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Cold Comfort: Systematics and Biology of Antarctic Bryozoans

Judith E. Winston

ABSTRACT. Antarctic bryozoans are spectacular. They are often larger and more colorful than their temperate relatives. Antarctic bryozoans are also outstanding in their diversity. Well over 300 species have been described, and new descriptions continue to appear. In the U.S. Antarctic Research Program (USARP) collections we have identified 389 species so far, mostly belonging to the Cheilostomata, the dominant order in Recent seas. Much about their ecology can be learned from study of the abundant material preserved in the USARP collections. Yearly growth bands demonstrate that colonies may live for decades and that growth rates are very close to those of related temperate species. The presence of embryos in the brood chambers of many species allows determination of seasonality of reproduction and fecundity of colonies of different sizes. A large proportion of Antarctic bryozoan species (81% for cheilostomes) are endemic. Endemic groups include bizarre and unusual forms in which polymorphism, the occurrence of individuals specialized to perform different tasks, is highly developed. Behavioral studies carried out with living colonies in the Antarctic have shown how different polymorphs function in cleaning and protecting colonies from trespassers or predators: capturing motile animals such as amphipods, polychaetes, and nematodes and sweeping colonies free of debris.

INTRODUCTION

The more than 5,000 members of the phylum Bryozoa, belonging to the Lophotrochozoa group of protostome invertebrates, are found in marine and freshwater habitats worldwide, including the seas that surround Antarctica. Bryozoans are colonial, benthic, sessile animals. They reproduce asexually by budding new members of a colony or, in some cases, by fragmentation of an existing colony. Colonies also reproduce sexually. Embryos, often brooded, develop into free-swimming larvae that settle and metamorphose to begin a new colony. Although individual bryozoan zooids are microscopic (ranging from about 0.30 to 2.0 mm in length), colonies can be quite large, consisting of many thousands of individuals and, in some places, creating three-dimensional benthic habitats that serve as shelter, feeding, and nursery grounds for other organisms. Bryozoans are suspension feeders, part of the benthic biological filter system made up of sessile filter-feeding animals. Bryozoans also produce physical and chemical defenses against their enemies. Many members of the dominant Recent order of bryozoans, the cheilostomes, have developed a high degree of polymorphism,

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with heterozooids specialized for reproduction, attachment, cleaning, and defense. Their chemical defenses consist of natural products such as alkaloids or terpenoids, which are toxic or discouraging to predators or disease agents (Sharp et al., 2007).

The chilly Antarctic seafloor, where seawater temperatures are near or below freezing year-round, might not seem like an ideal habitat for benthic organisms. Food is plentiful for only part of the year, and, in shallow water, icebergs may scour the seafloor, destroying everything they touch. Yet more than 300 species of bryozoans have been found there, including a large number of distinctive endemic taxa. This paper will discuss some results from more than 20 years of study of the U.S. Antarctic Research Program (USARP) bryozoan collections by the author and collaborators A. E. Bernheimer, P. J. Hayward, and B. F. Heimberg.

TAXONOMY AND DISTRIBUTION OF USARP BRYOZOANS

BRYOZOAN COLLECTION IN THE ANTARCTIC

The beginning of bryozoan collecting in the Antarctic dates from the last part of the nineteenth century and the early part of the twentieth, the era of the national expeditions for the exploration of the continent. Although a few species from Cape Adare in the Ross Sea were recorded by Kirkpatrick (1902), the first major report on the bryozoan fauna was by Waters (1904) on the 89 taxa collected in the Bellingshausen Sea by the *Belgica* Expedition. Analysis of collections from other expeditions followed (Calvet, 1904a, 1904b, 1909; Kluge, 1914; Thornely, 1924; Livingstone, 1928). A second wave of collecting began with a series of voyages carried out by the British Discovery Investigations (of which some of the bryozoans appeared in Hastings, 1943). The first U.S. specialist to study Antarctic bryozoans was Mary Rogick, who published 13 papers on the taxonomy of the bryozoans collected during the U.S. Navy's 1947–1948 Antarctic Expedition between 1955 and 1965 (summarized in Rogick, 1965).

THE USARP BRYOZOAN COLLECTIONS

The International Geophysical Year of 1957–1958 marked a new era of marine research and benthic collecting in the Antarctic. The USARP bryozoan collections consist of more than 5,000 lots collected by various U.S. research groups between 1958 and 1982. The earliest lots in the collection were obtained during benthic studies by Stanford University researchers working in the McMurdo

Sound and the Ross Sea. Later systematic collections of all benthos, including bryozoans, were made by scientists and technicians during oceanographic cruises of USNS *Eltanin* (1962–1968) and R/V *Hero* (1968–1982). These collections were returned to the United States to be processed by technicians at the Smithsonian Oceanographic Sorting Center (SOSC) and were distributed to taxonomic specialists on each group. The stations from which bryozoans were collected ranged from 10°W to 70°E but were concentrated in the following Antarctic and subantarctic areas: the Ross Sea, the Antarctic Peninsula, off the islands of the Scotia Arc, and from Tierra del Fuego to the Falkland Islands (Figure 1).

My involvement with the collections included training SOSC technicians in bryozoan identification and working with technicians and volunteers at SOSC, the American Museum of Natural History, and the Virginia Museum of Natural History to sort and identify those lots, now separated into almost 8,000 vials and jars. It also led to a 1985 NSF grant to work at Palmer Station to study ecology and behavior of living colonies of some Antarctic species. In spite of the large amount of marine biology carried out in Antarctica, relatively little attention had been paid to benthic community structure or to the ecology of benthic organisms. For this reason, as part of the project on behavioral and chemical ecology of Antarctic bryozoans,
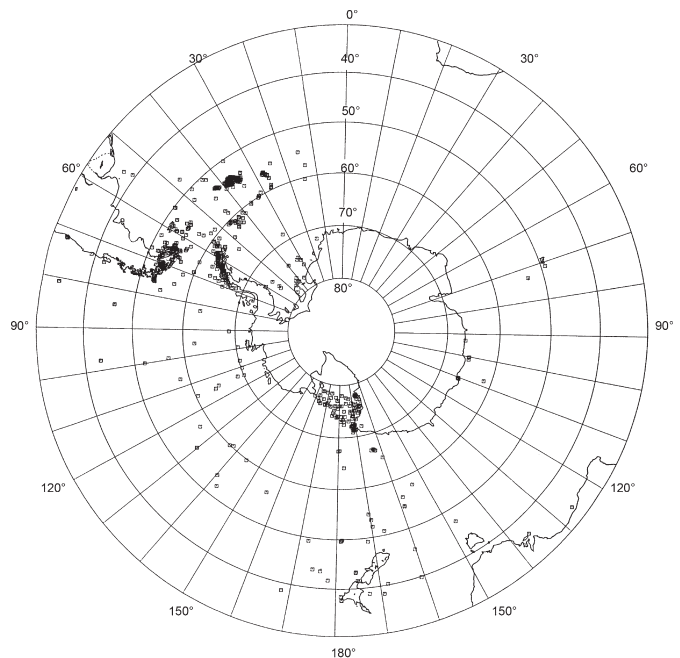

FIGURE 1. Location of USARP stations containing bryozoans processed by the Smithsonian Oceanographic Sorting Center.

we attempted to learn more about the role these animals played in one particular benthic community, that off the southern end of Low Island, South Shetland Islands. Finally, as a lecturer on the American Museum's Discovery tours, I made three additional trips to the Antarctic Peninsula and South Shetland Islands, where I was able to observe beach drift organisms and intertidal bryozoan habitats at a number of locations.

