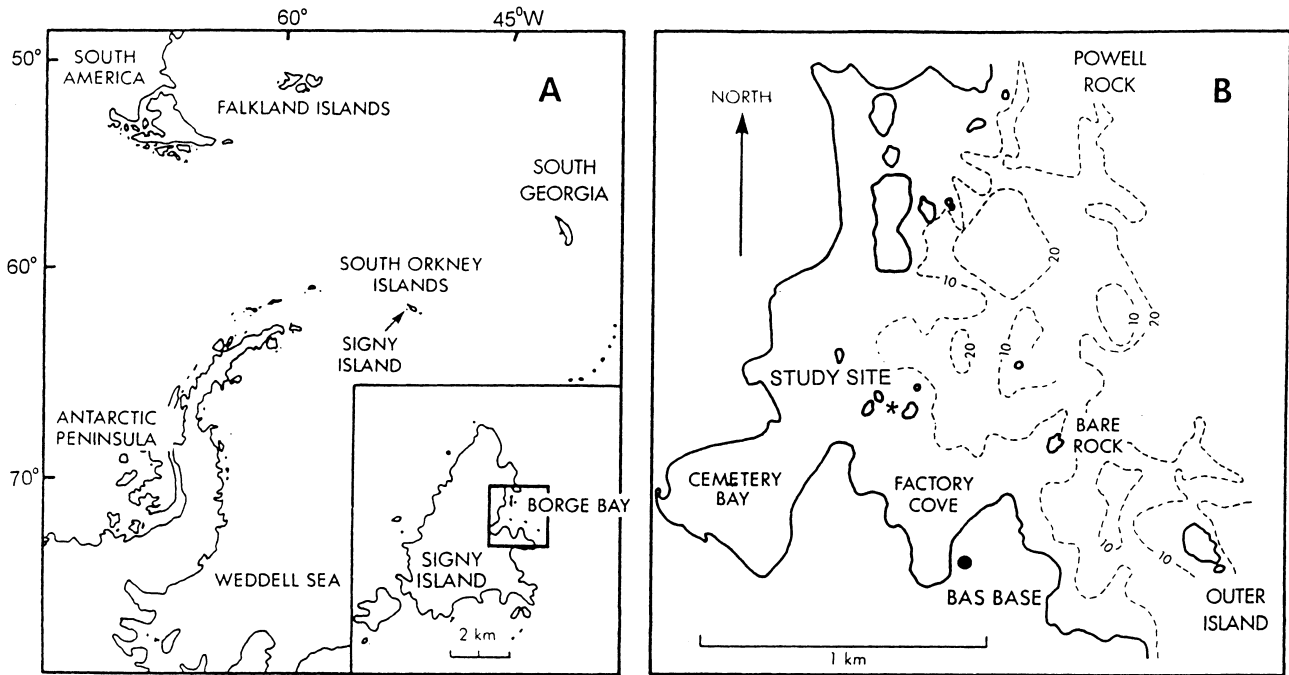


Fig. 2 **A** Dorsal and **B** ventral views of *Glyptonotus antarcticus* showing the sectors of the cuticle examined: 1 fused cephalothorax and pereon sectors, 2 fused pleon and telson sectors, a to f pereopod sectors (a coxa, b basis, c ischium, d merus, e carpus, f propodus, g dactylus). The sectors of the cuticle are not labelled on the ventral view. Pereopod segments are not shown and labelled on all pereopods. Modified from Eights (1852)

