

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN



Barnes D.K.A., Downey R.V., 2014.

In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. 195-199.

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SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

The "Biogeographic Atlas of the Southern Ocean" is a legacy of the International Polar Year 2007-2009 (www.ipy.org) and of the Census of Marine Life 2000-2010 (www.coml.org), contributed by the Census of Antarctic Marine Life (www.caml.aq) and the SCAR Marine Biodiversity Information Network (www.scarmarbin.be; www.biodiversity.aq).

The "Biogeographic Atlas" is a contribution to the SCAR programmes Ant-ECO (State of the Antarctic Ecosystem) and AnT-ERA (Antarctic Thresholds- Ecosystem Resilience and Adaptation) (www.scar.org/science-themes/ecosystems).

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Published by:

The Scientific Committee on Antarctic Research, Scott Polar Research Institute, Lensfield Road, Cambridge, CB2 1ER, United Kingdom (www.scar.org).

Publication funded by:

- The Census of Marine Life (Albert P. Sloan Foundation, New York)
- The TOTAL Foundation, Paris

The "Biogeographic Atlas of the Southern Ocean" shared the Cosmos Prize awarded to the Census of Marine Life by the International Osaka Expo'90 Commemorative Foundation, Tokyo, Japan.

Publication supported by:

- The Belgian Science Policy (Belspo), through the Belgian Scientific Research Programme on the Antarctic and the "biodiversity.aq" network (SCAR-MarBIN/ANTABIF)
- The Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium
 The British Antarctic Survey (BAS), Cambridge, United Kingdom
- The Université Pierre et Marie Curie (UPMC), Paris, France
- The Australian Antarctic Division, Hobart, Australia
- The Scientific Steering Committee of CAML, Michael Stoddart (CAML Administrator) and Victoria Wadley (CAML Project Manager)

Mapping coordination and design: Huw Griffiths (BAS, Cambridge) & Anton Van de Putte (RBINS, Brussels)

Editorial assistance: Henri Robert, Xavier Loréa, Charlotte Havermans, Nicole Moortgat (RBINS, Brussels)

Printed by: Altitude Design, Rue Saint Josse, 15, B-1210 Brussels, Belgium (www.altitude-design.be)

Lay out: Sigrid Camus & Amélie Blaton (Altitude Design, Brussels).

Cover design: Amélie Blaton (Altitude Design, Brussels) and the Editorial Team.

Cover pictures: amphipod crustacean (Epimeria rubrieques De Broyer & Klages, 1991), image © T. Riehl, University of Hamburg; krill (Euphausia superba Dana, 1850), image © V. Siegel, Institute of Sea Fisheries, Hamburg; fish (*Chaenocephalus* sp.), image © C. d'Udekem d'Acoz, RBINS; emperor penguin (*Aptenodytes forsteri* G.R. Gray, 1844), image © C. d'Udekem d'Acoz, RBINS; Humpback whale (*Megaptera novaeangliae* (Borowski, 1781)), image © L. Kindermann, AWI

Online dynamic version:

A dynamic online version of the Biogeographic Atlas is available on the SCAR-MarBIN / AntaBIF portal: atlas.biodiversity.aq.

Recommended citation:

De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (eds.), 2014. Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, XII + 498 pp.

For individual chapter:

(e.g.) Crame A., 2014. Chapter 3.1. Evolutionary Setting. In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. xx-yy.

ISBN: 978-0-948277-28-3



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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 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 kenozooids, 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 radiated, 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 1992).

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 (Kuklinkski & Barnes 2009, Hayward & Winston 2011). Bryozoans are typically viewed as pioneer, primary colonisers of surfaces, as most species are easily overgrown by ascidians, 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 *Alcyonidium* 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 2010).

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 Figuerola *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.

