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SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 5.5. PORIFERA.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.5. Porifera

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1. Introduction

Porifera (pore-bearers), commonly known as sponges, are sessile, colonial animals that are ubiquitous to most marine and freshwater environments. As an ecologically successful phyla, sponges having existed since the Precambrian (~580 Ma), and were major reef builders during the Palaeozoic and Mesozoic (542 to 65 Ma) (e.g. Krautter 1997, Li *et al.* 1998, Jackson *et al.* 2007). Even today, sponges are an abundant and highly diverse phylum, with approximately 8,500 valid species described so far (Van Soest *et al.* 2012a, b), but at least twice that number are predicted to be discovered in the near future (Hooper & Van Soest 2002; Van Soest *et al.*, 2012a).

Sponge architecture is unique, consisting of a basic system of water canals and chambers of cilia-bearing cells (choanocytes), which take oxygen and fine particulate food matter in from the surrounding water, and pump out waste and reproductive products. Sponge skeletons are relatively complex, providing a supporting framework for the living cells of the animal. Skeletal morphology is still the main identification method used to differentiate between species; but advances in molecular techniques are providing new insight into species differentiation and higher order classifications (Wörheide & Erpenbeck 2007, Wörheide *et al.* 2008, Cárdenas *et al.* 2011, Vargas *et al.* 2012, Wörheide *et al.* 2012). Sponges are currently divided into four classes (Demospongiae, Hexactinellida, Calcarea, and Homoscleromorpha), all of which are represented within the Southern Ocean (Hooper & Van Soest 2002, Gazave *et al.* 2010).



Photo 1 Photograph illustrating the variety of morphologies present in sponge communities in the Weddell Sea (118 m). Image: J. Gutt © AWI/Marum, University of Bremen, Germany.

To date, the demosponge class comprises the majority (75%) of sponge species recorded within the Southern Ocean and exhibits the greatest depth ranges (from shallow to abyssal) in sponge species distributions (Koltun 1969, Sarà *et al.* 1992, McClintock *et al.* 2005, Downey *et al.* 2012). Demosponges are often colourful and their skeletons are composed of either a combination of siliceous spicules and spongin fibres, or spongin fibres alone (e.g. bath sponges). Hexactinellid sponges are well-represented and contribute significantly to the biomass, species diversity and abundance in the Southern Ocean, especially on the Antarctic shelf, which is unusual, as they are regarded as typical deep-water fauna (Tabachnick 1994, Reiswig 2002, Leys 2003). Hexactinellid skeletons are composed of triaxial siliceous spicules, and many species possess long root tufts, which enable them to colonise soft-bottom sediment environments. Thus they are an important constituent of the abyssal plains community around Antarctica (Janussen & Tendal 2007). Calcarea are a small Porifera class with currently nine orders. Calcareous sponges are mostly small in body size, their spicules are made of calcium carbonate and most species of calcareous sponges are restricted to shallow coastal waters globally. This class is found to be shallow-dwelling and relatively rare in the Antarctic (McClintock *et al.* 2005), however, occurrences are known from the deep Antarctic shelf (Janussen & Rapp 2011, Rapp *et al.* 2013) and have recently been recorded from the abyssal Weddell Sea (Rapp *et al.* 2011). Homoscleromorpha are a class of siliceous and generally shallow-dwelling sponges, which was recently elevated to this taxonomic level. Currently, only seven genera and less than 100 species are known worldwide (Gazave *et al.* 2011), but despite their rarity, two genera (3 spp.) have so far been described from the Southern Ocean (Griffiths & Downey 2012).

Taxonomic richness is a characteristic of the Southern Ocean Demospongiae class, with both the Polymastiidae (8 genera) and Hymedesmiidae (7 genera) families being the most genera-rich, and the Chalinidae (48 spp.), Microcionidae (27 spp.), Coelosphaeridae (20 spp.) and Halichondriidae (19 spp.) families being particularly species-rich (Griffiths & Downey 2012). Species-rich genera are common in Southern Ocean

demosponges, particularly the genera *Isodictya* (17 spp.), *Myxilla* (15 spp.), *Iophon* (14 spp.), *Tedania* (14 spp.), *Mycale* (11 spp.), and *Suberites* (10 spp.). All other sponge classes have a lower taxonomic diversity within the Southern Ocean. For example, within the 7 families of the Hexactinellida found within the Southern Ocean, the majority are genus- and species-poor, except for the family Rossellidae (10 genera, 21 spp.), and particularly the Southern Ocean endemic genus *Rossella* (Barthel & Tendal 1994). Calcarea families are neither genus- nor species-rich, with the most species-rich families being the Achramorphidae and Leucettidae (9 spp. each) (Downey *et al.* 2012). The Homoscleromorpha class are also neither genus- nor species-rich; however, all currently known families in this class (Oscarellidae and Plakinidae) are represented in the Southern Ocean. Taxonomic richness of Southern Ocean sponges could be explained by several specific ecological phenomena, which include the reduced number of efficient sponge-predators and competitors for food and space, tolerance of varied substrata (McClintock *et al.* 2005), and low levels of sedimentation, which are all potentially important for the success and diversity of filter-feeding organisms (Hedgpeth 1969).

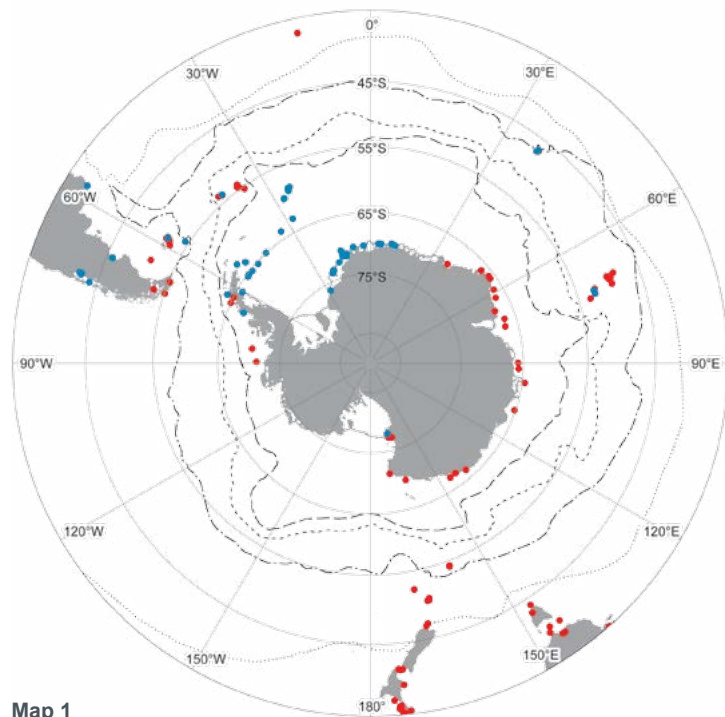
2. Sponge research highlights in the Southern Ocean

There have been a number of advances in Southern Ocean sponge research, particularly in the fields of taxonomy/systematics (Brandt *et al.* 2007, Plotkin & Janussen 2007, Janussen & Reiswig 2009, Göcke & Janussen 2013a, b, c, Rapp *et al.* 2011, 2013), ecology (McClintock *et al.* 2005, Rapp *et al.* 2011), habitat importance (Hogg *et al.* 2010) and biogeography (Sarà *et al.* 1992, Downey *et al.* 2012). An important step in advancing the progress in Southern Ocean sponge research has been the collection of all available sponge species distribution records from the Southern Ocean into one database (Griffiths & Downey 2012). Over 10,000 records of sponges have been collated as part of a SCAR-MarBIN/TOTAL Foundation project to map Southern Ocean bio-constructors (sessile animals that provide habitat). This database enhances our knowledge of sponge distributions, species richness and endemism, and also provides a visual aid of which areas are well-explored, and those that need further investigation (Maps 1–4). It also greatly helps in determining where habitat-forming species occur in the Southern Ocean, which is crucial for the conservation of Antarctic benthic biodiversity; as well as pinpointing potential vulnerable marine ecosystems (VMEs) within the Southern Ocean for organisations such as CCAMLR (Convention on the Conservation of Antarctic Marine Living Resources).

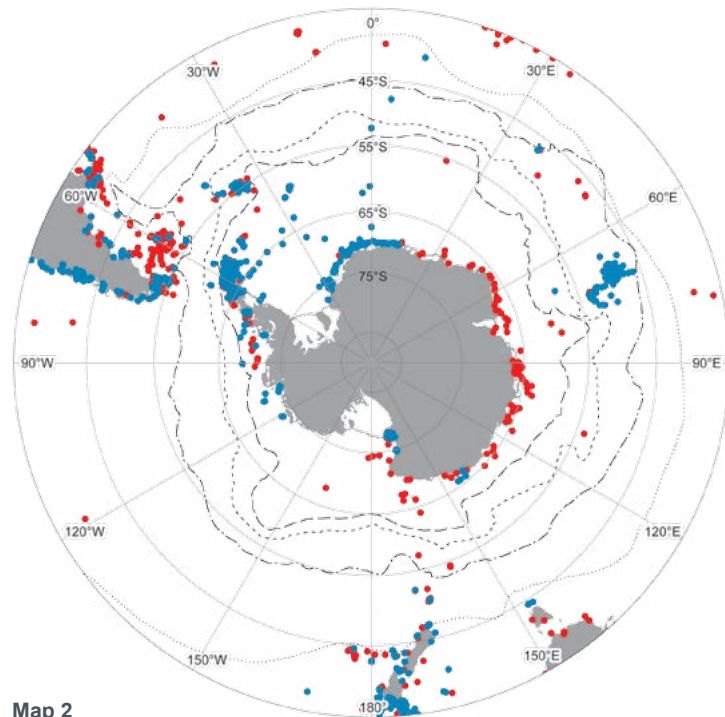
2.1. New species found, new regions explored

In recent decades significant advances have been made in global sponge taxonomy (Hooper & Van Soest 2002, Van Soest *et al.* 2012a, b), especially within the Southern Ocean where many new species and genera (e.g. the new genus *Astrotylus*) have been described (Plotkin & Janussen 2007), while other species and genera have been synonymised and validated (Van Soest *et al.* 2012b). Exploring new habitats and areas within the Southern Ocean has led to considerable changes in sponge taxonomy with regards to diversity, particularly within the Hexactinellida and Calcarea classes, where the number of species have doubled or even tripled since the first expeditions to the Southern Ocean (e.g. Janussen *et al.* 2004, Janussen & Tendal 2007, Janussen & Reiswig 2009, Rapp *et al.* 2011, De Broyer *et al.* 2011b). Advances in sponge natural product chemistry (Joseph & Sujatha 2011, Núñez-Pons *et al.* 2012, Turk *et al.* 2013), molecular techniques (e.g. Wörheide *et al.* 2007), together with the sponge bar-coding project (<http://www.spongebarcoding.org/>) and traditional taxonomy are likely to further increase our understanding of the uniqueness and diversity of Southern Ocean sponges.