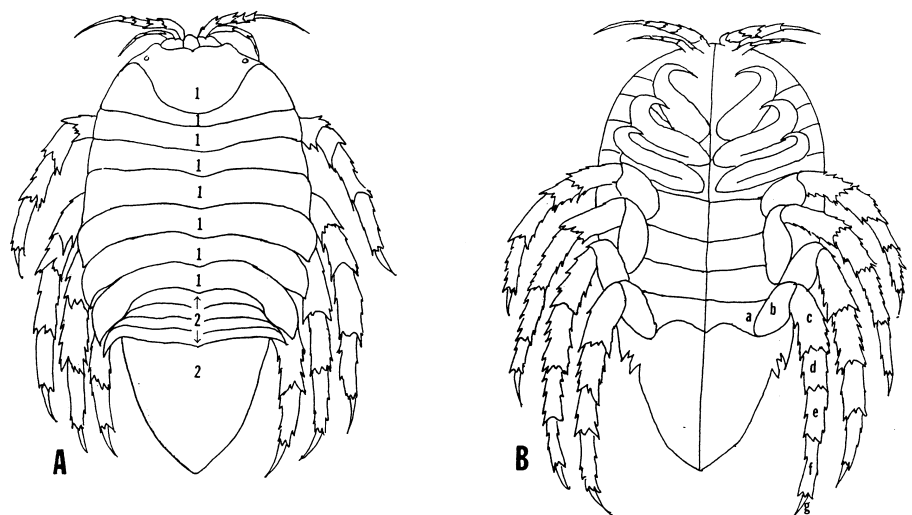


Table 1 Epizoic bryozoan species found living on *Glyptonotus antarcticus* and their previously documented depth ranges and substrata (1 Barnes and Clarke 1995a, 2 Hayward 1995, 3 Hayward and Thorpe 1988, 4 Barnes 1995a, 5 Barnes and Clarke 1994, 6 Barnes and Clarke 1995b, 7 Rogick 1956, 8 Moyano and Gordon 1980, 9 Moyano and Wendt 1981, 10 Hayward and Taylor 1984, 11 Moyano 1986, 12 Winston and Hayward 1994, 13 d'Orbigny 1847, 14 Busk 1876, 15 Busk 1879, 16 Jullien 1888, 17 Calvet 1909, 18 Powell 1967, 19 Androsova 1972, 20 Moyano 1972a, 21 Moyano 1975, 22 Moyano 1979, 23 Viviani 1977, 24 López-Gappa 1985, 25 Hayward 1993, 26 Calvet 1904, 27 Gordon 1982, 28 Hayward 1991, 29 Moyano 1972b, 30 Barnes 1995b)

Species	Depth range (m)	Rocks	Shells	Algal fronds	Ascidians	Brachio-pods	Bryozoans	Holothurians	Hydroids	Limpets	Octocorals	Polychaete setae	Pycnogonids	Sponge spicules	Ship hulls	Total substrata	References
<i>Aimulosia antarctica</i> (Powell)	6–19	x						x								2	1,2
<i>Arachnopusia inchoata</i> Hayward and Thorpe	5–250	x			x											3	1–6
<i>Celleporella antarctica</i> Moyano and Gordon	6–67	x		x	x	x	x	x	x	x	x	x	x			12	1, 2, 7–12
<i>Celleporella bougainvillei</i> (d'Orbigny)	0–165	x		x	x	x	x	x	x	x	x	x	x			13	1, 2, 6, 8, 11, 13–24
<i>Celleporella dictyota</i> Hayward	?														x	1	2, 25
<i>Harpezia spinosissima</i> (Calvet)	6–40	x		x							x					4	1, 2, 7, 12, 26, 27
<i>Hippadenella inerma</i> (Calvet)	8–30	x														1	2, 17, 28
<i>Inversula nutrix</i> Jullien	2–25	x				x			x							3	1, 2, 5, 6, 12, 22, 29, 30
<i>Lacerna eatoni</i> (Busk)	6–20	x				x										2	1, 2, 14, 15, 28
<i>Smittina rogickae</i> Hayward and Taylor	< 75	x														1	1, 2, 10
Total species		9	2	3	3	5	2	3	2	3	3	2	2	2	1		

Table 2 Prevalence and intensity of colonizing of *Glyptonotus antarcticus* for each bryozoan species (\pm SD)

