CHAPTER 5.23. BRYOZOA.

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN


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5.23. Bryozoa

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1. Introduction

Once referred to as ‘Ectoprocts’, bryozoans or moss animals are exclusively colonial animals formed of tens of thousands of modules called zooids. These colonies can encrust rocks, algae or other animals or they can form their own encrusting structures, which can resemble small macro algal fronds, bushes, twigs, coral-like plates or >1 m wide foliaceous reefs (Photo 1). The zooids of such colonies can take a variety of forms from autozooids, which suspension-feed on phytoplankton, to structurally supportive xenozooids, specialised reproductive ovicells and defensive ‘jawed’ avicularia. All Antarctic species, except one, are sessile and their ability to disperse and colonise regions is enabled by the production of numerous sexually produced larvae.

Bryozoans are now fairly ubiquitous across aquatic habitats from lakes to estuaries, shore to deep sea and tropics to polar oceans – using current data on all species they account for ~4.2% of all extant Antarctic fauna. For the last ~80 Ma, even with the brief but effective K-T extinction event (~65 Ma), gymnolaemates, the largest class of marine Bryozoa, have persisted, and become particularly speciose and abundant in the Southern Ocean (SO) (Hayward 1995). Stenolaemates, a less-speciose class of marine Bryozoa, have persevered over longer time scales, are also abundant globally, although their levels of richness in the SO are difficult to assess due to the paucity of research in the last half century. Outcrops of Antarctic fossil bryozoans are rare, with most reports limited to Eocene rocks of Seymour Island (north Antarctic Peninsula) (Taylor et al. 2008) and 4000 km away at McMurdo Sound (Hara 2013). However, fossils have also been found in more recent strata (Oligocene) in parts of the Antarctic Peninsula and South Shetland Islands (Hara 1982). Bryozoans, particularly the cheilostome order, could be argued to be one of the more successful taxa currently on Antarctica’s continental shelf. A single boulder can sometimes be encrusted by as many species of cheilostomes as all other mega and larger macrofauna found in a random hard surface ‘sample’ (Barnes & Clarke 1995, 1998). Few across-taxa studies have been undertaken at larger spatial scales, but bryozoans are amongst the most speciose groups recorded in the Deception Island caldera, the South Orkney Islands shelf (Barnes et al. 1996) and around South Georgia (Hogg et al. 2011). Currently, 412 Bryozoa species have been recorded from south of the Polar Front (PF), but there are still extensive under-sampled regions (such as the Amundsen Sea) where new species and genera are still being found (Kuklinski & Barnes 2009, Hayward & Winston 2011). Bryozoans are typically viewed as pioneer, primary colonisers of surfaces, as most species are easily overgrown by asasians, sponges and other fauna, however, by utilising SCUBA, remote operated vehicles or towed/drop cameras, bryozoans are found to be just as abundant and rich in more mature assemblages as cryptic epibionts (Gutt 2007).

In 1995, Hayward assembled all primary cheilostome taxonomic literature and combined this into a text, which greatly facilitated the use of this taxon by disciplines such as biogeography, ecology, and physiology. Since then, a number of new species have been described and others revised, but apart from an investigation of the ctenostome genus Aloyonidium by Porter & Hayward (2004), molecular methods have only just started to be applied to bryozoans south of the PF. The application of molecular genetics has revealed that many marine taxa, which were previously considered to have wide ranges, consist of many closely related species, and we expect that this will prove to be true of bryozoans. This would seem especially likely for bryozoans whose ranges currently cross the PF, as the few species for which cross-PF distributions have remained true are generally present in the deep sea; an environment where very few Antarctic bryozoans have been reported (Barnes & Kuklinski 2004).

2. Biogeography

The biogeography of bryozoans at high southern latitudes has been considered in a number of studies (e.g. Rogick 1965), and most recently by Barnes & Griffiths (2008) and Figueiroloa et al. (2012). Current and recent initiatives (e.g. CAML, SCAR-MarBIN) that have encouraged multinational efforts to create and expertly assess the taxonomy of open-access database records of marine species have increased the availability and quality of biogeographic information for scientists.

Photo 1 Variety of form in Antarctic cheilostomes and cyclostomes. (a) Hornera sp. (b) Kymella polaris (Waters, 1904). (c) Tubulipora sp. (d) Melicerita obliqua (Thomelly, 1924). (e) Reteporella sp. (f) Discoporella sp. (g) Iimidronaea sp. (h) Tubulipora sp. (i) Beania erecta Waters, 1904. (j) Arachnopusia inchoata Hayward & Thorpe, 1988. (k) Himantozoum antarcticum (Calvet, 1909). (l) Cellarinella watsersi Calvet, 1909. Image © J. Oliver, BAS.
Lattitudinal and longitudinal ranges are strongly linked in SO bryozoans (Fig. 1). Antarctic bryozoan species tend to show wider geographic ranges (especially in longitude) than those in the Arctic or southern temperate zones (Maps 1 & 4). Half of Antarctic species attain longitudinal ranges that are greater than 180°, with half circumpolar longitudinal ranges (>300°) found in many species, such as Nematomurula flagellata, Carbasea curva, Cellanichthys nudi, and Kymella polaris (Maps 1 & 9). Over 70% of Antarctic species have latitudinal ranges greater than 10° latitude, with only 6% (e.g. Acyonidium simulum, Arachnopodia aviculifera, and Stomatopora antarctica) having limited latitudinal ranges (<3°) in the Southern Ocean (Map 2). Currently, 40% of sub-Antarctic species are found to have limited latitudinal ranges (e.g. Foveolaria orbicularis, Anastigia kirkpatrici, and Galeopsis manoricensis), and over 90% of these species have limited longitudinal ranges (<10° longitude).