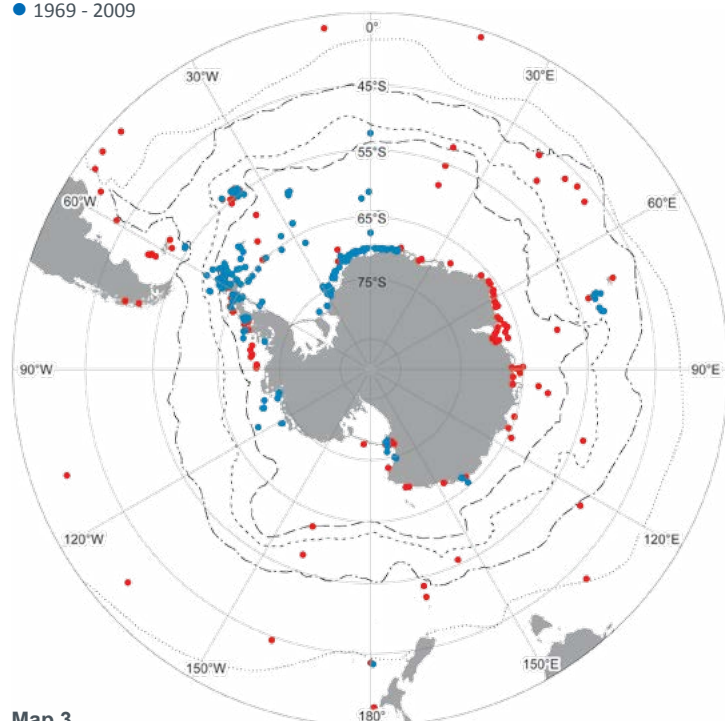
Current sponge distribution data can be used as an indication of how much research has been accomplished in the last 40 years in Southern Ocean sponges. Since Hedgpeth's report (1969), the number of demosponge records has more than doubled and hexactinellid records have tripled in the Southern Ocean (Fig. 1), (Maps 1–4). Calcarea and Homoscleromorpha records have both increased in the last 40 years, however, at a much slower pace than other sponge classes. Distribution records indicate which regions have been newly explored in the Southern Ocean, particularly along the coast of Dronning Maud Land (10°W to 20°E), and abyssal sites away from the coast (Maps 1–4). Much of this exploration has been accomplished by the recent ANDEEP and SYSTCO (ANtartic benthic DEEP-sea biodiversity, Pelagic-benthic SYS-Tem COupling) research programmes. Major breakthroughs in our understanding of Antarctic sponges achieved in these projects include: higher levels of sponge diversity found at bathyal and abyssal depths than previously known; nearly 50% of sponge species found were new to the Southern Ocean; the first recording of calcareous sponges from the Antarctic deep-sea; and 22% of species found were entirely new to science (Brandt *et al.* 2007, Janussen & Tendal 2007). Even regions that have been well-sampled before, such as South Georgia, are yielding discoveries, such as 15 previously undescribed endemic sponge species (Goodwin *et al.* 2012). In recent decades there have been concerted efforts made in exploring those Antarctic regions that have been under-sampled for benthic fauna, such as the BENTART cruise to the



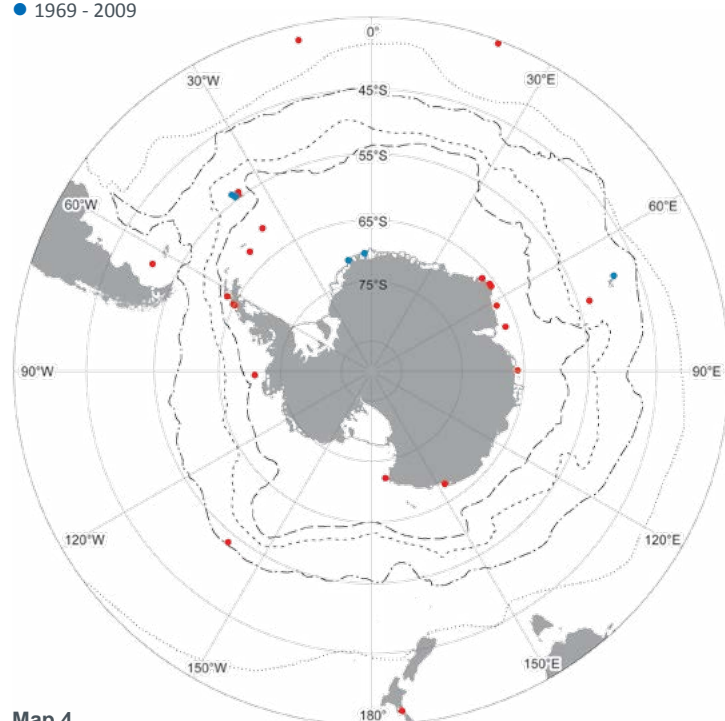
Map 1
Calcarea
● 1840 - 1969
● 1969 - 2009



Map 2
Demospongiae
● 1840 - 1969
● 1969 - 2009



Map 3
Hexactinellida
● 1840 - 1969
● 1969 - 2009



Map 4
Homoscleromorpha
● 1840 - 1969
● 1969 - 2009

Porifera Maps 1–4 Pre- and post-1969 records: Map 1. Calcarea. Map 2. Demospongiae. Map 3. Hexactinellida. Map 4. Homoscleromorpha.

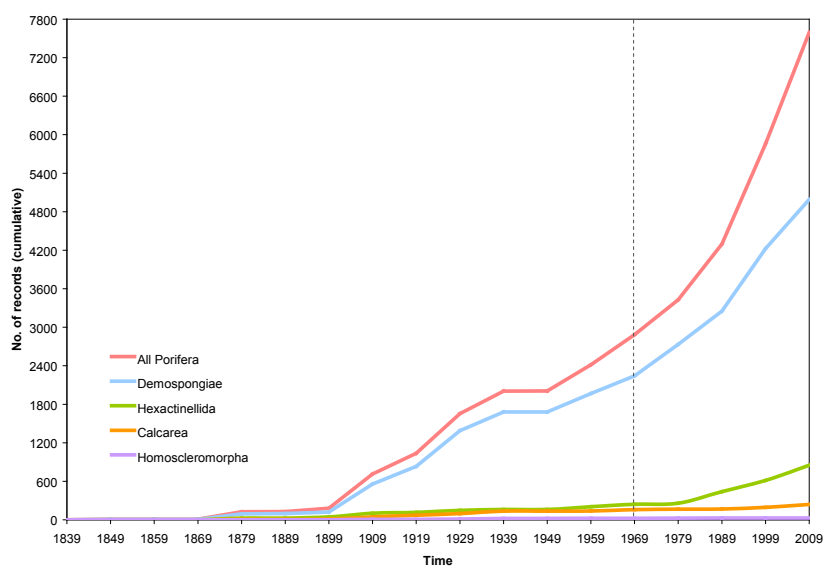


Figure 1 Graph illustrating the cumulative number of records of all sponges (including sponges not identified to class level), and each of the 4 classes of sponges in the Southern Ocean (data extracted from SOMBASE/TOTAL-Bioconstructors database). The hashed line illustrates the cumulative number of available records of Southern Ocean sponges at the time that Hedgpeth (1969) published.

Bellingshausen Sea (Ríos & Cristobo 2007), under ice-shelves in East Antarctica (Riddle *et al.* 2007), and in the recently ice-free former Larsen A and B shelves, east of the Antarctic Peninsula (Gutt *et al.* 2011, Fillinger *et al.* 2013).

2.2. Sponges: bioconstructing biomass and biodiversity

Antarctic shelf biomass for non-coral reef benthos is amongst the highest in the world (Barthel & Gutt 1992) but the global importance of these high biomass sponge habitats has only recently been reviewed (Hogg *et al.* 2010). Sponges are classed as ‘bioconstructors’ as they provide permanent, heterogeneous and complex habitats, nurseries and substrate for many marine organisms (Barthel 1992, Kunzmann 1996, Gutt & Schickan 1998, Cocito 2004). Morphological plasticity, which is common in sponges, is important in increasing habitat heterogeneity, which is thought to be one of the most significant drivers of biodiversity (Fagerstrom 1991). Hexactinellids can be vase-like in shape, particularly the genus *Rossella*, and are found to harbour a diverse fauna within and upon them (McClintock *et al.* 2005) (Photo 1). Many morphological arrangements are also seen within the demosponge class, as they have a leuconoid cell structure, which is believed to permit great diversity of shape (Bergquist 1978). Demosponges are typically irregular in form, and can be encrusting, branching, forming irregular mounds, string-like, foliaceous, tubular or urn-shaped. Homoscleromorpha sponges are typically found to be encrusting or cushion-shaped and calcareous sponges can be encrusting, urn-like or tubular in shape (Van Soest *et al.* 2012a).

Mobile species, such as holothurians and echinoderms use sponges as a platform for their filter feeding (Gutt & Schickan 1998) (Photo 2), and sponges are important in maintaining several fish species throughout their reproductive lifecycles (Barthel 1997). Many species of amphipods and isopods live in the cavities and within the sponge tissue and polychaetes are commonly found living in the outer spicule layer of sponges (Barthel & Tendal 1994). The co-evolution of sponges and their epifauna have been suggested as one of the major explanations for Antarctic benthic species richness (Gutt & Schickan 1998). For these reasons sponges have been recognised by Antarctic policy makers as important indicators of VME's for conservation purposes (Lockhart & Jones 2009).

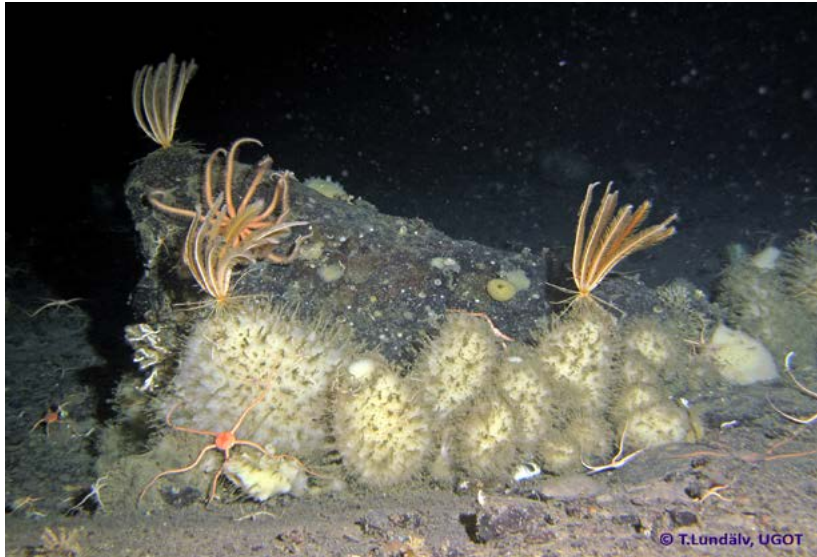


Photo 2 Photograph illustrating the variety of fauna (crinoids and ophiuroids) utilising sponges as a habitat, and particularly as a feeding platform in the Weddell Sea. Photo taken during the ANT-XXVII/3 expedition on RV *Polarstern*, 2011. Image © Tomas Lundälv, University of Gothenburg.