Species	No. of isopods colonized	% of isopods colonized	Range in no. of colonies per fouled host	Mean no. of colonies per fouled host	Total no. of colonies per fouled host
<i>Celleporella antarctica</i>	18	30.0	1–6	2.1	37
<i>Celleporella bougainvillei</i>	8	13.3	1–5	2.4	19
<i>Inversiula nutrix</i>	7	11.7	1–6	2.9	20
<i>Arachnopusia inchoata</i>	3	5.0	1	1.0	3
<i>Celleporella dictyota</i>	3	5.0	1	1.0	3
<i>Aimulosia antarctica</i>	2	3.3	1	1.0	2
<i>Harpecia spinosissima</i>	2	3.3	1–2	1.5	3
<i>Hippadenella inerma</i>	1	1.7	1	1.0	1
<i>Lacerna eatoni</i>	1	1.7	1	1.0	1
<i>Smittina rogickae</i>	1	1.7	1	1.0	1
Mean	4.6 \pm 5.3	7.7 \pm 8.9	1.0–2.5	1.5 \pm 0.7	9.0
All species combined	25	41.7	1–12	3.6 \pm 3.0	90

Table 3 Number of bryozoan species and colonies per sector of cuticle of isopod

Sector of cuticle	No. of bryozoan species	Range in no. of colonies per host	Mean no. of colonies per host	Total no. of colonies per host
Dorsal fused cephalothorax and pereon	5	0–3	0.17	10
Dorsal fused pleon and telson	5	0–4	0.23	14
Dorsal total	6	0–7	0.40	24
Ventral fused cephalothorax and pereon	8	0–5	0.55	33
Ventral fused pleon and telson	5	0–3	0.30	18
Coxa	1	0–1	0.02	1
Basis	0	0	0.00	0
Ischium	0	0	0.00	0
Merus	0	0	0.00	0
Carpus	2	0–1	0.03	1.3
Propodus	3	0–1	0.11	6.8
Dactylus	2	0–1	0.10	5.8
Pereopod total	3	0–3	0.25	15
Ventral total	10	0–8	1.10	66
Dorsal and ventral fused cephalothorax and pereon	9	0–5	0.72	43
Dorsal and ventral fused pleon and telson	6	0–6	0.53	32
Total	10	0–12	1.50	90

males are, on average, 47.5 mm wide and females 41.4 mm wide (White 1975). The 60 isopods in the present study (width range: 6–51 mm, mean = 40.5 mm) probably included a mix of immature and mature individuals with different molting frequencies.

The results from the present study indicate that the abundance and diversity of bryozoan colonies increase with host size. This may be caused by increasing target size for the bryozoan larvae and/or an ontogenetic decrease in the frequency of host molting. The latter has also been suggested for the marine isopod *Serolis* (Moyano 1989).

The physical disturbance of shallow benthic marine environments caused by ice creates a long-term hazard in both ecological and evolutionary time (White 1977). The frequency of ice scour in places such as the study site means that on an evolutionary time scale, ice scouring will have a major impact on benthic invertebrates (Peck and Bullough 1993). Barnes and Clarke (1995a) showed that the composition of the epizoic bryozoan community

at the study site is much different from that on adjacent abiotic substrata. This suggests that some epizoic bryozoans may have evolved a different substratum niche from those bryozoans on hard substrata.

Bryozoans are generally poor competitors for substratum space (Russ 1982) and as a result tend to be more common on ephemeral (McKinney and Jackson 1989) and/or recently disturbed substrata (Barnes 1995a,b). Bryozoans are an important part of communities in early stages of development on newly exposed substrata, especially at high latitudes (e.g., Barnes 1995a,b). They have a greater survivability on motile, ephemeral substrata such as those provided by the exoskeletons of isopods.

The most common organisms in the shallow, ice-impacted zone are transient populations of motile organisms such as limpets, amphipods, and isopods (Barnes 1995b). This is because epibenthic sessile organisms have little chance of escaping moving ice, unlike motile organisms such as *G. antarcticus* (Dayton et al. 1970).