The wide longitudinal ranges of Antarctic bryozoans are likely to have been driven by the strength of the Antarctic Circumpolar Current (ACC), similarity of environmental conditions around Antarctica, and the former seaways across West Antarctica. Key SO biogeographic distributions of bryozoans are shown on Maps 1–9, including circumpolar (Map 1); regional endemic species (Map 2); cross Polar Front (Map 3); sub-Antarctic (Map 4); and palaeo-seaways (Map 5).

Important examples of restricted deep water taxa (Map 6); shallow shelf-restricted species (Map 7); and eurybathic species (Map 8) are also highlighted. Current sampling has found few cheilostome species, compared with cheilostomes and cyclostomes in the SO (Maps 10–12). These maps illustrate that the location and intensity of sampling has changed over the last half century with regions including the Antarctic Peninsula, Weddell Sea, and sub-Antarctic better-sampled over the last 40 years.

3. Bathymetry

As many Antarctic bryozoan species appear to not just be restricted geographically, but also by depth, their narrow bathymetric range is proving to be a useful tool for interpreting glacial and palaeo-seaways (Brandt et al. 2010). Bryozoans occur sparsely in the intertidal zone but, cheilostomes at least, seem to be found wherever there has been a concerted effort to look for them, however, they have not been reported on shores south of 68° S to date. Currently, 40% of sub-Antarctic species are found to the uppermost section of shelf (0–100 m) and nearly 90% occur only on the shelf (<1000 m depth), indicating that the Antarctic shelf is the most biodiverse area for bryozoans. However, a significant number of Southern Ocean bryozoan species have wider depth ranges from the shallows to shelf break. Currently ~26% of species have been recorded from the continental slope and 3% from abyssal depths (e.g. Camptopodites latus and Melicertica obliqua (Map 8)); with the majority of abyssal records of these species only known from the Weddell Sea. Bryozoan abundance levels decrease ~1000 times from shelf to continental slope and are at least an order of magnitude rarer again in the abyss (Barnes & Kuklinski 2010). When combined with the paucity of sampling at such depths, it seems unlikely that we will have a good understanding of the true extent of the slope or deep sea bryozoan composition (and thus the lower depth limit or ranges of shelf fauna) for many decades until focused depth research is undertaken.

4. Recent progress in Antarctic bryozoan research

The first biological samples from the Amundsen Sea (which spans 40° of coastline, but with surprisingly few undescribed cheilostome species. However, new cheilostome species have been described from many localities around Antarctica throughout the last decade, particularly in the Weddell Sea (e.g. Gontar 2002). New specimens await description from the Amundsen and Weddell seas, as well as in CEAMARS and an East Antarctic Marine Census) samples off Oates Land (Dumont d’Urville Sea). About 0.4–0.7 of all new (geographic or bathymetric) records are reported per sample in the Southern Ocean, and one of the most recent finds is the first bryozoan (Calliopora westlawi) believed to be bipolar in distribution (Kuklinski & Barnes 2010). Progress in bryozoan research has occurred in several key areas, such as the increased access to exact species locations, molecular techniques to better determine Antarctic bryozoan taxonomy, and the development of both Arctic and Antarctic online identification guides, which include new and crucial electron-microscope images.

5. Using bryozoans as climate/environmental proxies

Increasingly, bryozoan species distributions are being used to test hypotheses about the origins of Antarctic biota (Brandt 2005); and one of the most important of these hypotheses is to determine the extent to which the deep sea vs. the shelf as source or sink regions of current marine fauna (i.e. the importance of emergent vs. submergent migrations) (Barnes & Kuklinski 2010). Both geological data and glaciological models have been used to infer that most life was removed from the Antarctic continental shelf by the last (and probably many previous) glaciations, and thus the key question is: where did the rich abundant fauna currently found there, re-colonise from? To date, very little has been found for this hypothesis that bryozoans are a subset of those in the abyss or the continental slope (emergent migration). If the slope and abyss were not the source of shelf fauna, another possibility is Antarctica’s outlying islands or southern margins of other continents. Similarly, little support has been found for this, and so the re-colonisation of Antarctic shelves from in situ refugia is currently thought to be the most likely scenario (Barnes & Hillenbrand 2010). This has important ramifications for Antarctic ice-mass balance and climate models — because it suggests that there may have been significantly less ice coverage and/or longer ice-free periods than previously thought. Thus, a number of areas (e.g. deep oceanic basins) have been identified as potential ice-free habitats during the LGM (Last Glacial Maximum), but so far no conclusive evidence of marine life surviving entire glaciation on Antarctic shelves have been found.