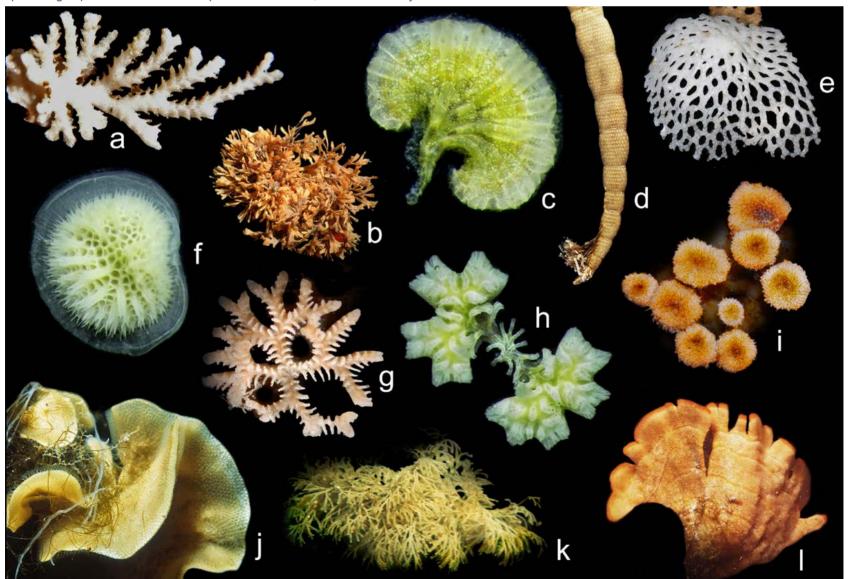


Photo 1 Variety of form in Antarctic cheilostomes and cyclostomes. (a) Hornera sp. (b) Kymella polaris (Waters, 1904). (c) Tubulipora sp. (d) Melicerita obliqua (Thornely, 1924). (e) Reteporella sp. (f) Discoporella sp. (g) Idmidronea sp. (h) Tubulipora sp. (i) Beania erecta Waters, 1904. (j) Arachnopusia inchoata Hayward & Thorpe, 1988. (k) Himantozoum antarcticum (Calvet, 1909). (l) Cellarinella watersi Calvet, 1909. Image © J. Oliver, BAS.

Latitudinal 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 sub-Antarctic or southern temperate zones (Maps 1 & 4), Half of Antarctic species attain longitudinal ranges that are greater than 180°, with near circumpolar longitudinal ranges (> 300°) found in many species, such as Nematoflustra flagellata, Carbasea curva, Cellarinella nutti, and Kymella polaris (Maps 1 & 9). Over 70% of Antarctic species have latitudinal ranges greater than 10° latitude, with only 6% (e.g. Alcyonidium simulatum, Arachnopusia 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, Amastigia kirkpatricki, and Galeopsis marionensis), 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 ctenostome 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.

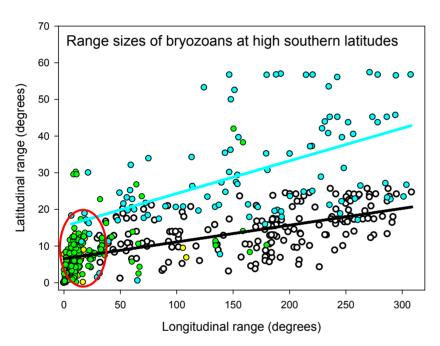


Figure 1 Range size of high latitude southern hemisphere bryozoans. The symbols are: Antarctic (unfilled), sub-Antarctic (yellow), southern temperate (green) and cross-Polar Front (blue) distributions. The relationships shown are significant linear regressions and the red circle highlights species with restricted ranges (suggested as potentially vulnerable to climate changes).

Southern Ocean Bryozoa biogeography has tended to use only cheilostome data (Map 10), as they constituted the majority (87%) of bryozoan species records south of 30° S (Barnes & Griffiths 2008). Although they probably do form the majority of species at high latitude, it is likely that such a high value largely reflects the bias of recent taxonomic studies. Cheilostomes have been reported from virtually every Antarctic shelf area examined to date, even underneath ice shelves (e.g. Post et al. 2007). More than half (57%) of currently described Antarctic cheilostomes are endemic, which is similar to that found in other isolated regions, such as New Zealand (Barnes & Griffiths 2008). The long term isolation caused by the ACC is perhaps best illustrated by the high generic and even occasionally family-level endemismof SO bryozoans (Barnes & Griffiths 2008). Despite the dominating force of the ACC, there is clear regional structure apparent in the geographic distributions of SO cheilostomes (Maps 2–5), which could be beneficial in reconstructing Antarctica's glaciological history.