TAXONOMIC DISTRIBUTION OF USARP BRYOZOANS

Two classes, Gymnolaemata and Stenolaemata, and three orders of bryozoans are recorded from the Antarctic. The Gymnolaemata include the orders Ctenostomata and Cheilostomata. The Cyclostomata are the only living order of the Stenolaemata.

The dominant bryozoans in Recent oceans are the cheilostomes, a group whose diversity and abundance has increased greatly since its origin in the Cretaceous. Cheilostomes have box-like zooids, variously reinforced with calcium carbonate skeletons, a hinged operculum protecting the orifice through which the polypide extends to feed, and colonies often displaying a high degree of polymorphism. Most cheilostomes brood their embryos to the larval stage in variously formed reproductive structures called ovicells.

Of the 389 species so far recorded in the sorted and identified USARP collections, 344 (88.5%) are cheilostomes. Four new species have been described so far from the collection (Hayward and Winston, 1994) with more to follow. Although most of the major groups of cheilostomes are represented in the Antarctic and subantarctic, several groups have undergone a good deal of radiation with numerous species, most of them endemic. Families especially well represented (10 or more species) include the Flustridae, Calloporidae, Bugulidae, Cabereidae, Cellariidae, Arachnopusiidae, Exochellidae, Sclerodomidae, Smittinidae, Microporellidae, Celleporidae, and Reteporidae (Hayward, 1995). This pattern is reflected in the USARP collections. Some representative species are shown in Figure 2.

Although cyclostome bryozoans rank well below cheilostomes in terms of species diversity, they are abundant in the Antarctic, forming large colonies, easily recognizable as cyclostomes, although often difficult or impossible to determine to species level because colonies lack gonozooids, a vital taxonomic character in the group. Like cheilostomes, cyclostome bryozoans have calcified walls. Their zooids are tubular. The zooid orifice, at the distal end of the tube, has no operculum but closes by a sphinc-ter instead. Polymorphism is much less common, but some species have nanozooids. They brood embryos in one or more brood chambers or gonozooids, and sexual reproduction is unusual, involving polyembryony: larval fission in which the original fertilized egg results in many genetically identical larvae. Thirty-seven cyclostomes (9.55% of the total USARP bryozoan fauna) were found in USARP collections. Figure 3 (left) shows an erect branching cyclostome of the genus *Hornera*.

Members of the order Ctenostomata have chitinous and/or gelatinous walls. Some form encrusting or massive colonies. Others form delicate vine-like colonies consisting of single or clumps of tubular zooids along stolons or with zooid bases constricting into stolonate tubes that join adjacent zooids. They have no operculum but close the orifice by muscular constriction. Sexual reproduction may involve brooding embryos in body cavities of maternal zooids or broadcasting fertilized eggs into seawater, where development into larvae takes place. Although the first bryozoan described from the Antarctic continent was a ctenostome, *Alcyonidium flabelliforme* (Kirkpatrick, 1902), in terms of species diversity the group is less well represented there than in some other environments. Only eight species (2%) of the total bryozoan fauna were found in the USARP collections, but three of them represented new species (Winston and Hayward, 1994), one encrusting on other bryozoans and the other two boring into live bryozoan colonies or living in dead zooids or crevices (e.g., *Bowerbankia antarctica*, Figure 3).

The most abundant species in the Antarctic Peninsula and South Shetland Islands form foliaceous, lightly calcified colonies (*Carbasea ovoidea, Kymella polaris, Flustra astrovae, Himantozoum antarcticum,* and *Nematoflustra flagellata*), delicate jointed branching colonies (*Cellaria divisa*), or encrusting colonies (e.g., *Micropora brevissima, Inversiula nutrix, Celleporella antarctica, Ellisina antarctica, Harpecia spinosissima, Lacerna hosteensis, Escharoides tridens*, and *Lichenopora canaliculata*). From the Ross Sea, the most abundant species in the USARP collections in shallow water (less than 50 m) is *Eminoecia carsonae*, with rigidly branching erect colonies. In deeper water, erect forms are also common, including *Cellaria monilorata, Arachnopusia latiavicularis, Antarcticaetos bubeccata, Thryptocirrus phylactellooides, Melicerita obliqua*, species of Cellarinellidae, *Reteporella antarctica* and other Reteporidae, with well-calcified branching or reticulate colony forms (see Figure 4), as well as some of the same epizoic species found in the Antarctic Peninsula area: *Celleporella antarctica, Ellisina antarctica,* and *Harpecia spinosissima*.
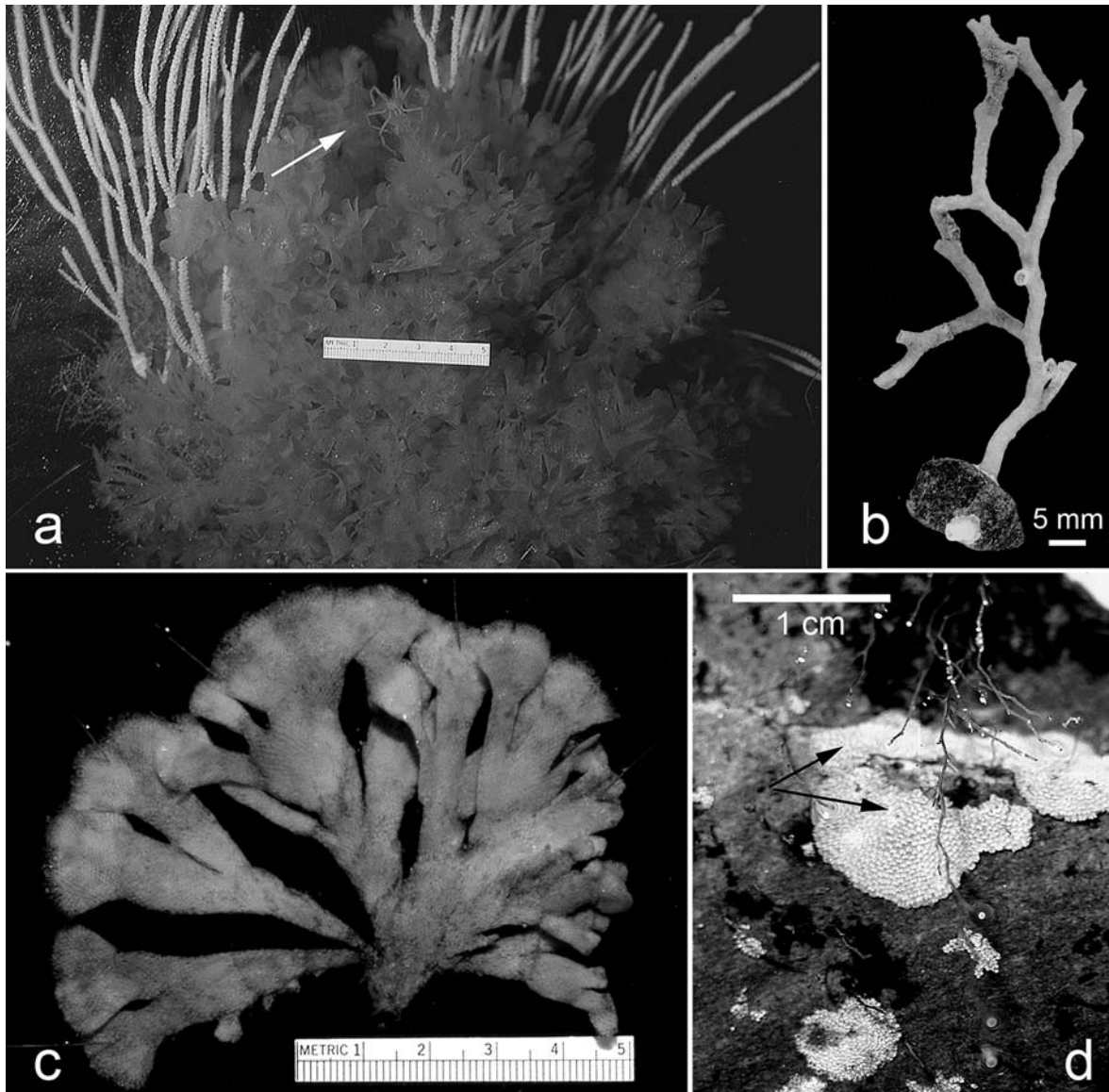
FIGURE 2. Morphologies common in bryozoans from USARP collections. (a) Large foliaceous colony of *Carbasea ovoidea* from Low Island. Scale = 5 cm. Arrow points to pycnogonid. (b) Rigid branching colony of *Cellarinella foveolata* attached to glacial pebble. (c) Living colony of *Kymella polaris* pinned out for study of reproduction and fouling. (d) Encrusting colonies of *Inversiula nutrix* on underside of an intertidal rock, shown by arrows. Branching hydroid above colonies and crustose algae (dark patches) are also visible.