3. Antarctic sponge biogeography

3.1. Range characteristics of Southern Ocean species

Circumpolarity is a relatively common feature in the Southern Ocean with 35% of species found to have wide longitudinal ranges ($>200^\circ$) (Fig. 2). A third of all Southern Ocean hexactinellids and 35% of demosponges are found in this wide longitudinal range group. Notable wide ranges are observed in the hexactinellid *Rossella racovitzae* (290°) (Map 5), the demosponge *Cinachyra barbata* (289°) (Map 6), and the calcareous sponge *Leucascus leptoraphis* (229°) (Map 7) (Downey *et al.* 2012). Sampling is more limited in the sub-Antarctic, but a small number of species (e.g. *Craniella coactifera* and *Hymeniacidon kerguelensis*) are also found to have wide longitudinal ranges in this Southern Ocean sector (Map 22). A small percentage (15%) of Southern Ocean species are found to have a restricted longitudinal ranges ($<10^\circ$), with the majority of these species restricted also by latitude and depth, to the shelf around sub-Antarctic islands (e.g. *Isodictya dufresni*, *Haliclona pedunculata*, and *Leucettusa vera* around the Kerguelen, Heard and MacDonald Islands), and the remainder either rare and/or represented by few records in under-sampled regions of the Antarctic (e.g. *Uncinatera plicata* and *Pararete gerlachei* in the Bellingshausen Sea). Latitudinal ranges are distinctly narrow for most Southern Ocean sponges, with 37% of species currently found to have ranges $<10^\circ$ (range determined by 3 or more known locations in the Southern Ocean) (Fig. 3). Over 40% of all Southern Ocean calcareous sponge species are found in this limited latitudinal range group. A small number of species have wide latitudinal ranges that extend significantly beyond the Southern Ocean, such as the demosponge *Suberites caminatus* (51°), the hexactinellid *Anoxycalyx ijimai* (44°), and the calcareous sponge *Leucettusa lancifera* (43°).

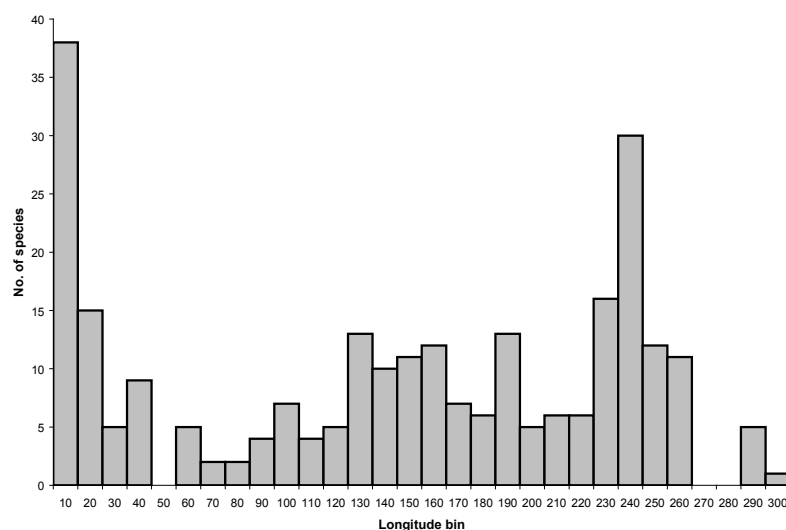


Figure 2 Longitudinal ranges of sponges found at 3 or more locations in the Southern Ocean. Longitudinal range size is calculated as the minimum continuous arc that included all the distribution points of the taxon. This method in calculating longitudinal range prevents any species from having a truly circumpolar distribution due to sampling gaps. Each taxon was grouped into one 10° longitudinal bin dependent upon its range size.

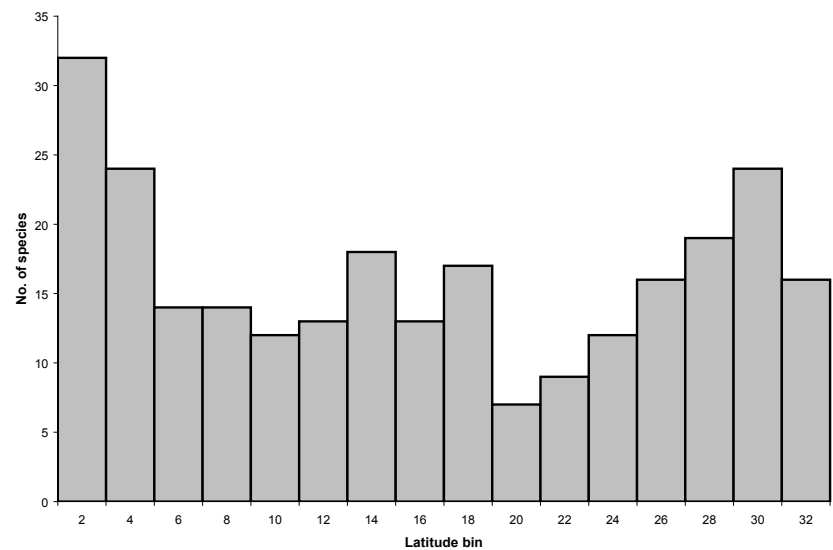
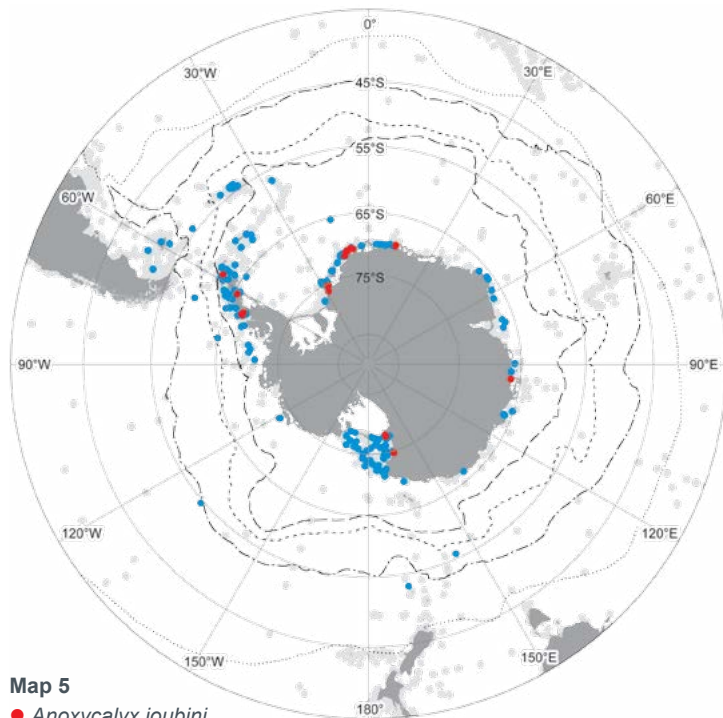


Figure 3 Latitudinal ranges of sponges found at 3 or more locations in the Southern Ocean. Latitudinal range size is the difference between the maximum and minimum range points and does not imply that an organism is found everywhere in-between. Each taxon was grouped into one 2° latitudinal bin dependent upon its range size.

Circumpolarity and latitudinal restriction in Southern Ocean sponges are driven by several processes. The main physical process is the ACC (Antarctic Circumpolar Current), which is the dominant current flow in the Southern Ocean (Dayton *et al.* 1994, Barker *et al.* 2007). The eastward flowing ACC and associated currents and coastal gyres, have given sponges the opportunity to be widely distributed longitudinally along the entire Antarctic coastline and sub-Antarctic (McClintock *et al.* 2005). Similar environmental conditions in many parts of the Southern Ocean help to generate circumpolarity by reducing barriers, such as isothermal waters, varied substrate from icebergs and glaciers, and comparable nutritional and hydrochemical conditions (Koltun 1969). While the ACC is an important mechanism in dispersing Antarctic fauna around the Southern Ocean, it also is a physical and environmental barrier (Polar Front) which limits the latitudinal ranges of many Antarctic species and reduces migration opportunities for species outside the Southern Ocean (Rogers 2012). It has been found that some wide longitudinal and latitudinal ranges in sponge species are composed of cryptic species complexes (morphologically similar but reproductively isolated organisms) (Usher *et al.* 2004). Future application of molecular techniques will be aimed at determining if wide-ranging Southern Ocean sponge species are in fact cryptic species complexes and what processes could be important in driving this phenomenon.