Records for the Antarctic ctenostomes (Map 11) are generally recent and reveal an Antarctic distribution with four main centres, as well as outlying islands with 'gaps' of a thousand kilometers or more between them. Records for Antarctic cyclostomes (Stenolaemata) are older, reflecting intense Swedish efforts prior to 1970, and suggest a much wider coverage across shelf areas (Map 12). Many of the more recent records are identified only to family or genus, indicating a strong need for taxonomic work on this phylum particularly for cyclostomes from the eastern Amundsen Sea, which are awaiting description.

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 biological and glaciological history (Barnes & Hillenbrand 2010). Bryozoans occur sparsely in the intertidal zone but, cheilostomes at least, seem to be found wherever there has been concerted effort to look for them, however, they have not been reported on shores south of 68° S to date. Currently, 42% species found are restricted 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 are eurybathic, found at wide depth ranges from the shallows to shelfbreak. Currently ~26% of species have been recorded from the continental slope and 3% from abyssal depths (e.g. Camptoplites latus and Melicerita 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

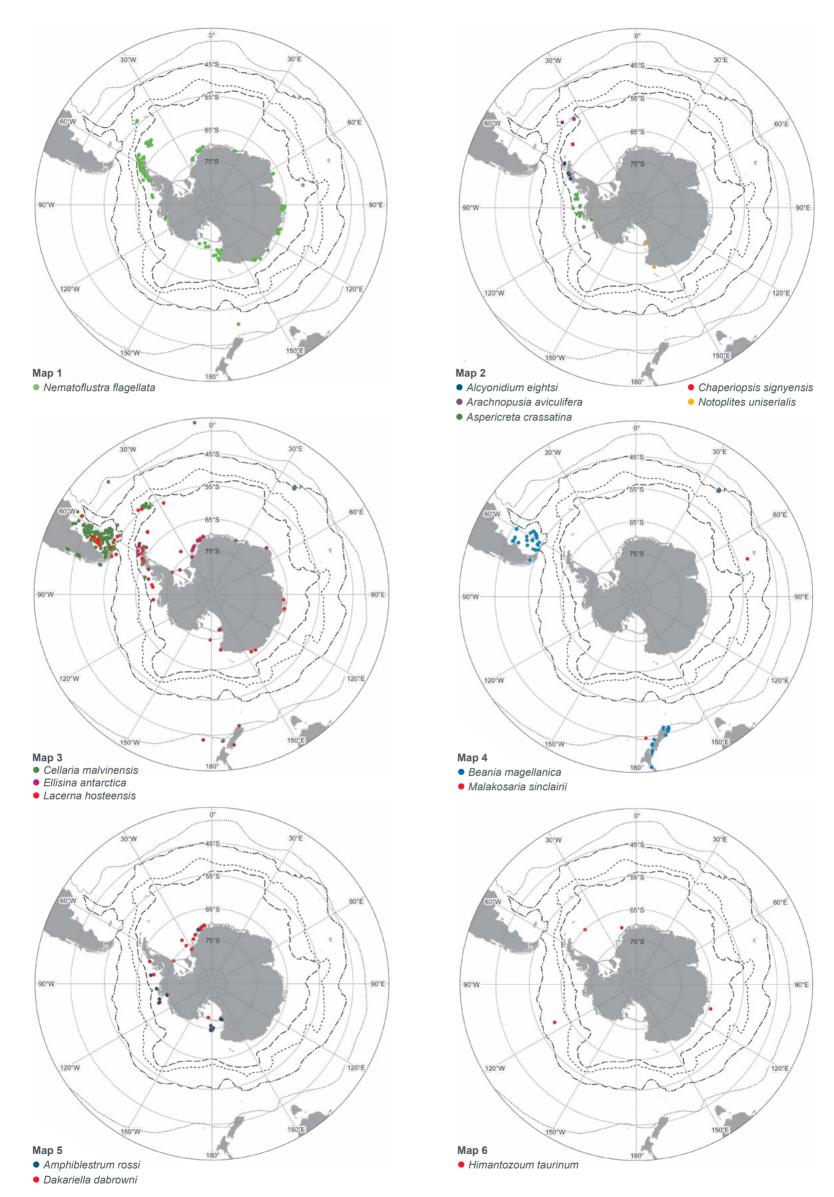
The first biological samples from the Amundsen Sea (which spans 40° longitude) yielded a rich bryozoan fauna, but with surprisingly few undescribed cheilostome species. However, new cheilostome species have been described from many localities around Antarctica throughout the last decade, particularly in the Weddell Sea (e.g. Gontar 2002). New specimens await description from the Amundsen and Weddell seas, as well as in CEAMARC (Collaborative 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 (*Callopora weslawski*) 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 on-line 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 determining 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 support has been found for the hypothesis that bryozoans on the shelf are a subset of those in the abyss or the continental slope (emergent migration). If the slope and abvss 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 recolonisation of Antarctic shelves from in situ refugia is currently thought to be the most likely explanation (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 shelfves have been found.