The Antarctic intertidal zone has been considered to be almost barren due to scouring by seasonal sea ice (Barnes, 1994a; Knox, 2007). This is not the case, however, in many localities along the Antarctic Peninsula and in the South Shetlands. Sheltered intertidal sites, often with plankton-rich eutrophic water due to runoff from adjacent colonies of birds or marine mammals, contain tide pools and crevices whose inhabitants include calcareous and macroalgae, limpets, amphipods, *Glyptonotus*, brittle stars, starfish, and sea urchins. A number of bryozoans, of which *Inversiula nutrix* (Figure 2d) was most common, encrust intertidal rocks or attach to seaweed in intertidal to shallow subtidal habitats (Winston and Hayward, 1994).
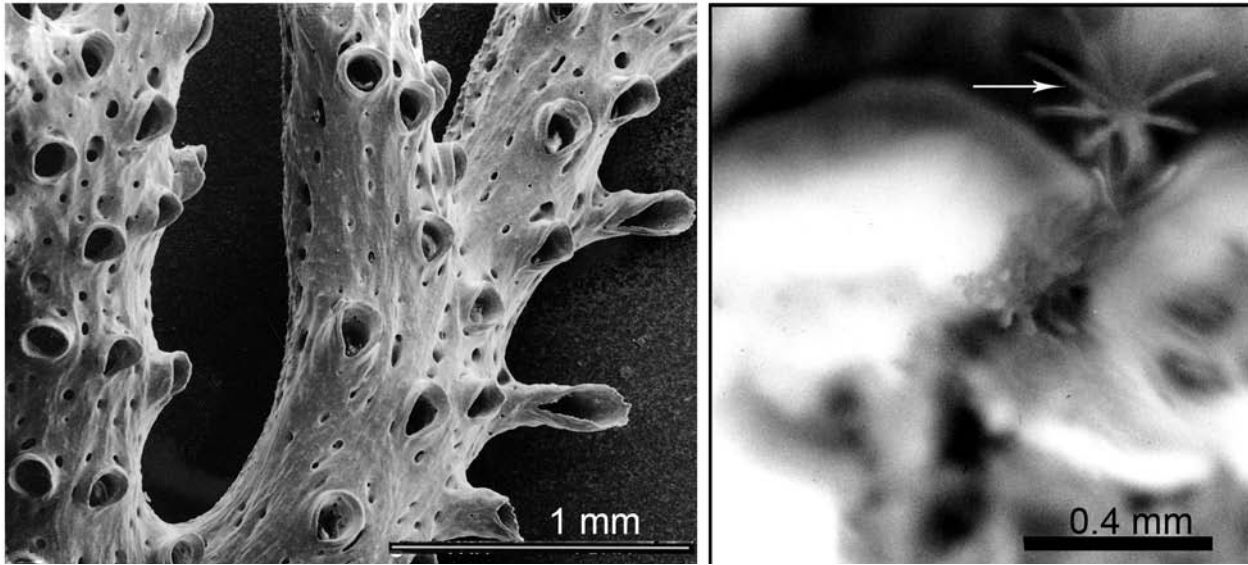
FIGURE 3. (left) An Antarctic cyclostome, *Hornera* sp. (scanning electron microscope image). (right) Living colony of an Antarctic ctenostome, *Bowerbankia antarctica*. Arrow points to lophophore emerging from crevice between two spirorbid tubes. Tentacle crown of spirorbid is visible below that of bryozoan.

BIOLOGY AND ECOLOGY OF ANTARCTIC BRYOZOANS

Study Areas, Methods, and Materials

In addition to long-term taxonomic projects, other studies using preserved USARP material, ecological and behavioral work on living Antarctic bryozoans, were carried out during the austral summer and fall of 1985 at Palmer Station and off the southernmost of the South Shetland Islands. Low Island (latitude 63°25′S, longitude 62°10′W) lies off the western coast of the Antarctic Peninsula. The Low Island area was a favorite collecting site for fish biologists working out of Palmer Station during our stay. It was close enough to the station (within 12 hours' cruise time) that fish could be maintained in good condition, and the sea bottom off its southern side slopes off to a relatively flat surface, free of projecting ledges or pinnacles that would tear the trawls used to collect specimens. By sharing cruise time with fish and krill biologists we were able to return to the site several times during the summer and fall. A 4 × 10 ft (1.2 × 3 m) otter trawl was used to collect both fish and bryozoans. Proportionate biomass of benthic organisms was determined on shipboard by averaging the blotted wet weights of different groups of organisms taken in three timed trawls of equal length. For studies of the food of the bryozoans we froze a number of freshly trawled colonies of the most common species in the ultracold freezer on the ship. They were later defrosted in the lab, and polypides were dissected and gut contents were examined by light and epifluorescence microscopy. For other studies of living material the bryozoans collected were maintained in holding tanks with running seawater until the ship returned to Palmer Station. On return to the lab they were placed in running seawater tanks and examined as soon as possible. Specimens for behavioral studies were collected both from Low Island by trawling and from Arthur Harbor, using a hand dredge from an inflatable boat. Autozooid feeding and behavior of avicularian polymorphs was recorded using a macrovideo setup in the lab at Palmer Station. Freshly collected material was maintained at close to normal seawater temperature during behavioral observations by an ice bath surrounding the observation dish.

To analyze growth and injury, colonies were pinned out in seawater in a shallow dissecting tray. A piece of clear Mylar film was then placed over them, and the colony outline, including growth checks, was traced with a waterproof marking pen. The traced version was immediately copied and used as a map to record areas of injury and fouling. Each colony was examined under the dissecting microscope, and all injuries, discoloration, bites, rips, empty zooids, and fouling organisms were recorded.

Growth of individual colonies was analyzed by measuring the distance between yearly growth checks.

For the reproductive study five colonies (if possible) were examined after each collection. Each colony was pinned out flat in a dissecting tray filled with seawater. It was then examined under a dissecting microscope for the following: developing ovicells, developing embryos, mature embryos, and empty ovicells. The colonies were also photographed and finally preserved in 70% ethanol.

BIOLOGICAL CHARACTERISTICS

Outstanding characteristics of invertebrates occurring in Antarctic benthic communities include a high degree of endemism, large body size in comparison with temperate or tropical relatives, and the prevalence of suspension feeding organisms (Hedgpeth, 1969, 1970; Dell, 1972; Arnaud, 1974; White, 1984; Gallardo, 1987; Arntz et al., 1994, 1997; Clarke and Johnston, 2003; Knox, 2007).