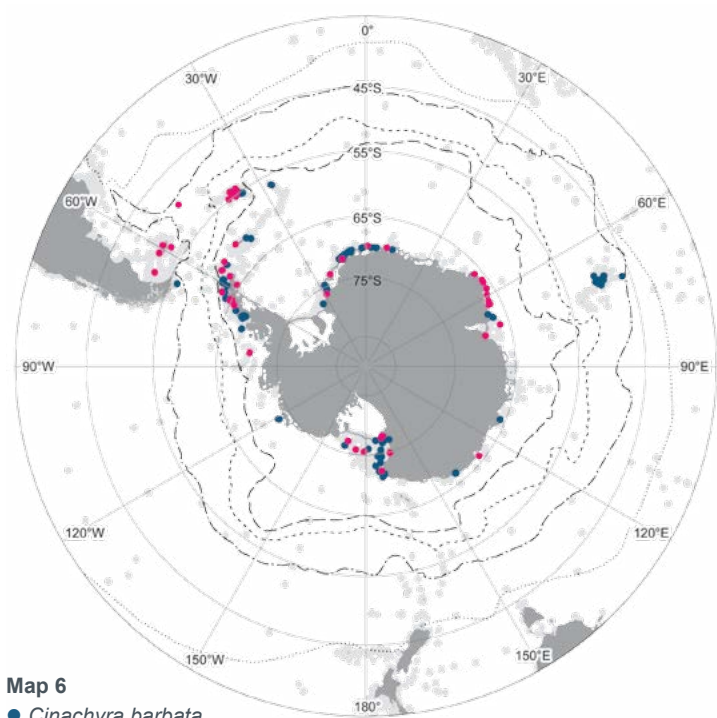
Despite this barrier to migration, a number of species have been able to colonise the Southern Ocean (Fig. 5 in Downey *et al.* 2012). The impact of the Polar Front (PF) reduces with depth, so that some eurybathic and deep-dwelling fauna have been able to migrate into the Southern Ocean (e.g. *Eurypon miniaceum* and *Clathria terraenovae*) (Clarke *et al.* 2009). A significant number of eurybathic Antarctic species have also increased their latitudinal ranges by colonising sectors of the sub-Antarctic (e.g. *Homaxinella balfourensis*, *Inflatella belli*, *Mycale acerata*, *Tetilla leptoderma* and *Isodictya kerguelensis*) (Maps 10 & 20). Tolerance of varied substrates could enable some species to become cosmopolitan within the Southern Hemisphere, given enough time and opportunities for range expansion (e.g. *Myxilla kerguelensis* has been found growing on a wide variety of substrates) (Boury-Esnault & Van Beveren 1982). Furthermore, an ability to grow on biological substrates could be an important dispersal mechanism (e.g. kelp rafting) in the colonisation of the sub-Antarctic islands (Fraser *et al.* 2010, Nikula *et al.* 2010). A number of species have ranges restricted to the Magellanic / West Antarctic Peninsula region; these species are found to be a sub-set of South American sponges with extended southerly ranges within the Southern Ocean (e.g. *Clathria membranacea* and *Mycale lapidiformis*) (Map 8). A significant number of Antarctic species have northerly ranges that extend into the Magellanic region (e.g. *Latrunculia apicalis* and *Isodictya erinacea*) (Map 9). The variable topographic connectivity between South America and the Antarctic Peninsula from the Scotia Ridge, and the former link with the continent before the opening of the Drake Passage (McClintock *et al.* 2005) are believed to be important in explaining these two-way range patterns.

Reproductive mode and dispersal capabilities are an important biological parameter in determining species range, and therefore potentially important in understanding sponge biogeographic patterns observed in the Southern Ocean. Reproductive mechanisms are varied, with sexual reproduction utilising lecithotrophic larvae of both oviparous and viviparous sponges (Bergquist 1978) and/or asexual reproduction through bipartition and budding (Teixidó *et al.* 2006). Lecithotrophic larvae generally have a short-lived existence in temperate environments, however, little is known about their longevity in the Southern Ocean (McClintock *et al.* 2005). The co-occurrence of sexual and asexual reproduction in the Southern Ocean has been theorised to be an adaptation to persistent ice-scour disturbance during glacial-interglacial cycles (Dell 1972). A long-term study of the Antarctic hexactinellid *Anoxycalyx joubini* illustrates the impact of recent changes in Ross Sea ice-sheet dynamics on phytoplankton productivity, which are hypothesised to have strongly affected regional sponge reproduction and recruitment (Dayton *et al.* 2013). Asexual budding is hypothesised to have improved short-distance colonisations, whereas longer-distance larval dispersal increased the survival of species



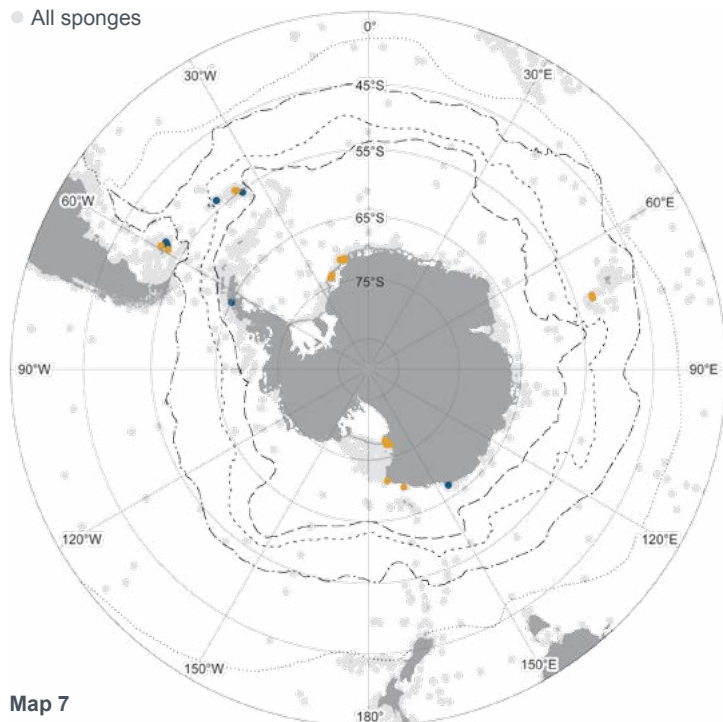
Map 5

● *Anoxycalyx joubini*
● *Rossella racovitzae*
● All sponges



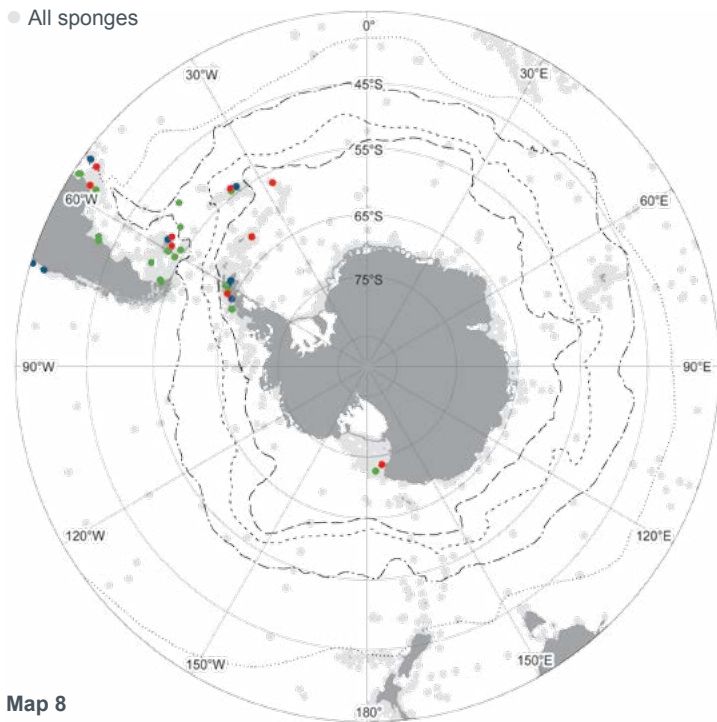
Map 6

● *Cinachyra barbata*
● *Microxina benedeni*
● All sponges



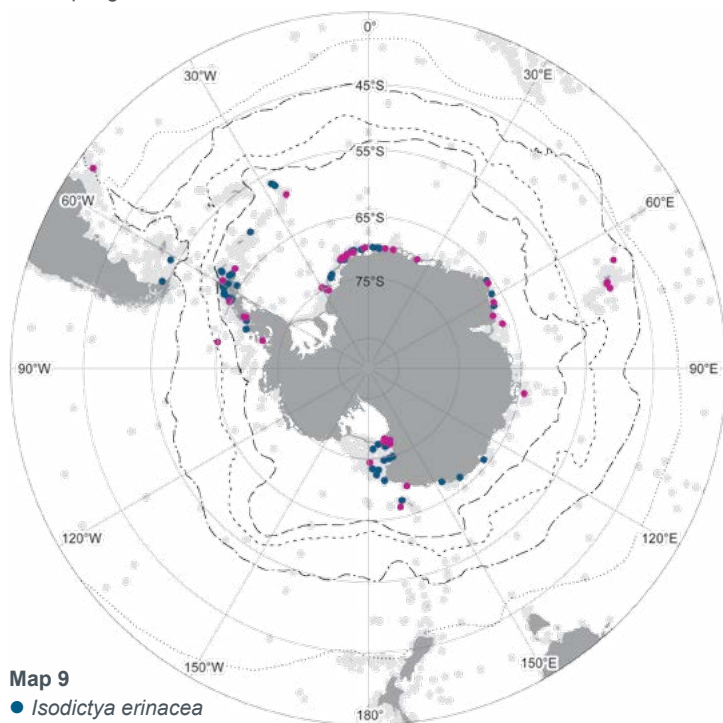
Map 7

● *Grantia hirsuta*
● *Leucascus leptoraphis*
● All sponges



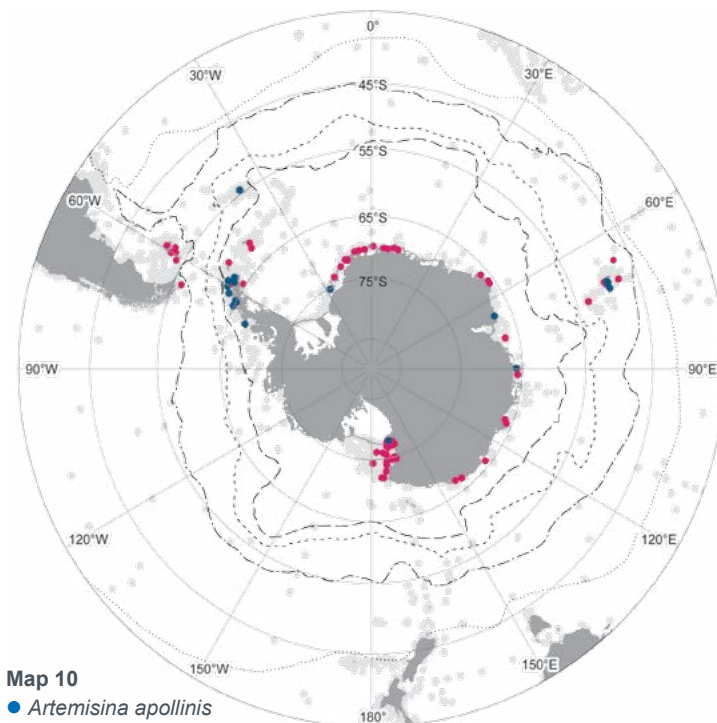
Map 8

● *Clathria membranacea*
● *Haliclona bilamellata*
● *Mycale lapidiformis*
● All sponges



Map 9

● *Isodictya erinacea*
● *Latrunculia apicalis*
● All sponges



Map 10

● *Artemisina apollinis*
● *Inflatella belli*
● All sponges

Porifera Maps 5–7 Circumpolar and generally PF-restricted latitudinal ranges: Map 5. Hexactinellida: *Anoxycalyx joubini*, *Rossella racovitzae*. Map 6. Demospongiae: *Cinachyra barbata*, *Microxina benedeni*. Map 7. *Grantia hirsuta*, *Leucascus leptoraphis*. **Maps 8–10** Wide latitudinal ranges: Map 8. Faunal colonisation from South America to Antarctica: *Clathria (Thalysias) membranacea*, *Haliclona bilamellata*, *Mycale (Mycale) lapidiformis*. Map 9. Faunal colonisation from Antarctica to South America: *Isodictya erinacea*, *Latrunculia apicalis*. Map 10. Faunal colonisation between Antarctica and sub-Antarctic islands: *Artemisina apollinis*, *Inflatella belli*.

around Antarctica, thereby maintaining longitudinally-wide distributions (McClintock *et al.* 2005). Sexual reproduction is a feature of all sponge classes (Shanks 2001); however asexual reproduction has only been observed in demosponges and hexactinellids (Teixidó *et al.* 2006). Recent research has indicated that asexual reproduction is a common feature of present-day Antarctic shelf hexactinellids (Teixidó *et al.* 2006). Wider ranges are found to be a more common feature in hexactinellids and demosponges (Downey *et al.* 2012), and the ability to utilise two modes of reproduction could have been important in maintaining this feature in the Southern Ocean. Further research is needed to understand dispersal potential of different reproductive modes in order to determine possible evolutionary impacts on current Southern Ocean sponge range and distribution.