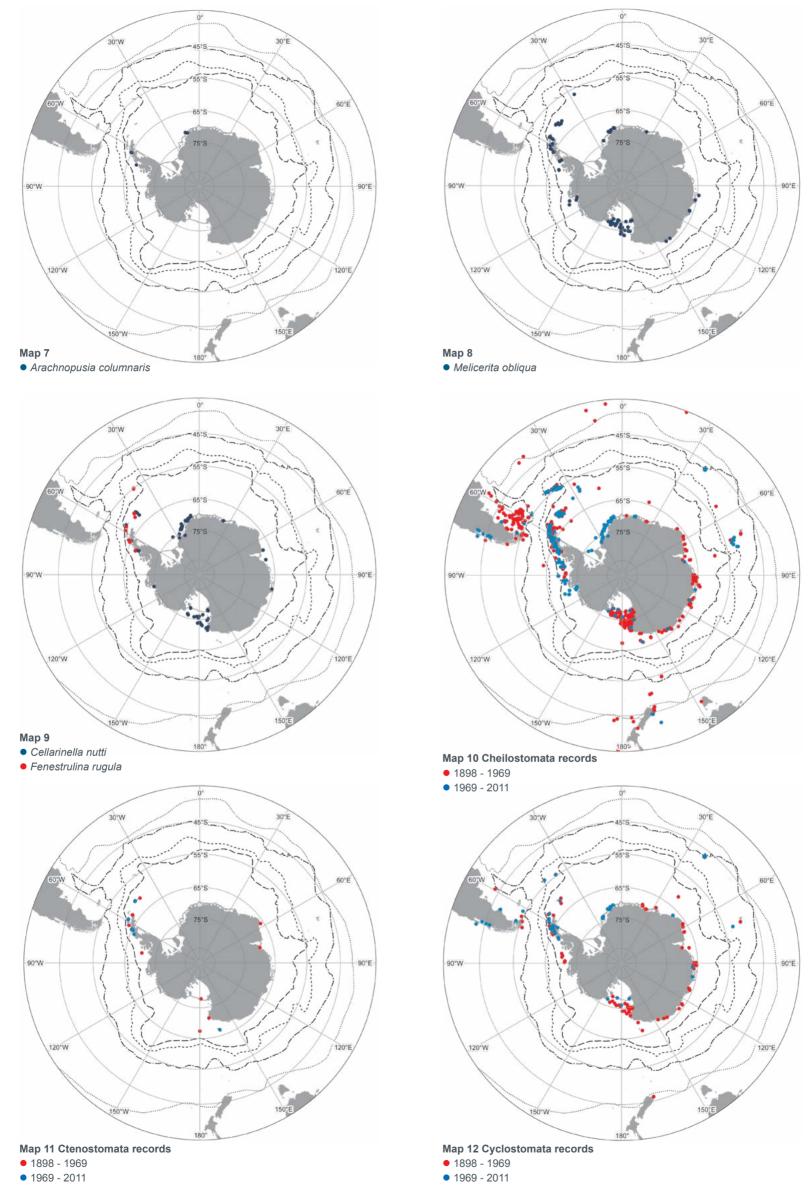
should approximately relate to the distances between them. Bryozoans are poor dispersers, as most larvae, are lecithtrophic (lives off yolk supplied via the egg) and benthic, which potentially both limit significant range expansion. However, analysis of local and regional composition has shown significant 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 ice sheet modelling, that palaeo-connections between these two seas 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 closed. By combining biogeographical 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 should lead to stronger predictions of how sea level is likely to change under current and projected rapid regional warming.