Many Antarctic bryozoans are large in size. Figure 2a shows a large colony of *Carbasea ovoidea*, a flexible, lightly calcified, foliaceous species collected at Low Island, South Shetland Islands. The size of the colony is approximately 20 cm in width by 15 cm in height. Individual zooids of many Antarctic species also are large in size, many of them between 1 and 2 mm long, versus the more common 0.4–0.9 mm zooid length of species found in warmer waters.

Figures 2 and 3 show some of the range of colony morphology found in species in the USARP collections. Branching colonies consisting of rooted seaweed-like fronds, wide or narrow, are abundant, especially in the Antarctic Peninsula and South Shetland Islands. Jointed and rigid erect forms, branching, unbranched, or anastomosing and reticulate, may be attached to other substrata, such as glacial pebbles (Figure 2b), vertical walls, or the dead colonies of other bryozoans or rooted in sediment (Figure 2c). Encrusting species are also abundant and diverse. Some form massive or nodular colonies consisting of several layers of frontally budded zooids. Other species form single-layered crusts, loosely or tightly attached to other bryozoans, other organisms, or hard substrata (Figure 2d).

Many Antarctic bryozoans are also more colorful than their temperate relatives. Bryozoans derive their pigment from the carotenoids in their phytoplankton food or, in some cases, from coloration present in symbiotic bacteria inhabiting zooids (Sharp et al., 2007). Colors of living colonies range from dark red (e.g., *Carbasea curva*) to orange brown (e.g., *Nematoflustra flagellata*), to yellow orange (e.g., *Kymella polaris*), to peach (e.g., *Orthoporidra* spp.), purple, pink (e.g., chaperiids and reteporids), and tan to white. The one *Bugula* species known, *Bugula longissima*, has dark green coloration when living, apparently derived from bacterial symbionts (Lebar et al., 2007).

The dark red *Carbasea curva*, which lacks the physical defense of avicularia, was found to show moderate haemolytic activity, killing 60% of human and 50% of dog erythrocytes (Winston and Bernheimer, 1986). Some of the species from Low Island were also tested for antibiotic activity. *Kymella polaris* and *Himantozoum antarcticum* both strongly inhibited the growth of *Staphylococcus aureus*. *Nematoflustra flagellata*, *Caberea darwinii*, and *Austroflustra vulgaris* moderately inhibited growth. Only *Beania livingstonei* was noninhibitory (Colon-Urban et al., 1985).

STUDIES OF BRYOZOANS FROM THE LOW ISLAND BENTHIC COMMUNITY

Shallow shelf environments (less than 500 m) in many areas of the Antarctic are dominated by communities made up largely of sessile suspension feeders like sponges, bryozoans, hydroids, gorgonians, and tunicates, whose colonies may form dense thicket-like growths spreading over large areas of the sea bottom (Belyaev, 1958; Uschakov, 1963; Propp, 1970; White and Robins, 1972; Barnes, 1995b, 1995c; Saíz-Salinas et al., 1997; Saíz-Salinas and Ramos, 1999; San Vincente et al., 2007). In contrast to epifaunal communities elsewhere, which are mostly limited to hard substrata, such communities in Antarctica commonly rest on or are rooted in soft sediments or are attached to scattered rocks and pebbles. Gallardo (1987) first called attention to the need to for recognizing the distinctiveness of this epi-infaunal or soft-bottom epifaunal community as a prerequisite to the study of its structure. The community we studied fit this epi-infaunal pattern.

Biomass

Inshore, in depths of 70 m or less, benthic biomass consisted primarily of macroalgae and echinoderms, a community similar to that reported at a number of localities along the peninsula (Gruzov and Pushkin, 1970; Delaca and Lipps, 1976; Moe and Delaca, 1976) and in the South Orkney Islands as well (White and Robins, 1972).

Between about 80 and 110 m a soft-bottom epi-infaunal community of the type discussed by Gallardo (1987) occurred. By wet weight (Figure 4) the dominant components of this community were sponges (31.4%); echinoderms, chiefly holothurians (24.6%); ascidians (18.7%);
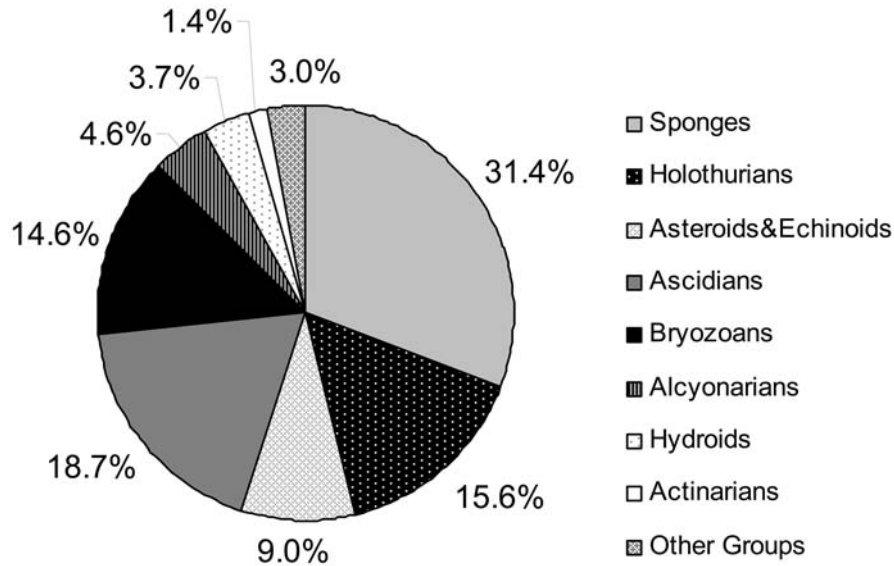
FIGURE 4. Biomass of organisms from three trawl collections at 100 m, Low Island, Antarctic Peninsula.

bryozoans (14.6%) and coelenterates, mostly gorgonians, especially *Ophidogorgia paradoxa* and *Thouarella* spp.; and hydroids (10.0%) (Winston and Heimberg, 1988). Over 30 species of bryozoans occurred. The five most abundant species (*Carbasea ovoidea, Nematoflustra flagellata, Austroflustra vulgaris, Kymella polaris,* and *Himantozoum antarcticum*) all have flexible, foliaceous, lightly calcified colonies (e.g., Figure 2a,c). Therefore, in terms of volume or area of sea bottom covered, bryozoans are an even more important component of the community than would be indicated by biomass alone. Although not the highest bryozoan biomass reported from Antarctic benthic communities (Starmans et al., 1999, reported 22% bryozoan biomass in Amundsen and Bellingshausen seas), the biomass of bryozoans is typical of the multilayered, microhabitat-rich, filter-feeding community reported from many areas of the Antarctic shelf from the Ross Sea (e.g., Bullivant, 1959:488, fig. 3; Dayton et al., 1974; Dayton, 1990), to King George Island (e.g., Rauschert, 1991:67, fig. 23), to Signy Island (Barnes, 1995b), to the Weddell Sea (Starmans et al., 1999).