3.2. Southern Ocean eurybathy

Eurybathy (wide depth range) is found to be a relatively common feature of Southern Ocean sponges (Table 1), with over a quarter of sponges currently classed as eurybathic. Demosponges and hexactinellids display the greatest eurybathic tendencies in the Southern Ocean, with this characteristic found in close to 30% of all species found within each of these sponge classes. Demosponge families with dominant eurybathic tendencies are the Suberitidae, Polymastiidae, and Cladorhizidae (range >5000 m) in the Southern Ocean (Fig. 7 in Downey *et al.* 2012) (Map 12). Hexactinellid families with eurybathic tendencies include the Rossellidae, Euplectellidae, and Euretidae (range >3000 m) (Göcke & Janussen 2011) (Map 11). The structure of eurybathy is different in demosponges and hexactinellids, with the majority of eurybathic demosponges found distributed between the shallower shelf and continental slope (e.g. Acarnidae, Niphatidae and Microcionidae families), whereas hexactinellid eurybathy is split fairly equally between sponges distributed between the shelf and continental slope (e.g. Rossellidae and Euretidae families), and those distributed between the abyss and the continental slope (e.g. Euplectellidae family). Unlike demosponges, nearly a third of all hexactinellid species are found to be restricted to abyssal depths, particularly species in the genera *Caulophacus*, *Holascus*, and *Malacosaccus*. Close to 90% of Southern Ocean calcareous and two-thirds of homoscleromorph sponges are stenobathic, being found only on the shelf; however, two calcareous (*Breitfussia chartacea* and *Achramorpha truncata*) and one homoscleromorph species (*Plakina trilopha*) have been found to be eurybathic (Map 13).

Eurybathy is believed to be a common feature of Southern Ocean benthic fauna (e.g. Brey *et al.* 1996). Environmental explanations for this biogeographic characteristic concentrate on three different processes that reduce vertical zonation in sponges. Firstly, Southern Ocean waters are typically isothermal as ocean waters extend all the way up to the Antarctic shelf, which implies that abyssal sponges can colonise shelf habitats without altering their current environmental tolerance. Secondly, bottom currents flow out from the coast promoting the movement of sponges from the shelf to the continental slope and deep-sea (Koltun 1969). Lastly, it has been postulated that some Antarctic shelf species escaped extinction by migrating to deeper waters during glacial cycles of ice sheet advance, thereby promoting eurybathy as a survival strategy (Dell 1972, Brey *et al.* 1996). The effect of last two processes, although impossible to determine the relative impact of each, could potentially be seen in the significant number of sponges (21%) with a shelf-continental slope range. Further sampling, particularly at bathyal and abyssal depths in the Southern Ocean, is expected to greatly improve our understanding of sponge eurybathy.

Eurybathy is not a common characteristic of Southern Ocean calcareous and homoscleromorph sponges. The CCD (carbonate compensation depth), which is found to be multi-bathyal and typically shallower in the Southern Ocean compared to other oceans, is a potentially important factor in determining depth distributions of calcifying organisms (Griffiths 2010, Hillenbrand *et al.* 2003). This process could limit the depth ranges of calcareous sponges found on the inner section of Antarctic shelves, such as the Amundsen and Bellingshausen, where the CCD is exceptionally shallow and would impede these organisms ability to calcify. Globally, homoscleromorph sponges are rare and shallow-dwelling (Gazave *et al.* 2010) and this characteristic is also seen in the Southern Ocean. Globally, the majority of hexactinellid sponges are found to inhabit deep oceanic environments. The expansive area of the Southern Ocean abyss and its connectivity to other deep-sea regions in the Southern Hemisphere (as similar abyssal environmental conditions reduce potential barriers) could be an important factor in the significant presence of stenobathic abyssal hexactinellid genera.

3.3. Centre of richness & endemism

At present, 400 valid species, represented by 139 genera in 70 families (Table 2), are described from the Southern Ocean. Estimates in recent years have varied from 250 to 530 species and this approximation is likely to change in the future with increased sampling and improved taxonomy (Koltun 1969, Barthel 1992, Brandt *et al.* 2007, De Broyer 2011a). At present, approximately 5% of global sponge species are found in the Southern Ocean (Van Soest *et al.* 2012b), which is lower than expected, considering that ~9% of global continental shelf areas are found around the Antarctic (Barnes & Peck 2008). At class level, hexactinellid and calcareous sponges are better-represented in the Southern Ocean, and individually each account for ~8% of global sponge species in their respective classes, whereas Southern Ocean demosponges and homoscleromorph sponges are poorly represented compared to the total number of known demosponge species. Demosponges are found to be exceptionally diverse at tropical and certain temperate latitudes (Van Soest *et al.* 2012a), most likely due to more intensive sampling and research; however, ecological hypotheses concerning photo-symbiont promotion of speciation in host sponges (Erwin & Thacker 2007, Erwin *et al.* 2012) and the greater intensity of predation (Ruzicka & Gleason 2008), have been posited to explain this latitudinal cline of demosponge species richness. The relatively lower level of Southern Ocean sponge species diversity is most likely due to under-sampling, especially of the expansive continental slope and deep-sea, and limited taxonomic knowledge compared to other regions (Arntz *et al.* 1997).

Table 2 Numbers of Antarctic families, genera, and species within the Porifera phylum, and within each sponge class. Numbers in brackets indicate the number of Antarctic endemic genera or species. Data extracted from the SOMBASE/TOTAL-Bioconstructors database.

	Antarctic Families	Antarctic Genera	Antarctic Species
Porifera	70	139 (10)	400 (175)
Demospongiae	47	97 (4)	293 (112)
Hexactinellida	7	21 (4)	53 (36)
Calcareia	14	19 (2)	51 (27)
Homoscleromorpha	2	2 (0)	3 (0)

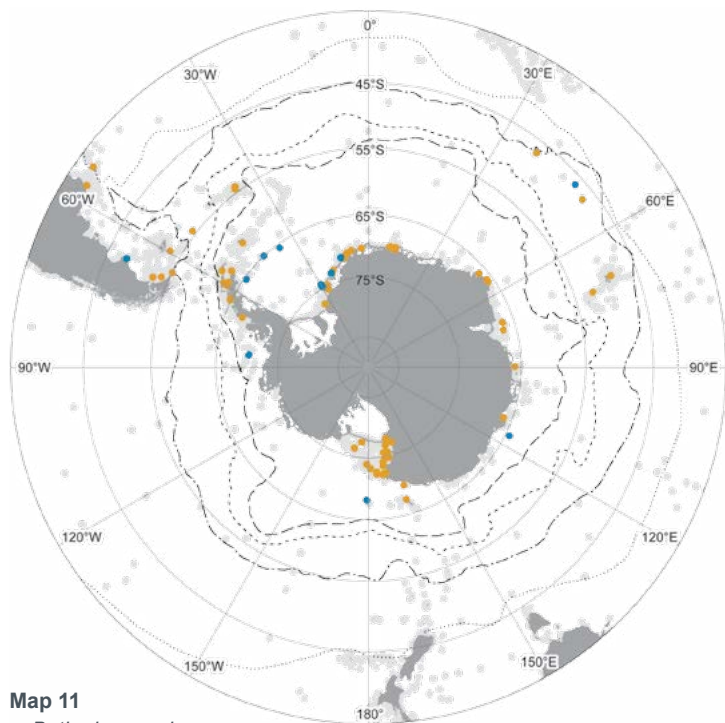
Currently, 44% of Southern Ocean sponge species and 7% of genera found are believed to be endemic. Class level endemism is striking in sponges, with 69% of Hexactinellida, 53% of Calcareia and 38% of Demospongiae species are endemic to the Southern Ocean. The highest proportion of Southern Ocean generic endemism occurs in hexactinellids (19%), compared to 11% endemism in calcareous sponges and 4% in demosponges. Currently, no endemic homoscleromorph sponges have been found in the Southern Ocean. Endemic Southern Ocean demosponge genera include: *Cladothenea*, *Acanthorhabdus*, *Pachypellina*, and *Astrotylus*. Hexactinellid endemic genera include: *Acoelocalyx*, *Docosaccus*, *Rossella*, and *Uncinatera*. Calcareia endemic genera include: *Jenkina* and *Dermatreton*. Interestingly, all Southern Ocean endemic Calcareia genera and one endemic hexactinellid genus (*Rossella*) are polytypic, whereas all endemic demosponge genera are currently found to be monotypic.

Gradual long-term physical and climatic barriers are believed to have been important in creating and maintaining Antarctic endemism through isolation (allopatric speciation). The separation of Antarctica during the Gondwana break-up and the oceanographic isolation of the Southern Ocean by the ACC, after the opening of the Drake Passage, are both important processes that have isolated Antarctic fauna from the rest of the Southern Hemisphere (Clarke & Crame 2010). The gradual and long-term cooling of Antarctica (from ~33 Ma) is believed to have led to unique compositional changes in Antarctic fauna (extinctions of warm-adapted taxa and the radiation of cold-adapted taxa), which are still apparent today (Clarke & Crame 1992).