The level of similarity of bryozoan shelf assemblages between regions



Bryozoa Maps 1–6 Distribution types of Antarctic bryozoan species. Map 1. Circumpolar: Nematoflustra flagellata (Waters, 1904). Map 2. Regionally endemic: Alcyonidium eightsi Winston & Hayward, 1994; Arachnopusia aviculifera Hayward & Thorpe, 1988; 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 5. Either side of palaeo-seaways: Amphiblestrum rossi Hayward & Thorpe, 1989, Dakariella dabrowni (Rogick, 1962). Map 6. Deep water: Himantozoum taurinum Harmer, 1926.

Bryozoa



Bryozoa Maps 7–8 Distribution types of Antarctic bryozoan species. Map 7. Shallow-water only: *Arachnopusia columnaris* Hayward & Thorpe, 1988. Map 8. Eurybathic: *Melicerita obliqua* (Thornely, 1924). Map 9. Distribution shown to have recently changed. Maps 10–12 High latitude species level data for bryozoans over time. The data shown are at the time of Hedgpeth 1969 (red dots) and up to March 2011 (blue dots). Map 10. Cheilostomata. Map 11. Ctenostomata. Map 12. Cyclostomata.

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 temporalspatial 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 ${\rm CO_2}$ in the atmosphere. One of the key biological responses to these recently measured environmental changes, has been the spatial (bathymetric 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 investigate potential performance changes (e.g. by comparing the growth of a species at 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 Cellarinella 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 refuges 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 substratum 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),



Photo 2 Bryozoan bioconstuctor assemblages on the Ross Sea shelf. Image © D.

foliaceous (Arachnopusia, Isoschizoporella, and Lageneschara), fenestrate/ reticulate (Reteporella), and flustriform (Isosecuriflustra and Nematoflustra) (Hageman et al. 1998) (Photo 1). Bryozoan families that are encrusting (Smittina and Osthimosia), create nano-habitats and act functionally as 'binders', which unite and expand other erect bioconstructions (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.

Globally, Antarctica holds the greatest expanses of habitat-forming bryozoans (Wood et al. 2012), with extensive communities (> 1000 km) found in the Weddell and Lazarev seas (Gutt & Starmans 1998) and densely structured communities found in the Ross Sea (Parker & Bowden 2010). Currently, at least 25% of all bryozoan species found in the SO are deemed to be major bioconstructors. Cheilostome bryozoa are major bioconstructors globally, with families such as the genera- and species-rich Flustridae and Cellaridae particularly important habitat-formers within the SO. Unusually,

cyclostome bryozoans, which are only abundant around the New Zealand coast, have also been found to be bioconstructing in the SO (Gutt & Starmans 1998). Over 95% of bioconstructing bryozoa species are distributed only on the Antarctic shelf (0-1000 m); however, important habitat-forming species (e.g. Melicerita obliqua) have been found at depths of up to 5000 m in the Weddell Sea (Map 8). There are few studies to date which quantify the importance of bryozoans in creating and maintaining localised biodiversity on the Antarctic shelf. One notable study has indicated the capacity of Bryozoa as bioconstructors, finding over 30 species of epibionts on two species of cheilostomes around the South Orkney Islands (Barnes 1994). Globally, some of the most diverse faunal communities are indirectly associated with bryozoa habitat (e.g. Echinodermata, Annelida, Porifera, and Mollusca), have been found along the Weddell and Lazarev seas (Gutt & Starmans 1998). However, the continued paucity of bioconstructor studies within the SO has limited our ability to fully understand and summarise the importance of bryozoans for benthic biodiversity in this region.

Acknowledgments

Dr. Huw Griffiths (BAS, Cambridge) is thanked for the preparation of the maps. This is CAML contribution # 121.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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

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 biotic 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.aq) 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.

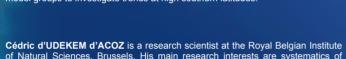
The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)
In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and 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.

The Editorial Team



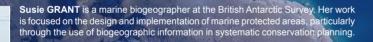
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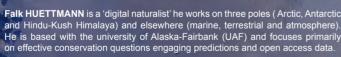


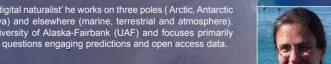


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