Large motile invertebrates found in this habitat included the isopods *Glyptonotus antarcticus* and *Serolis* sp., the echinoid *Sterechinus neumayeri,* and various asteroids, e.g., *Odontaster validus* and *Labidaster annulatus.* Demersal fish species included nototheniids (*Notothenia gibberifrons, N. larseni, N. nudifrons,* and *N. coriiceps*) and the icefish *Chaenocephalus aceratus.*

Growth and Longevity of Most Abundant Species

Life history characteristics of Antarctic bryozoans are amenable to analysis for the following three reasons: (1) Growth is in discrete modules (zooids), making increments of growth easy to measure. (2) Colony fronds of perennial Antarctic species, like those of some temperate species, show yearly growth checks where growth stops during winter months, making it possible to determine the age of fronds as well as their yearly growth rate by back measurement (Stebbing, 1971b; Winston, 1983; Pätzold et al., 1987; Barnes, 1995c; Brey et al., 1998). (3) Embryos, usually brooded in zooid cavities or in ovicells, are easily detectable in living colonies, making it possible to quantify reproductive effort.

Carbasea ovoidea was the most abundant bryozoan species in the Low Island community, often comprising more than half the bryozoan biomass in a trawl sample. The delicate, tan, unilaminar fronds of *Carbasea* colonies showed no growth checks, indicating that all the growth of a particular frond took place during one season, although basal rhizoids and stolons (of this and the other species) might be perennial, producing new fronds yearly. The mean increase in height for *Carbasea* fronds was 8.6 cm per year.

In the other dominant species, both colonies and fronds were perennial. The narrow, curling fronds of *Himantzoum* could not be accurately measured and so were excluded

from this part of the study. The other three perennial species grew much more slowly than *Carbasea*. Figure 5 compares growth in height for individual colonies of all three species as determined by back measurement. Two of them, *Austroflustra vulgaris* and *Nematoflustra flagellata* are related to *Carbasea* (family Flustridae). *Nematoflustra* fronds showed a mean increase in height of only 0.92 cm per year, whereas *Austroflustra* fronds increased 1.2 cm per year. The ascophoran cheilostome *Kymella polaris* is not closely related to the other species but grew at a similar rate. On average, *Kymella* fronds increased 1.3 cm in height per year.

The oldest fronds of *Kymella* were at least six years in age, and those of *Austroflustra* and *Nematoflustra* were seven years. As none were complete colonies, the genetic individuals they represented may have persisted much longer. The life spans of these species appear somewhat shorter than the 10–50+ year life spans of some of the rigid erect bryozoan species found in deeper Antarctic shelf habitats (Winston, 1983; Brey et al., 1998). However, both growth rates and life spans for both *Austroflustra* and *Nematoflustra* were in the same range as those of temperate perennials like *Flustra foliacea* (12 years) (Stebbing, 1971b). Barnes (1995c) also studied growth of *Nematoflustra* in shallow water at Signy Island. He found an average yearly increase in height of 0.7 cm and estimated that the oldest colonies at that location were 26 years old.

Reproduction

Three methods of protecting developing embryos were represented among the dominant species. *Austroflustra vulgaris* and *Nematoflustra flagellata* brood eggs internally in zooid body cavities, while *Kymella polaris* broods eggs in ovicells of maternal zooids. In contrast, *Carbasea ovoidea* broods developing embryos externally in embryo sacs attached in clusters of four or five to the orifice of each fertile zooid.

The reproductive pattern of *Carbasea* also contrasted with that of the other common species. Reproductive effort in *Carbasea* was very high (averaging 2953 embryos per colony) at the time of our first census in late austral summer (1 March) and may have peaked earlier in the summer. By the next sampling period, reproduction had ceased entirely, although zooids, like those of other species, continued to contain actively feeding polypides throughout the study period.

The mean number of embryos per colony was lower in the other species studied: *Nematoflustra, Austroflustra,*

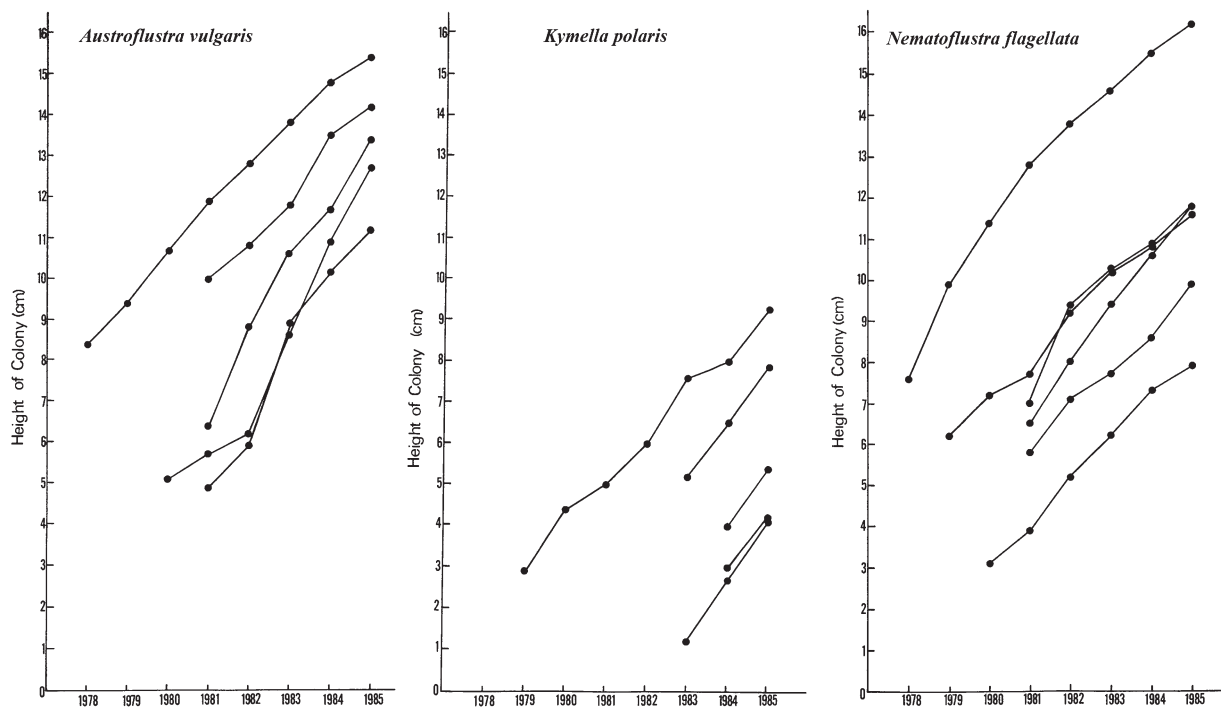

FIGURE 5. Annual growth of individual colonies of three species of Low Island bryozoans determined by back measurement.

Himantozoum, and *Kymella*, averaging a few hundred per colony at any one census (Table 1). In these species, sexual reproduction was still occurring at the last date sampled. For *Kymella* and *Himantozoum*, the two species in which embryos were brooded in ovicells, we could determine the percentage of ovicells brooding embryos versus empty ovicells over the course of the season (Table 2). The percentage of empty ovicells gradually increased until by 20 April, 72% of all *Kymella* ovicells and 95% of all *Himantozoum* ovicells were empty, indicating that the end of the reproductive season was approaching for at least these two species. In *Nematoflustra* the number of embryos fluctuated slightly from census to census but showed no significant decline as of 20 April. *Austroflustra vulgaris* colonies contained mature embryos at the 7 March census (mean of 258 per colony), while colonies collected on 20 April had an average of 227 embryos per colony. Although there was no way for us to tell how long the embryos present in late April would be brooded, it may well be as later workers (e.g., Barnes and Clarke, 1995; Bowden, 2005; Knox, 2007) have suggested, that "winter" may not be as long for the benthos as predicted on the basis of light and phytoplankton abundance.

TABLE 1. Mean number of embryos produced per colony for most abundant Low Island species.