Previous research on Weddell Sea demosponge and hexactinellid sponges indicated that endemism appeared to decrease with depth, particularly below 2000 m (Janussen & Tendal 2007). Utilising all available records, currently half of Southern Ocean endemic genera and almost 70% (120 spp.) of all endemic species are shelf-restricted. This bathymetric restriction indicates the probable importance of the Antarctic shelf as a centre for sponge endemism in the Southern Ocean. Two endemic demosponge genera (*Acanthorhabdus* and *Pachypellina*), one endemic hexactinellid genus (*Uncinatera*), and two endemic calcareous genera (*Dermatreton* and *Jenkina*) are shelf-restricted in the Antarctic (Maps 14–16). The majority (13 spp.) of shelf-restricted

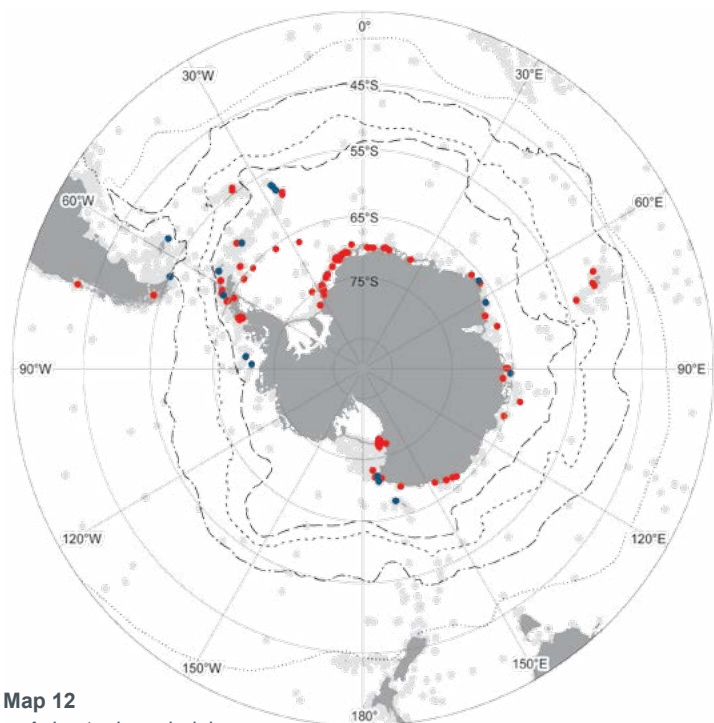
Table 1 Number of Antarctic species found in each depth zone within the Porifera phylum and within each sponge class. Species found to be restricted to one depth zone were categorised within one of the three stenobathic zones. Eurybathy in sponges was determined by the representation of sponge species in more than one zone.

	Porifera	Demospongiae	Hexactinellida	Calcareia	Homoscleromorpha
Stenobathic zones					
Shelf: Zone I (0–1000 m)	252	190	18	45	2
Continental Slope: Zone II (1000–3000 m)	16	7	7	2	0
Abyssal: Zone III (3000 m +)	23	8	14	1	0
Eurybathic zones					
Shelf & Continental Slope: Zones I+II (0–3000 m)	83	72	7	3	1
Continental Slope & Abyssal: Zones II+III (1000–3000 m+)	9	4	5	0	0
All depth zones: Zones I+II+III (0–3000 m+)	9	7	2	0	0



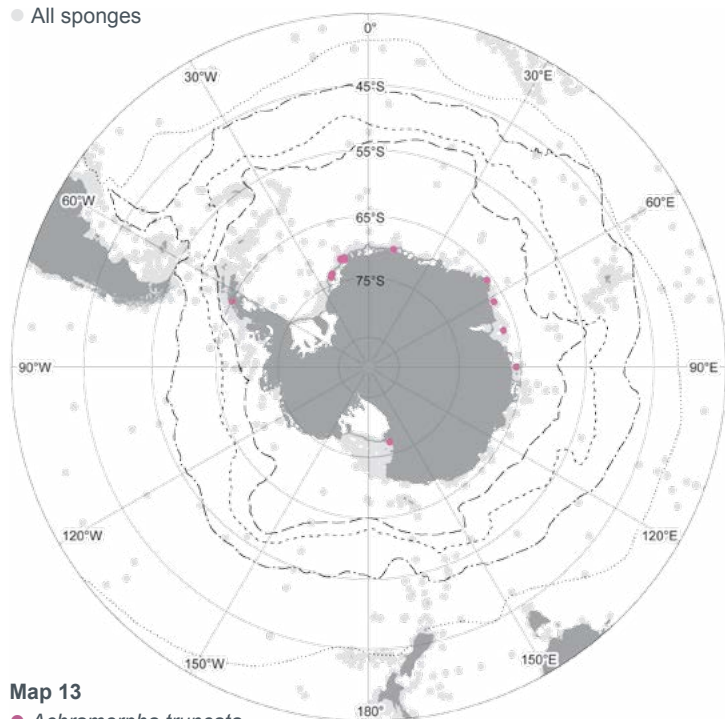
Map 11

● *Bathydorus spinosus*
● *Rossella antarctica*
● All sponges



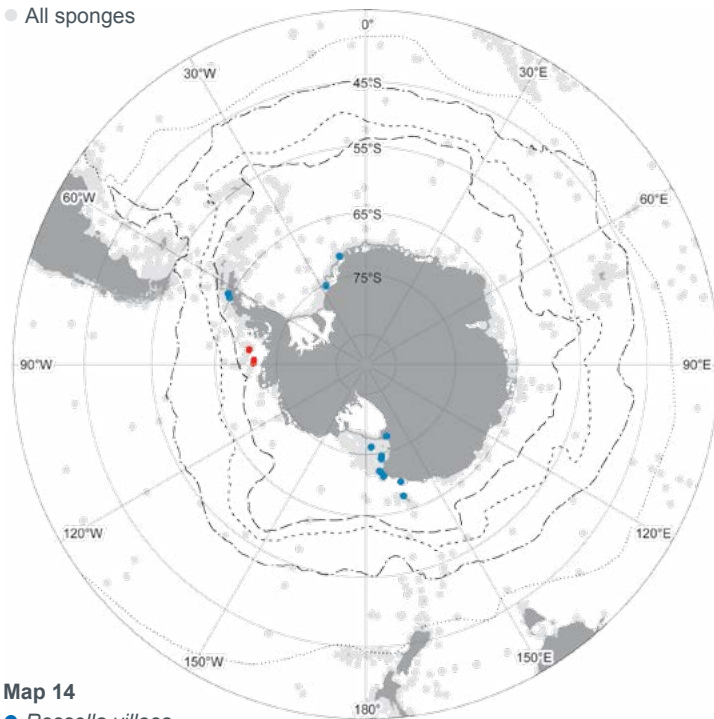
Map 12

● *Asbestopluma belgicae*
● *Polymastia invaginata*
● All sponges



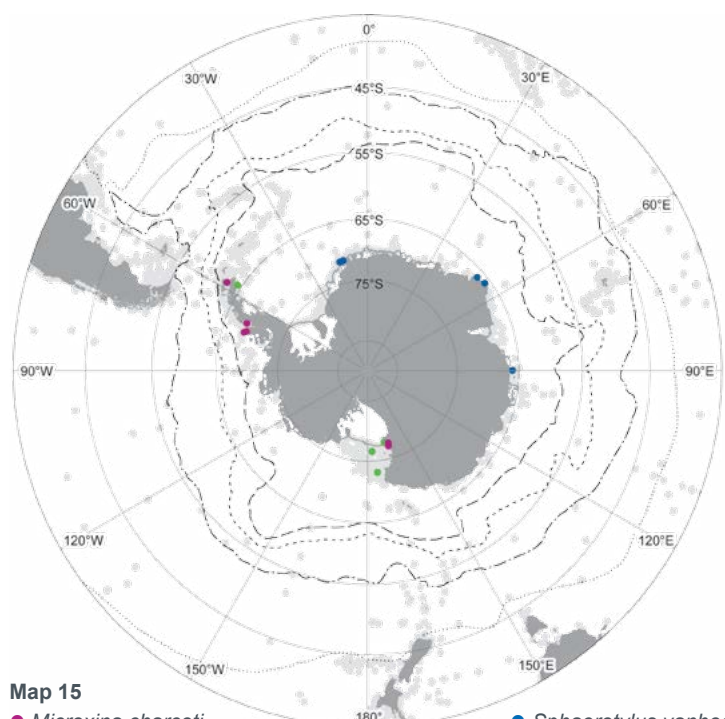
Map 13

● *Achramorpha truncata*
● All sponges



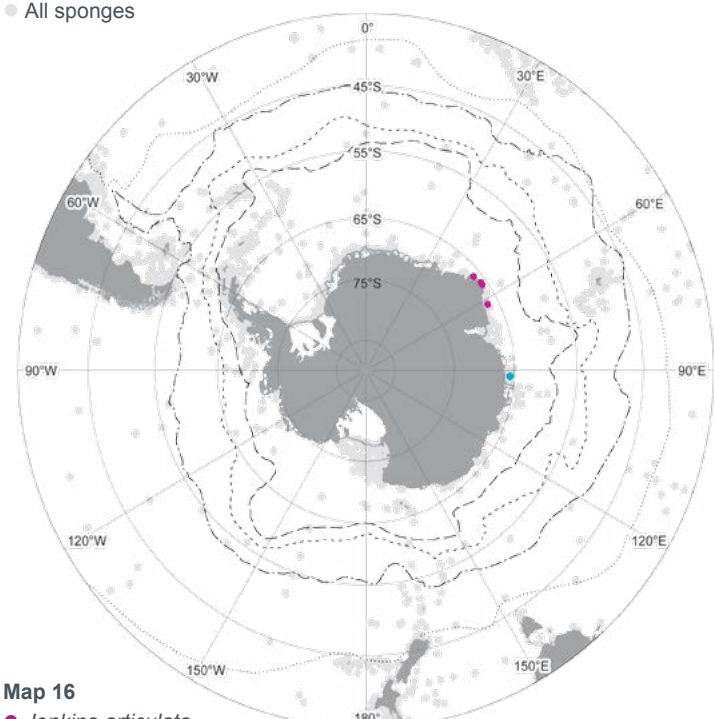
Map 14

● *Rossella villosa*
● *Uncinatera plicata*
● All sponges



Map 15

● *Microxina charcoti*
● *Pachypellina fistulata*
● *Sphaerotylus vanhoeffeni*
● All sponges



Map 16

● *Jenkinsia articulata*
● *Leucandra mawsoni*
● All sponges

Porifera Maps 11–13 Eurybathy: colonisation within the Southern Ocean, and to and from the Southern Ocean: Map 11. Hexactinellida: *Bathydorus spinosus*, *Rossella antarctica*. Map 12. Demospongiae: *Asbestopluma belgicae*, *Polymastia invaginata*. Map 13. Calcareia: *Achramorpha truncata*. **Maps 14–16** Antarctic shelf-restricted endemism: Map 14. Hexactinellida: *Rossella villosa*, *Uncinatera plicata*. Map 15. Demospongiae: *Microxina charcoti*, *Pachypellina fistulata*, *Sphaerotylus vanhoeffeni*. Map 16. Calcareia: *Jenkinsia articulata*, *Leucandra mawsoni*.

endemic hexactinellid species are in the endemic genus *Rossella* (Map 5, 11, 14). However, the majority of shelf-restricted endemic demosponge and Calcareous species are found to be from common Southern Hemisphere genera (81 endemic demosponge species from 38 genera; and 17 endemic calcareous species from 9 genera). Long-term isolation of the Antarctic shelf must have been important for genera evolution in sponges. The PF, vast abyssal depths surrounding the shelf, the biodiversity pump hypothesis (population separations of marine fauna on the shelf due to ice sheet disturbance on habitat availability during glacial-interglacial cycles) (Clarke & Crame 1992), and the CCD, are all hypothesised to have been important in isolating the Antarctic shelf. Opportunistic but isolated dispersal events from wide-ranging Southern Hemisphere genera to the Antarctic shelf appear to have been important in the evolution of many endemic demosponge and calcareous species. Functional traits of some Antarctic sponges, such as stenobathy and a low dispersal potential, could have potentially enhanced this isolation further on the Antarctic shelf.