The diversity of bryozoan species on motile ephemeral substrata in environments without frequent disruption of the benthos by ice (e.g., Key et al. 1995, 1996a,b, in press a,b) is an order of magnitude lower than the diversity of epizoic bryozoan species on *G. antarcticus*. Because of the previously mentioned frequent ice scour in the study area, there may be more intense selective pressure for epibiosis to evolve in multiple lineages. Epibiosis on motile ephemeral substrata in the Antarctic may be the evolutionary result of the long-term disturbance of the shallow benthos by ice.

Epibionts that are more opportunistic in their substratum selection can be considered generalists as compared to specialists, which exhibit greater substratum selectivity. The 10 bryozoan species found on *G. antarcticus* have also been reported on 14 other substrata (Table 1). *Celleporella bougainvillei* and *C. antarctica*, which have previously been reported on 12–13 of these substrata, could be considered low specificity (i.e., generalist) colonizing species. The other species, which have been reported on four or fewer substrata, could be considered as higher specificity (i.e., specialist) species. The diversity of substrata (both inorganic and animal) utilized by a species is a function of substratum selectivity and of how common or well studied the species is. Species may be found on a lower diversity of substratum types because: (1) they truly specialize on fewer substrata; (2) because they are rare or less well studied and have simply not been found on a higher diversity of substrata; or (3) because they live at depths with a lower diversity of available substratum types. *Arachnopusia inchoata* and *I. nutrix* are two of the most common species in the study area (Barnes and Rothery 1996), so their small number of substrata exploited probably does represent a higher degree of substratum specificity. *C. bougainvillei* and *C. antarctica* are also very common in the study area (Barnes and Rothery 1996).

It appears that this relationship between the epizoic bryozoans and their isopods is not just opportunistic and fortuitous. The high diversity of epizoic bryozoans in this environment where the substratum is frequently scoured by ice suggests that epibiosis may be selectively advantageous even though the host molts. This is supported by the high specificity in substratum selection exhibited by most of the bryozoans and the lower diversity of bryozoans found on rocks at the site (Table 1).

Alternatively, other environmental factors may be involved or these Antarctic bryozoans may be more opportunistic in their substratum utilization. This is supported by the higher prevalence of rocks with bryozoans (56%) compared to the isopods (42%) (Barnes et al. 1996).

Finally, why did the bryozoans preferentially settle on certain sectors of the isopods' cuticles? Bryozoan larvae do not haphazardly select settlement sites. They show preferences for specific substrata which are often based on the orientation of the substratum (e.g., Pomerat and Reiner 1942), how cryptic the substratum

is (e.g., Lescinsky 1993), or the presence of a certain microflora (e.g., Scholz and Krumbein 1996).

Various host behaviors can affect the distribution of epizoans, as has been shown with epizoic foraminiferans on Arctic isopods (Svavarsson and Davidsdottir 1994, 1995). Host feeding could make small food particles available to ventrally located bryozoans. The spatial distribution of epizoic bryozoans on motile hosts may reflect those areas (e.g., dorsal surface) incurring the least abrasion and/or the least fouling by sediment during motion of the host. This host species does not burrow (Meyer-Rochow 1980), and therefore potential abrasion of epizoans is reduced as compared to some burrowing brachyuran Crustacea and xiphosuran Chelicerata whose behavior has been implicated in negatively impacting epizoans (Key et al. 1996a,b, 1997, in press a,b).

In addition, host copulation could abrade bryozoans. Extended, pre-copulative pairing is common in isopods, and in this species, males carry pre-adult females for as long as 190 days preceding the ecdysis of the female to maturity (White 1970). Copulation occurs with the male and female ventral sides in apposition (White 1970). It was expected that this extended pairing and copulation would result in the abrasion of epizoic bryozoans and a reduced intensity of bryozoans on the ventral surface. However, no difference in colonization was found between the dorsal and ventral surfaces.

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