Species	Total number of embryos	Mean number per colony	Number of colonies
Carbasea	15,355	1536	10
Austroflustra	5920	321	20
Himantozoum	6326	452	14
Kymella	3698	247	15
Nematoflustra	19,277	741	26

TABLE 2. Percent of ovicells empty for two Low Island species at three census periods.

Species	1 March	2 April	20 April
Kymella	19%	40%	75%
Himantozoum	46%	62%	95%

Partial Mortality and Predation

Like most clonal organisms, bryozoans have retained extensive powers of regeneration and can tolerate a high degree of injury or death of portions of the colony without death of the entire colony. Such partial mortality may be caused by physical disturbance of the environment or by predators or grazers. A few invertebrates, including some pycnogonids and nudibranchs, are specialized as single-zooid predators of bryozoans. These animals pierce a zooid with proboscis or radula and suck out body fluids and tissues, leaving an empty or broken zooid behind. Single or small patches of empty zooids were probably the result of such predators. The grazing or browsing activities of fish, echinoids, and mollusks leave larger scrapes, rips, and bites on colony fronds. We examined colonies for injuries of the different types and noted where they occurred on the fronds. Table 3 shows that all species sustained a considerable amount of damage. *Carbasea* colonies showed the least amount of injury to growing tips (the most delicate and accessible portion of the frond). This is most likely due to their much higher growth rate.

Evidence from studies of gut contents of associated macrobenthic organisms also suggested that most of the injuries observed were not due to feeding by specialized bryozoan predators. A search of the literature revealed that small quantities (from less than 1% to about 3%) of bryozoans had been found in gut contents of several Antarctic fish and echinoderms (Dayton et al., 1974; Dearborn, 1977). We examined gut contents of a number of invertebrates from Low Island trawls (including polychaetes, echinoderms, and crustaceans) to learn whether any of them were feeding on bryozoans. Two Low Island invertebrates, the echinoid *Sterechinus neumayeri* and the isopod *Glyptonotus antarcticus*, did contain bryozoan fragments. But our results, like those of later workers, indicated that gut contents of invertebrate carnivores and scavengers, like those of the demersal fish, consisted primarily of small motile invertebrates: amphipods, isopods, polychaetes, and mollusks (Schwartzbach, 1988; Ekau and Gutt, 1991: McClintock, 1994).

Another source of damage to colonies is caused by fouling of colonies by other organisms. Table 4 shows the most common organisms found attached to frontal surfaces of colonies of the five most abundant Low Island species. Some of them, such as the stalked barnacles found in branch bifurcations or the colonies of the bryozoan *Beania livingstonei*, which attach loosely to the host colony, may benefit the host, augmenting colony water currents by their own feeding activities. Others, such as

TABLE 3. Mean number of injuries per colony and percent of branch tips injured.

Species	Number of rips torn in branches	Number of injuries to branch tip (growing edge)	Number of bites to branch edges (sides of branches)	Number of injuries to center of a branch	Number of empty zooids	Percentage of branch tips injured
Carbasea	1.7	3.4	1.1	1.4	130	4.4%
Nematoflustra	4.0	3.5	5.0	7.2	41	23.5%
Austroflustra	1.4	2.8	3.0	3.8	81	52%
Kymella	1.2	4.1	0.5	0.2	50	53%

encrusting bryozoans like *Ellisina* and *Harpecia*, disable the host zooids they overgrow. Table 5 shows the diversity and density of fouling on Low Island species compared with that on NE Atlantic *Flustra foliacea*, as studied by Stebbing (1971a). The overall number of taxa and number of epizoans per colony was lower for all the Low Island species studied than for *Flustra*. However, when the number of epizoans per square centimeter was calculated, two species, *Austroflustra* (1.10/cm^2) and *Kymella* (1.2/cm^2), were in the same range as *Flustra foliacea* (1.0/cm^2). Barnes (1994) studied the epibiota of two erect species, *Alleoflustra tenuis* and *Nematoflustra flagellata,* from shallow (36–40 m) and deeper (150 m) habitats at Signy Island. The frontal surface of *Nematoflustra* showed fewer colonizers than the abfrontal surface, and for both species the amount of fouling decreased to almost zero at 150 m. The number of taxa encrusting both species was also low (median = 3.0 for *Alleoflustra* and 2.0 for *Nematoflustra*). Our methods were somewhat different, but it appears that overall diversity of epibiotic taxa was higher at Low Island, but the diversity of epibiotic bryozoan taxa was much higher at Signy Island.

Food Sources

Gut contents of the bryozoans studied are summarized in Table 6. Each autozooid polypide has a mouth at the base of the lophophore funnel. Mouth size is slightly variable, as the mouth expands and contracts slightly with particle swallowing, but it is closely correlated with zooid size (Winston, 1977). These Antarctic species had large mouths compared to species from warmer water but, somewhat surprisingly, were still feeding primarily on very small plankton cells, mostly tiny diatoms and dark, rough-walled cysts less than 20 μm in size, probably resting stages of either choanoflagellates (Marchant, 1985; Marchant and McEldowny, 1986) or diatoms (Bodungen et al., 1986). Most of the phytoplankton component of their diet was thus within the nanoplankton, a size range which has been shown to account for much of the primary productivity in some areas of Antarctic seas (Bracher, 1999; Knox, 2007). The Bransfield Strait area is an important breeding ground for krill, which feed on larger plankton. Nanoplankton and picoplankton populations increase as microplankton blooms diminish (Varela et al., 2002). Some studies have found

TABLE 4. Dominant epizoans attached to dominant Low Island bryozoan species; a "+" indicates their presence on a particular bryozoan species.

Epizoan organisms	*Carbasea*	*Nematoflustra*	*Flustra*	*Himantozoum*	*Kymella*
Foraminiferans	+	+		+	
Diatoms				+	
Hydroids		+	+		
Stalked barnacles		+			+
Beania livingstonei		+			+
Harpecia spinosissima				+	
Ellisina antarctica			+	+	
Osthimosia sp.	+				
Cyclostome bryozoans				+	

TABLE 5. Diversity and density of epizoans fouling Low Island bryozoans compared with fouling on northeast Atlantic *Flustra foliacea*.

Species	Number of epizoic taxa	Mean number of epizoans/colony	Mean number/cm^2 of colony surface
Carbasea ovoidea	9	28	0.56
Nematoflustra flagellata	13	14	0.24
Austroflustra vulgaris	12	36	1.10
Himantozoum antarcticum	9	9	—
Kymella polaris	9	28	1.2
Flustra foliacea	42	558	1.0

TABLE 6. Gut contents of Low Island bryozoans.

Species	Mean mouth size (μm)	Dominant particle types[a]	Particle size range (μm)
Carbasea ovoidea	59	BPM, diatoms, cysts	3–66
Austroflustra vulgaris	96	BPM, cysts	3–45
Kymella polaris	94	BPM, sediment grains	6–60
Nematoflustra flagellata	87	Cysts, diatoms	9–69
Beania livingstonei	114	BPM, diatoms, cysts, sediment grains	3–93

[a]BPM = brown particulate material.

nanoplankton making up 83% of phytoplankton carbon in February and March (Kang and Lee, 1995). Sediments in the peninsula are also rich in organic matter (Bodungen et al., 1989). Benthic microalgae (Vincent, 1988; Gilbert, 1991) may also be important in areas reached by light.