Recent findings illustrate that species endemism could be more common at abyssal depths in the Southern Ocean than previously thought (Göcke & Janussen 2013c). A third of endemic genera (*Acoelocalyx*, *Docosaccus*, and *Astrotylus*) and a number of endemic species are currently found only at abyssal depths in the Southern Ocean (e.g. *Leucetta weddelliana* and *Cladorhiza mani*) (Maps 17–19). Abyssal endemic genera appear to be monotypic; with nearly half of all abyssal endemic species currently found within the Southern Hemisphere deep-sea hexactinellid genus *Caulophacus*. It has been hypothesised that the presence of closed and semi-closed basins are important in maintaining endemism of abyssal genera and species through long-term isolation in the Southern Ocean (Brandt *et al.* 2012). However, limited sampling of the abyss should be considered when reviewing current Southern Ocean abyssal endemism levels.

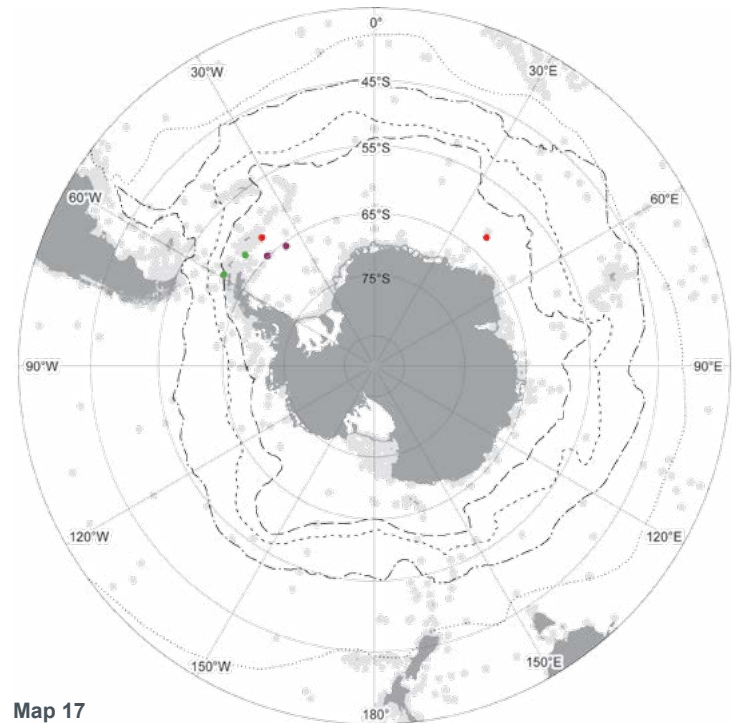
Currently 7 endemic species (demosponge and calcareous sponges) are only found on the shelf around the Kerguelen Islands (*Chondrocladia fatimae*, *Haliclona pedunculata*, *Hymedesmia mariondufresni*, *Isodictya dufresni*, *Leucandra kerguelensis*, *Leucettusa vera*, and *Sycon kerguelense*). Fifteen new endemic demosponge species have also been found at shallow depths around South Georgia (Goodwin *et al.* 2012). This evidence indicates the possible importance of these islands as regions of endemism within the Southern Ocean. Reasons for high levels of endemism around the Kerguelen Islands and South Georgia could be because both are geologically old, relatively isolated from the Antarctic continent, and have a comparatively large shelf area (Lebouvier *et al.* 2010, Hogg *et al.* 2011). Both islands are close to the northern mean position of the PF; however, as this front shifts position, their benthic shelf fauna can be exposed to unique changes in currents and water masses, which would not impact fauna on the Antarctic shelf (Barnes *et al.* 2006). The dual impacts of isolation and disturbance could have driven sponge speciation around these islands.

Endemism levels in sponges tend to be lower than other benthic taxa found in the Southern Ocean (Clarke & Johnston 2003). Current evidence indicates that the Antarctic shelf, large, isolated islands, and the abyss are all possibly important centres of sponge genera evolution and speciation in the Southern Ocean. Physical barriers within and around the Southern Ocean have been important in creating and maintaining endemism, however, Southern Hemisphere species with wide environmental tolerances, excellent dispersal potential, and eurybathic traits are (given enough time) able to colonise the Antarctic. Connectivity through the Scotia Ridge continues to be an important route for the migration (both ways) of sponges between southern South America and the Antarctic. It is likely that with continued exploration of the Southern Ocean and the greater application of DNA sequencing, that a greater understanding of sponge evolution will be gained.

4. Southern Ocean marine biogeographic region

All species whose origin coincide in place, time and conditions of initial adaptation, respond similarly to changes in physical and chemical factors, therefore these species will have a similar distribution that can be grouped into a biogeographic region (Golikov *et al.* 1990). All studies on sponge fauna have concluded that Antarctica itself forms a distinct biogeographic region (Koltun 1969, Sarà *et al.* 1992, McClintock *et al.* 2005, Downey *et al.* 2012, Van Soest *et al.* 2012a). The most recent faunal analysis of demosponges in the Southern Hemisphere concluded that the Southern Ocean sponge biogeographic region encompasses the entire Antarctic continent, as well as the sub-Antarctic islands of South Georgia, Kerguelen, Heard and MacDonald, and Macquarie (Downey *et al.* 2012). Biogeographic analyses of Southern Hemisphere demosponges also found little species-level faunal similarity between Antarctica and South Africa, New Zealand, and southern Australia (Sarà *et al.* 1992, Downey *et al.* 2012). This situation is believed to largely reflect the timing of past continental connectivity in the Southern Hemisphere (Clarke & Crame 2010). Further research is needed to determine if calcareous, hexactinellid and homoscleromorph sponges share this evolutionary path, or reveal different drivers in each of their potentially unique histories in the Southern Ocean.

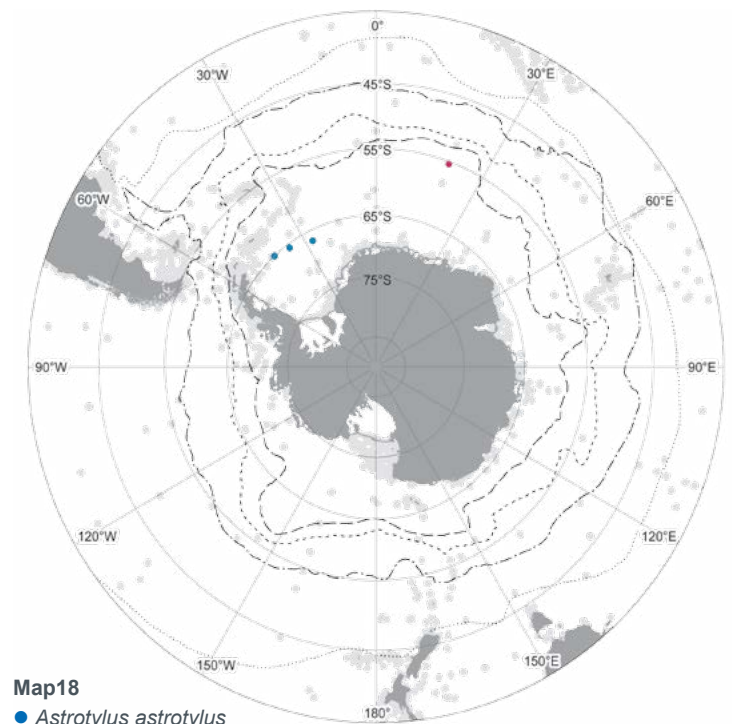
Connectivity between the Antarctic and South America is believed to be stronger due to two phenomena, the more recent linkage of the two continents before the opening of the Drake Passage and the potential for eurybathic species to colonise along the Scotia Ridge (e.g. Brey *et al.* 1996, Clarke *et al.* 2004, Linse *et al.* 2006, Primo & Vázquez 2007, Griffiths *et al.* 2009). Previous sponge studies have combined the Magellanic biogeographic region (southern South America and the Falkland Islands) into the Southern Ocean biogeographic region (Sarà *et al.* 1992). However, the most recent research confirms the importance of Magellanic sponge fauna within Antarctica (parti-



Map 17

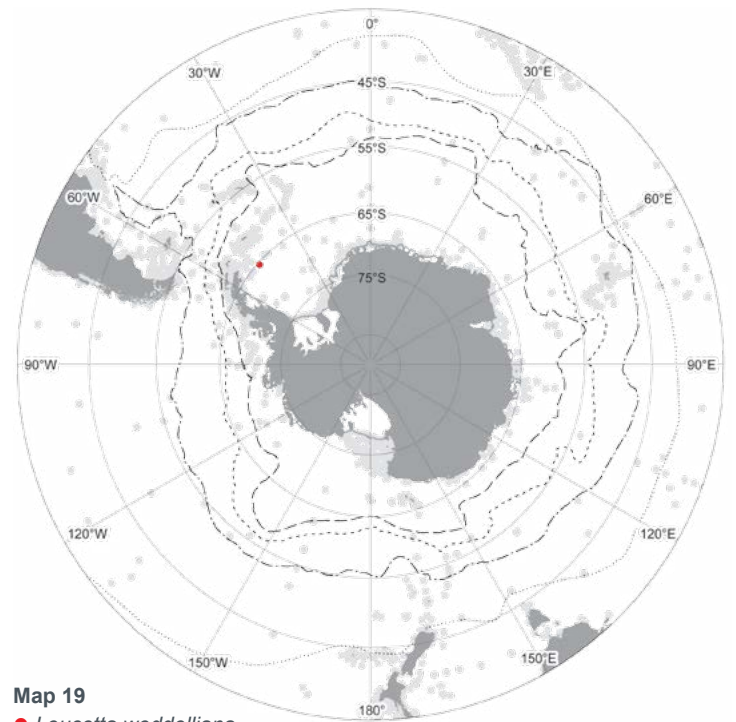
● *Acoelocalyx brucei*
● *Caulophacus instabilis*

