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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.8. Antarctic Hexacorals (Cnidaria, Anthozoa, Hexacorallia)

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1. Introduction

Subclass Hexacorallia (Cnidaria, Anthozoa) comprises sea anemones (members of order Actiniaria), black corals (members of order Antipatharia), tube anemones (members of order Ceriantharia), mushroom anemones (members of order Corallimorpharia), stony corals (members of order Scleractinia) and mat anemones (members of order Zoanthidea). Members of Hexacorallia, which currently contains about 4300 extant species (Daly *et al*. 2007), are characterised by hexamerous symmetry (although eight- or ten-part symmetry is not uncommon) and spirocysts, a type of cnida with a single-walled capsule and a tubule with tiny entangling threads. Actiniaria (~1100 species) and Scleractinia (~1600 species) are the most species-rich orders; the other four orders represent less than a quarter of the diversity (Antipatharia 235 species; Ceriantharia 100 species; Corallimorpharia 45 species; and Zoanthidea ~200 species).

Hexacorals are important components of macrobenthic communities in the Southern Ocean in terms of biomass and as part of the suspension feeder communities that dominate some habitats. The most recent taxonomic and biogeographic reviews of members of this taxon in the Southern Ocean identified 42 species of order Scleractinia (Cairns 1982) and 116 species of order Actiniaria (Dunn 1983, Fautin 1984, Rodríguez *et al.* 2007). Fautin (1984) reported two species of Corallimorpharia and described another (Fautin 2011a) that reaches the waters we inventory. Rodríguez *et al.* (2007) included six species, four of which we recognise here; they listed one that we consider a synonym, and the other was included because of differences in the geographical limits of their inventory. The other three hexacoral orders are understudied and represent perhaps only about 15 species.

Actiniaria and Scleractinia in the Southern Ocean follow the general biogeographic pattern of other invertebrates — high endemism, circumpolar species, differentiation between East and West Antarctica faunae, etc. (Cairns 1982, Rodríguez *et al*. 2007). Although baselines for biogeography of these two major hexacoral orders have been written, new data are available (particularly for sea anemones). No synthesis exists for any of the other orders in the Southern Ocean. Here we provide an overview of the entire subclass; our main generalisations are relatively high levels of endemism and complementarity in the distribution the six orders of hexacorals.

Photo 1 *Hormathia lacunifera* (Stephenson, 1918). Det. E. Rodríguez. Larsen B (*Polarstern* ANT-XXIII/8, st. 720-2). The elongate organisms on the column of the sea anemone are antarcturid isopods. Image: J. Gutt © AWI/Marum, University of Bremen, Germany.

2. Methods

We include bibliographic records of hexacorals (Cairns 1982, Cairns *et al.* 2005, Rodríguez *et al.* 2007, Fautin 2011b, Rodríguez & López-González 2013). The limits of our geographical coverage are those of SCAR-MarBIN for the Southern Ocean in its broad sense (e.g. Deacon 1984, Rintoul 2007). We consider the Antarctic Region (ANT) to be the zone south of the Polar Front (PF) (or Antarctic Convergence; 48°S to 63°S, average 55°S); the Sub-Antarctic Region (SBA) to extend from the Polar Front in the south to the Sub-Tropical Front in the north (30°S to 47°S, average 43°S); and the limit of the Southern Ocean (O) starts north of the Sub-Tropical Front.