The bryozoans studied also ingested large amounts of "brown particulate material." This material contained chlorophyll and may have been derived from the fecal pellets of zooplankton or those of other benthos. Fecal material could also have derived from benthos (Nöthig and von Bodungen, 1989; Tatián et al., 2004). Feeding on dead organisms or fecal material has been shown to occur in other Antarctic animals and may aid them in surviving seasons of low food supply. Sediment particles may indicate the importance of an advected food supply, as Gutt (2007) has speculated, which might explain the sediment grains found in bryozoan gut contents.

Some food resource besides phytoplankton seems likely to be part of Antarctic bryozoan life histories. Polypides of colonies of all species we observed were still actively feeding at the end of our stay in late April. This is in keeping with the observations made by Barnes and Clarke (1994), who monitored colony activity every month for a two-year period at Signy Island. Most bryozoans they observed stopped feeding for only a two- to three-month period in mid–austral winter.

Habitat and Ecosystem Role

The primary role of bryozoans in the Low Island ecosystem appeared to be that of habitat and foraging ground for demersal fish and motile invertebrates. To assess their importance in that regard, we selected three large clusters of *Carbasea ovoidea* from a single trawl and immediately immersed them in large jars of seawater formalin to kill and preserve their inhabitants for later analysis. Table 7 shows the results. When living, these clumps contained about 0.09 m^3 of habitat space (in overall volume, not counting areas of each frond) and held almost 500 individual invertebrates. Most were arthropods (81.6%), of which amphipods comprised the majority: 345 individuals (69.6%). Nematodes were the next largest group present, with 54 individuals (10.8%). Other motile and sessile groups made up the remainder of the inhabitants. Most of them figure in the diets of demersal fishes and benthic invertebrates of the Antarctic Peninsula region (Targett, 1981; Daniels, 1982).

Figure 6 is a diagrammatic representation of a Low Island food web, placing the bryozoans within it as part of the link to the benthos. The major role of bryozoans within the Low Island ecosystem is as a three-dimensional, layered habitat and shelter for the small invertebrates on which larger demersal fish and benthic invertebrates feed

TABLE 7. Animals inhabiting three *Carbasea ovoidea* colonies collected at Low Island.

Group	Number of specimens
Amphipods	345
Nematodes	54
Isopods	41
Pycnogonids	19
Ascidians	17
Bivalves	12
Holothurians	4
Sponges	2
Sipunculans	1
Asteroids	1
Total	496

and a part of the epibenthic nursery ground for juveniles of demersal fish and motile invertebrates. Along with other sessile epifauna, they may also provide large epibiotic filter-feeding invertebrates with a higher perch and better access to food (Gutt and Shickan, 1998). The bryozoans themselves are suspension-feeding consumers of microplankton and nanoplankton, as well as fecal material or detritus supplied from above their colonies. They may also play a minor role as a food source for single-zooid predators and a few fish and invertebrates.
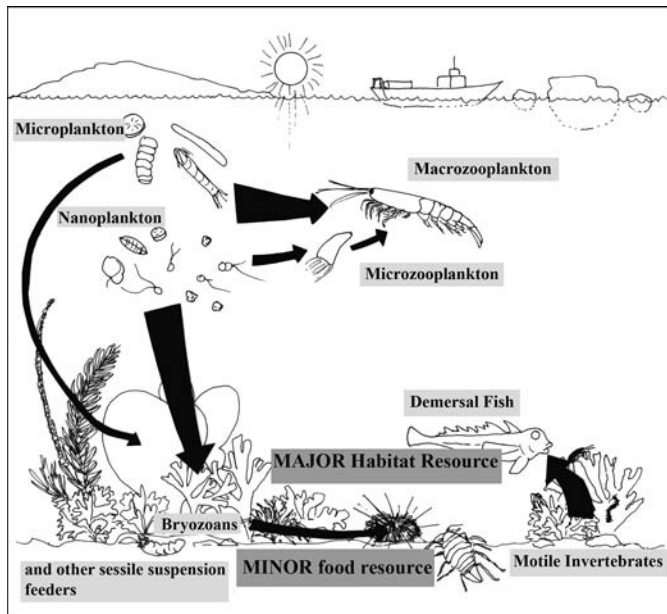

FIGURE 6. Low Island food web. Diagrammatic representation of links between benthic and pelagic communities.

BEHAVIOR OF ANTARCTIC BRYOZOANS

Morphological studies of avicularia and vibracula (Winston, 1984) and behavioral studies carried out with living colonies (Winston, 1991) have shown how different polymorphs, including those of Antarctic species, function within colonies. These functions include sweeping debris from zooids and colonies, protecting the colony from trespassers, and capturing motile organisms and possible predators.

NEMATOFLUSTRA—VIBRACULA

Distal to each autozooid of *Nematoflustra flagellata* is a vibraculum zooid with a long, curved, bristle-like mandible (Figure 7a). Mechanical stimulation or the vibration of a small organism, such as a pycnogonid or polychaete, triggered a wave of vibracular movement over a part or all of the colony surface. The circumrotary reversal of the vibracula mandibles was sequentially synchronized at first, traveling proximally from the branch tip, but later waves became less synchronous. The waves of moving setae effectively carried organisms or debris from the branches (Figure 7b) (Winston, 1991).

BEANIA—BIRD'S HEAD AVICULARIA

Unlike sessile avicularia and vibracula, the pedunculate (bird's head) avicularia found in the cellularine group of bryozoans close and open mandibles frequently, even when undisturbed, showing a species-specific pattern of ongoing activity. For example, in *Beania livingstonei* (Figure 7c) the avicularium bends forward on its peduncle, then snaps back into an upright position, while the mandible closes. Once the avicularium is upright, the mandible slowly reopens. Although the avicularian movements did not increase in the presence of trespassers, their activity was still effective as organisms caught by one avicularium were usually captured by the mandibles of several more in their struggles to free themselves (e.g., Figure 7d). Some were eventually able to pull free, detaching the avicularia from their peduncles in the process (Winston, 1991).