● *Lophocalyx topsenti*
● All sponges



Map 18

● *Astrotylus astrotylus*
● *Cladorhiza mani*
● All sponges



Map 19

● *Leucetta weddelliana*
● All sponges

Porifera Maps 17–19 Abyssal endemism (13 spp. In total, 10 Hexactinellida, 2 Demospongiae, 1 Calcareous): Map 17. Hexactinellida: *Acoelocalyx brucei*, *Caulophacus instabilis*, *Lophocalyx topsenti*. Map 18. Demospongiae: *Astrotylus astrotylus*, *Cladorhiza mani*. Map 19. Calcareous: *Leucetta weddelliana*.

cularly at South Georgia and the Antarctic Peninsula), but it is found to be a southerly extension of the distinctive South American cold-temperate biogeographic region (Downey *et al.* 2012: Fig. 8a–c). New research has indicated that South Georgia is an important ‘mixing ground’ for both South American sponge communities at their southern range limit and Weddell Sea/Antarctic Peninsula sponges at their northern range limit (Hogg *et al.* 2011). South Georgia’s position at the confluence of both Antarctic and South American currents and connectivity along the Scotia Ridge are believed to have been important in the migration of sponges between South America and Antarctica.

The sub-Antarctic islands of Kerguelen and Macquarie, alongside the islands of Prince Edward and Crozet, had in previous studies been classed as a separate sub-Antarctic region (Hedgpeth 1969). However, new analyses have found the islands of Kerguelen, Heard, MacDonald, and Macquarie to be strongly Antarctic in faunal composition (Downey *et al.* 2012). Connectivity along the Kerguelen Plateau, which links the Kerguelen, Heard and MacDonald Islands with the Antarctic continent at deep shelf depths, and the islands presence within the ACC are believed to have been important in maintaining strong faunal migration links between the two (Griffiths *et al.* 2009). Colonisation of species along the southern section of the Macquarie Ridge is believed to explain the current level of faunal similarity between Macquarie Island and the Antarctic. Distinct, but weaker Magellanic faunal connections are also apparent at these sub-Antarctic islands (e.g. *Myxilla chilensis*, *Iophon proximum* and *Haliclona topsenti*) (Map 21). This faunal connectivity is believed to be aided by strong westward-flowing currents in the Southern Ocean which have enabled the passive long-distance dispersal of larvae (Barnes & De Grave 2001, Helmuth *et al.* 1994, O’Hara 1998, Waters 2008, Nikula *et al.* 2010, 2013). Colonisation of the northern sector of the Macquarie Ridge is believed to have enabled the establishment of a small number of cold-temperate New Zealand species at Macquarie Island (e.g. *Asbestopluma desmophora* and *Myxilla novaezealandiae*) (Map 21).

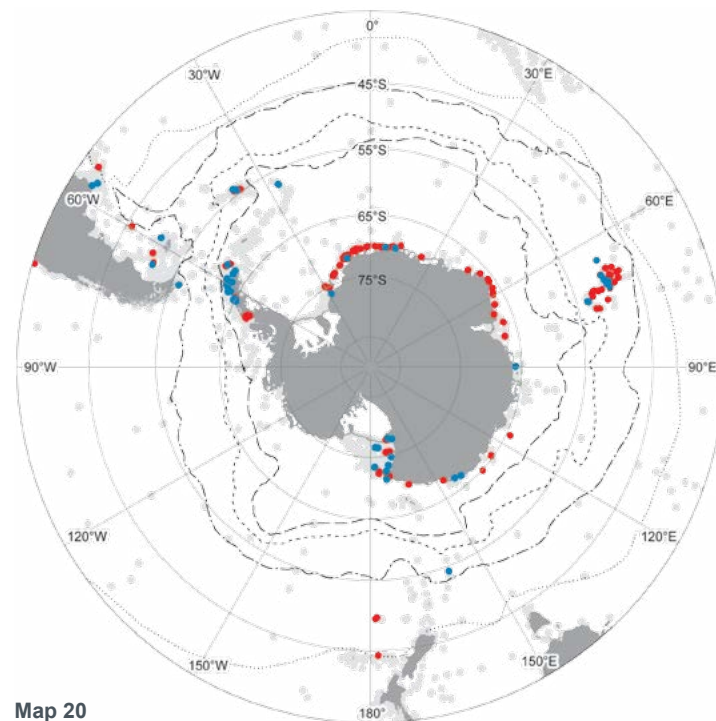
Despite their relative proximity to the Kerguelen Islands, the Prince Edward and Crozet Islands are found to form their own distinct sub-Antarctic sponge biogeographic region. This region does include a small number of species in common with the Antarctic (e.g. *Rossella antarctica* and *Bathydorus spinosus*), a large number of potential endemics (e.g. *Iophon abnormale*, *I. laminale* and *Mycale mammiformis*), and a small proportion of species from Magellanic South America (e.g. *Fibulia ramosa* and *Iophon cheliferum*); which indicate that eurybathic migration, isolation and west-wind drift migration are important in maintaining this unique faunal community. The New Zealand sub-Antarctic islands are found to be the southerly range limit of the New Zealand cold-temperate sponge fauna, faunistically dissimilar to both the sub-Antarctic and Antarctic demosponge regions (Downey *et al.* 2012). In order to gain an improved understanding of Southern Ocean biogeography, further research is needed to determine migrational links between the Antarctic and sub-Antarctic islands, as well as the importance of colonisation between cold-temperate regions of the Southern Hemisphere and the Southern Ocean.

Acknowledgements

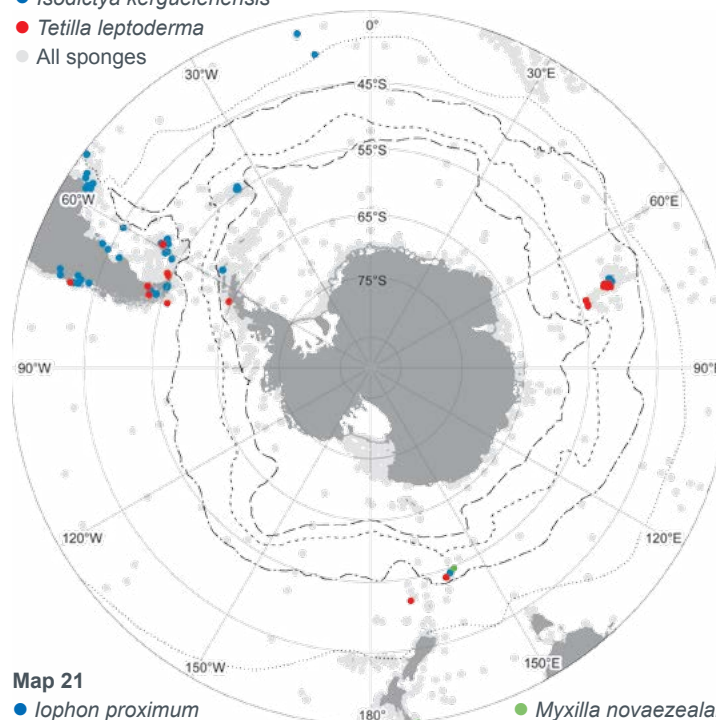
Huw Griffiths (BAS, Cambridge) is thanked for the preparation of the maps. This is CAML contribution # 103.

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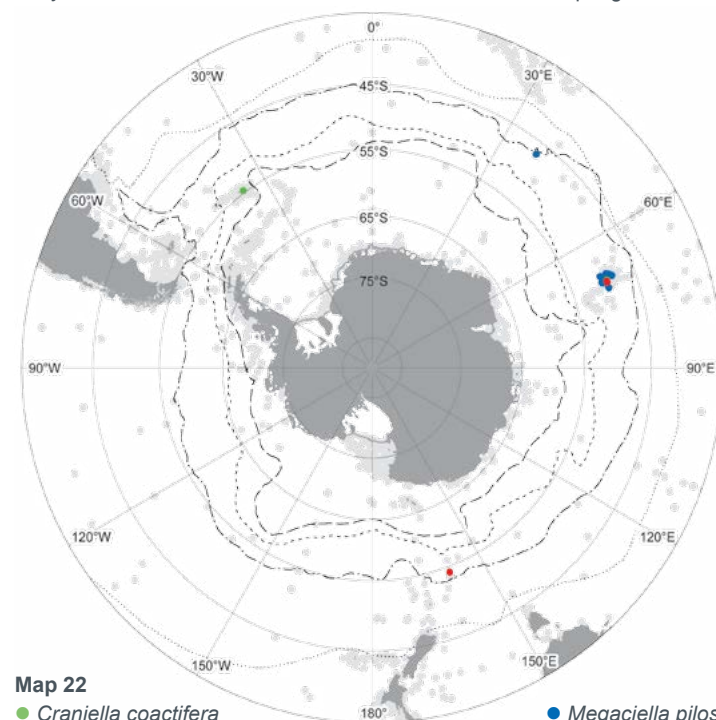
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Map 20
● *Isodictya kerguelensis*
● *Tetilla leptoderma*
● All sponges



Map 21
● *Iophon proximum*
● *Myxilla chilensis*
● *Myxilla novaezealandiae*
● All sponges



Map 22
● *Craniella coactifera*
● *Hymeniacidon kerguelensis*
● *Megaciella pilosa*
● All sponges

Porifera Maps 20–22 Long-distance dispersal in the sub-Antarctic islands (continental and island sources in the Southern Hemisphere): Map 20. Antarctic species: *Isodictya kerguelensis*, *Tetilla leptoderma*. Map 21. Magellanic and Falkland Islands species: *Iophon proximum*, *Myxilla chilensis* and New Zealand species: *Myxilla novaezealandiae*. Map 22. Sub-Antarctic species: South Georgia species: *Craniella coactifera*; Kerguelen, Heard and McDonald Islands species: *Hymeniacidon kerguelensis* (excluding the var. *capensis*); Prince Edward and Crozet Islands species: *Megaciella pilosa*.



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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 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



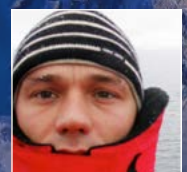
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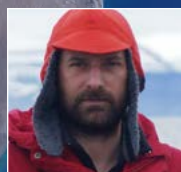
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