The level of similarity of bryozoan shelf assemblages between regions should approximately relate to the distances between them. Bryozoans are poor dispersers, as most larvae, are lecithotrophic (lives off yolk supplied via the egg) and benthic, which potentially both limit significant range expansion. However, analysis of local and regional biogeographic and glacial/glacimarine anomalies in distance-similarity indices, which indicate strong shared species links between the Weddell and Ross seas (Barnes & Hillenbrand 2010). These findings support theories, based on diatom distributions and in situ refugia, that the southern continent had not existed. This would require the partial collapse of the third largest ice mass on Earth — the West Antarctic Ice Sheet. New samples from the Amundsen Sea are helping to further explore where such seaways were potentially located and when those connections were closed. By combining this bryozoan data, with glaciological (ice sheet stability and ice melt rate patterns) and geomorphological (bed mapping underneath the current ice shelf), we are better able to investigate and model ice sheet behaviour under past climatic conditions. Ultimately this is key to understanding how the ice sheet level is likely to change under current and projected rapid regional warming.
Bryozoa Maps 1–6: Distribution types of Antarctic bryozoan species.

Map 1: Circumpolar: Nematoflustra flagellata (Waters, 1904).

Map 2: Regionally endemic: Alcyonidium eightsii, Arachnopusia aviculifera, Aspericreta crassatina (Waters, 1904), Chaperiopsis signyensis (Hayward, 1993), Notoplites uniserialis (Hastings, 1943).

Map 3: Across the Polar Front: Cellaria malvinensis (Busk, 1852), Ellisina antarctica (Hastings, 1945), Lacerna hosteensis (Jullien, 1888).

Map 4: Sub-Antarctic: Beania magellanica (Busk, 1852), Malakosaria sinclairii (Busk, 1857).


Map 6: Deep water: Himantozoum taurinum (Harmer, 1926).
6. Using bryozoans to investigate biological response to environmental change

The two most fundamental physical oceanographic changes measured over the last half a century have been sea surface warming and temporal-spatial changes in sea ice extent. One of the most important projected global environmental changes is increased surface ocean acidification, due to the increasing concentration of CO₂ in the atmosphere. One of the key biological responses to these recently measured environmental changes, has been the spatial (bathymeric and latitudinal) depression of phytoplankton blooms (Montes-Hugo et al. 2009). Bryozoans are a potentially useful taxon for monitoring each of these environmental changes, as they are abundant, common and species-rich in the predicted zones of warming and pH change (as well as in adjacent areas that are projected to have few changes) in the SO. Bryozoans are influenced by sea ice, in terms of disturbance (fast ice duration reduces ice scour by minimising iceberg travel) and food availability (fast ice duration is related to phytoplankton bloom timing and duration). Spatial distribution data, both bathymetric and geographic, can be used to select the most appropriate species to sites of differing levels of environmental change, and by sampling at different depths and geographic localities. Two of the species to have shown significant change in the last few decades are Cellairellina nutti and Fenestrulina rugula (Map 9) (Barnes et al. 2011).

7. Bryozoans as bioconstructors

Bryozoans are one of a number of marine organisms that are classed as ‘bioconstructors’ due to their ability to construct a permanent, dynamic structure (Cocito 2004). Bryozoans are both a pioneering phylum, as their larvae can attach and grow quickly in new areas, and an integral part of stable, long-standing benthic communities in Antarctica (Photo 2). Bryozoans are important bioconstructors, as they create habitat heterogeneity and structural complexity, which have been found to enhance local biodiversity in marine environments, by increasing and creating new habitat spaces, providing cryptic refugia for species, altering the localised physical environment for better larval recruitment, and multiplying resources for dwellers and scavengers (Cocito 2004). Taxa, such as sponges and corals, can positively influence the presence and distribution of bryozoans, by providing a suitable substrate for colonisation in regions which would otherwise be incompatible for successful migration. Mobile taxa, such as echinoids, also impact distribution, as they passively transport Bryozoa on their spines to new areas, including recently ice-scoured regions. The variety of structural growth forms of bryozoan bioconstructors are diverse, and include erect/rigid (Cellarinella and Cellaria), folaceous (Arachnopusis, Isoschizoporella, and Lagenscharca), fenestrae/reticulate (Reteporella), and flustriform (Isoschizoporella and Fenestrulina) (Hagen et al. 1998) (Photo 1). Bryozoa families that are encrusting (Smittina and Ostomisia), create nano-habitats and act functionally as ‘binders’, which unites and expand other erect bioconstructors (Cocito 2004). Within these structural forms, rigidity and shape (lobate, cylindrical, spiral, or conical) are important, as these features potentially increase the types and numbers of species that can utilise the Bryozoa as habitat.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope
Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of global and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)
CAML (www.caml.ai) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)
In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

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