CAMPTOPLITES—LONG-STALKED BIRD'S HEAD AVICULARIA

The long-stalked avicularia of *Camptoplites* species (Figure 7e) show an even more complex pattern. The long, slender peduncles of these avicularia sway slowly back and forth across the frontal surface of colony branches. As they sway, the mandibles of the avicularia snap open and
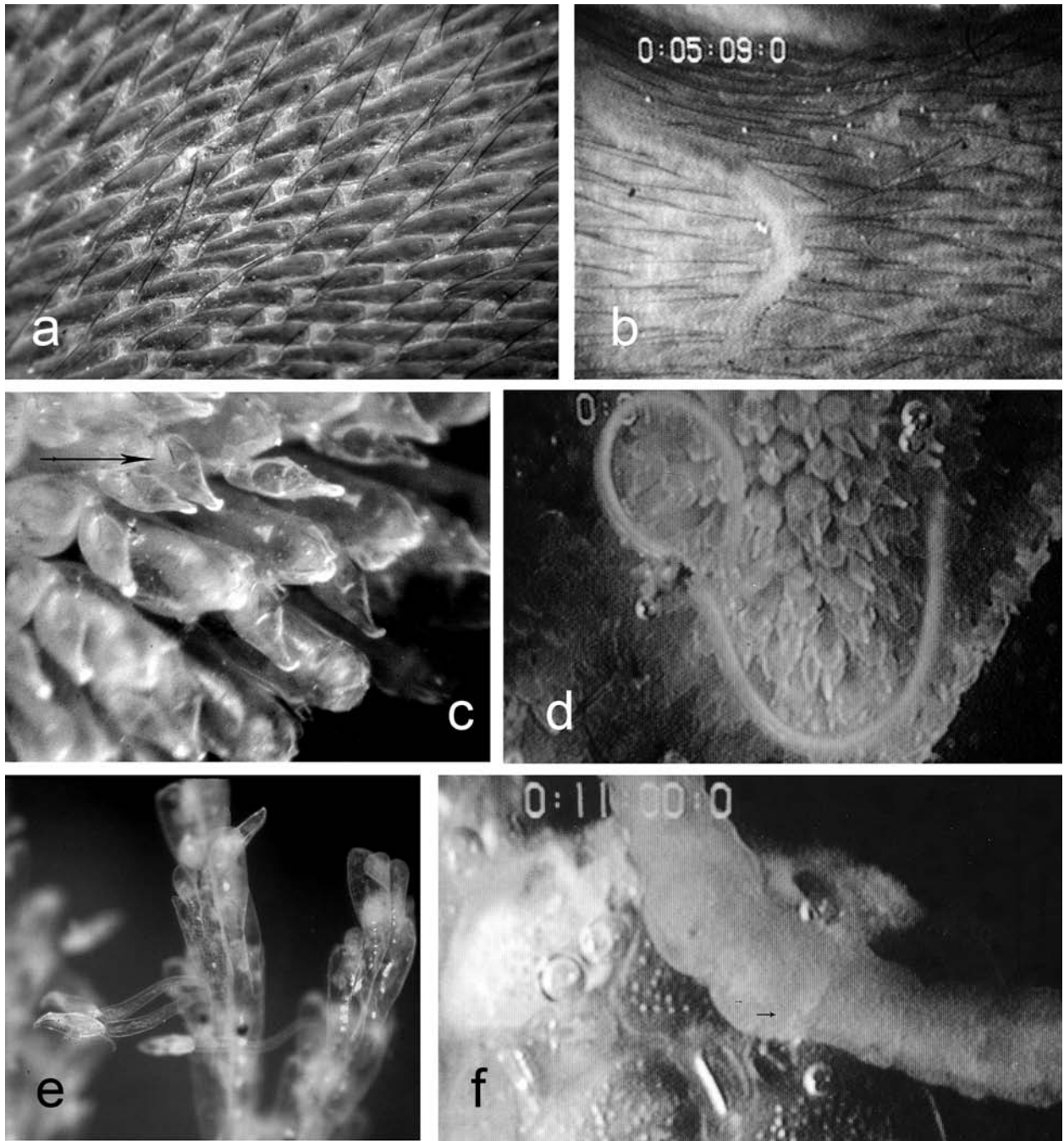
FIGURE 7. Avicularia and vibracula of some Antarctic bryozoan species studied. (a) Living branch of *Nematoflustra* with vibracula in undisturbed position. (b) Vibracula-sweeping polychaete from colony surface (still photo from video). (c) *Beania livingstonei*. Arrow points to one of the bird's head avicularia. (d) Nematode caught by several avicularia (still photo from video). (e) Long-stalked bird's head avicularia of *Camptoplites* colony. (f) Worm speared by one of the sharp-pointed mandibles of *Micropora brevissima*. Tiny arrow points to mandible inside worm's translucent body.

shut. They show no increase in activity when a trespassing organism touches the branches, but when a mandible intercepts an object soft and narrow enough to grasp (such as a polychaete chaeta or arthropod appendage), it snaps shut upon it. The swaying activity then carries the organism toward the edge of the colony (Winston, 1991).

MICROPORA—SESSILE AVICULARIA

Micropora brevissima (Figure 7f) has sessile avicularia with sharply pointed mandibles. In avicularia of this type, the bodies of the avicularia are fixed on the colony, and their mandibles close rarely, remaining in an open position even when zooid opercula are shut. The mandible shuts in response to physical stimuli, probing, jarring, or vibration of palate or mandible. Despite their small size, such avicularia are able to capture and hold relatively large trespassers by their appendages, e.g., cirri of polychaetes or legs of amphipods or pycnogonids. During observations of living colonies of this species carried out at Palmer Station, avicularia of *Micropora* captured several annelids and held them despite their much greater size (Winston, 1991).

CONCLUSIONS

Antarctic bryozoans are taxonomically rich and, like many other Antarctic organisms, show a high degree of endemism. Preliminary analysis of USARP bryozoan collections from the Ross Sea and Antarctic Peninsula yielded 222 species from all three marine orders: five ctenostomes, 28 cyclostomes, and 189 cheilostomes. Hayward (1995) studied Antarctic cheilostomes, primarily from British Antarctic research programs but also including some information from USARP collections. He listed 264 species of cheilostomes, of which 215 (81%) were endemic. Moyano (2005) took a different approach in summarizing taxonomic research on Antarctic bryozoans through 2004. He included taxa from all three orders, but some of his totals included subantarctic species. His list totaled 315 species, 250 (79%) of which were endemic.

Antarctic bryozoans are abundant. It is hard to find a published underwater benthic photograph from the Antarctic in which a bryozoan colony cannot be seen, and in many areas, their skeletons, along with sponge spicules and glacial pebbles, make up a significant component of the sediment. As shown in results from work at Low Island and elsewhere, bryozoans play a significant role in benthic ecosystems, providing habitat and foraging ground as well as a minor food resource for fish and motile invertebrates.

Many of the erect, branching, and foliose bryozoans which form such three-dimensional habitats are perennial, with life spans lasting several years, perhaps several decades. Their growth rates are slow and their fecundity low. *Carbasea ovoidea*, the exception to this pattern at Low Island, is a species whose northernmost range extends into the subantarctic and probably reaches the southernmost extent of its range somewhere along the peninsula (Hayward, 1995).

Most of the Antarctic fish and many other benthic invertebrates that feed among the bryozoans are similarly slow growing and long-lived. Their survival has depended on long-term stability of their environment. Two factors, trawling (illegal fishing), which has already decimated stocks of the most desirable fish species, and global climate change, could have severe consequences for such communities.

The impact of climate change will differ depending on the temperature scenario. As pointed out by Thatje et al. (2005), the lowering of temperatures, leading to a glacial period, could almost completely eliminate the benthic fauna of the Antarctic shelf and slope. Increasing temperatures (as seen today, especially in the West Antarctic) will probably lead to enhanced diversity in a few habitats (e.g., the intertidal zone of the peninsula) but also to a change in present-day communities due to human impact and temperature stress. Human impact, including increased travel, both scientific and touristic, will increase the likelihood of ship fouling (Lewis et al., 2005; Barnes and Conlan, 2007). In addition, an increase in growth rate with higher temperatures has already been detected in one bryozoan, *Cellarinella nutti* (Barnes et al., 2006).

As Collie et al. (2000) noted in their analysis of the impacts of fishing on shelf benthos, there are large gaps in our knowledge of the effects of trawling on three-dimensional epifaunal communities. Reduction in habitat complexity caused by intensive bottom fishing may have long-term negative consequences for fish communities (loss of nest sites and nursery and breeding grounds).

Although benthic habitats with a high degree of structural heterogeneity occur in areas besides Antarctica, such as New Zealand (Bradstock and Gordon, 1983; Batson and Probert, 2000) and Helgoland (de Kluijver, 1991), they are rare. In only one (Tasman Bay, New Zealand) have erect bryozoan communities been protected in an attempt to restore a fishery (Bradstock and Gordon, 1983).

Finally, despite all the biological work that has occurred in the Antarctic since the 1980s, we still have a very poor idea of the link between what happens in pelagic communities and the benthos. A solid understanding

of benthic-pelagic coupling, factoring in life histories of structural epibenthos and their epibionts as well as resting stages of phytoplankton, importance of fecal pellets, and the role of benthic meiofauna in food chains and shelf ecosystems, has hardly begun (Marcus and Boero, 1998).

Acknowledgments

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