3. Biodiversity and biogeographic patterns of Antarctic and sub-Antarctic hexacorals

3.1. Actiniaria (Maps 1–5)

The sea anemone fauna of the Southern Ocean includes 116 species (Table 1), 54 in the Antarctic region (29 ANT + 23 ANT-SBA + 2 ANT-SBA-O) (Rodríguez *et al.* 2007, Fautin 2011b). Endemism is high at the species level (53% for the Antarctic Region, 81% for the Southern Ocean) but low at higher taxonomic levels (25% endemic genera and no endemic families). The Antarctic Peninsula area has the highest proportion of endemic species (e.g. *Stephanthus antarcticus* Rodríguez & López-González, 2003), several of which extend to the Weddell Sea. More than 25% of species in the Antarctic Region are circumpolar (e.g. *Glyphoperidium bursa* Roule, 1909 and *Stomphia selaginella* (Stephenson, 1918)). However, only 15% of species cross the Polar Front — that is, are shared with the Magellan Province (e.g. *Isocicyonis alba* (Studer, 1879), and *Antholoba achates* Drayton in Dana, 1846) — or extend to the islands near New Zealand. Only two Southern Ocean species are documented to extend beyond the Southern Ocean, *Liponema multiporum* Hertwig, 1882, and *Galatheanthemum profundale* Carlgren, 1956, presumably having invaded the Southern Ocean from the deep sea. More than 61% of species in the Antarctic Region are restricted to the continental shelf (<1000 m). Most eurybathic species occur in both Antarctic and Sub-Antarctic Regions.

3.2. Antipatharia (Map 6)

Seventeen species of black corals have been documented in the Southern Ocean, nine in deep waters of the Antarctic Region (5 ANT + 2 SBA + 2 ANT-SBA-O: Table 1): *Abyssopathes lyriformis* Opresko, 2002 (Ross Sea, 3500 m), *Schizopathes affinis* Brook, 1889 (north of Amundsen Sea, 4895 m), *Dendrobathypathes grandis* Opresko, 2002 (West Antarctica, 417–686 m), *Bathypathes bifida* Thompson, 1905 (Weddell Sea and Antarctic Peninsula, 2569–3018 m), *B. alternata* Brook, 1889 (West Antarctica, 3914–4863 m), and *B. tenuis* Brook, 1889 (off Amundsen Sea, 4005–4755 m) also cited extending north of the Sub-tropical Front (Indian Ocean, 4755 m). *Heliopathes heterorhodzos* (Cooper, 1909) (3475–4667 m) and *Schizopathes crassa* Brook, 1889 (2836–3040 m) have a circumpolar distribution; the latter and *B. alternata* also extend into the Sub-Antarctic Region. Only *B. patula* Brook, 1889, is distributed across the entire Southern Ocean; in the Antarctic Region, it is known from East and West Antarctica (2500–4200 m) whereas in the Sub-Antarctic Region it is known only from the eastern and southwest Pacific (Chilean fjords, 1583–1908 m; southwest Pacific islands, 604 m); in the southwest Pacific it also occurs north of the Sub-Tropical Front (4863 m). Eight other species occur in the Sub-Antarctic Region: *D. isocrada* Opresko, 2002 (off Auckland Island, 728 m), *Stauropathes staurocrada* Opresko, 2002 (off Auckland Island, 814 m), *Trissopathes tristicha* (van Pesch, 1914) (off Auckland Island, 728 m), *Cladopathes plumosa* Brook, 1889 (off Auckland and Prince Edward islands, 566–728 m), *T. tetracrada* Opresko, 2003 (east Pacific, 1150 m), *Antipathes speciosa* (Brook, 1889) (east Pacific, 320 m), and *Antipathella fiordensis* (Grange, 1990) (east Pacific, 15 m). An unidentified species of *Cirripathes* was reported off Auckland Island (728–837 m) (de Blainville 1830).

3.3. Ceriantharia (Map 7)

One species of tube anemone is recorded in the Southern Ocean; identified only to order (Arntz & Brey 2001), the specimens were collected off the Antarctic Peninsula (so in the Antarctic Region) at a depth of 150–300 m. Although this order is not very speciose (Daly *et al.* 2007), its remarkable sparsity in the Antarctic Region might be an artefact of collecting. Ceriantharians live in a tube burrowed into soft sediment; because they are able to retract rapidly into the tube when disturbed, collecting them is difficult, particularly with trawls (this conventionally used collecting gear also damages the animals).

Table 1 Species of hexacorals in each region of the Southern Ocean (SO). Numbers in brackets are species shared by ANT and SBA (therefore, number is in both columns).

Order	Antarctic region (ANT)	Sub-Antarctic region (SBA)	SBA and north (SBA-O)	All 3 regions (ANT-SBA-O)	Total (proportion endemic)
Actiniaria	29 [23]	42 [23]	20	2	116 (81%)
Antipatharia	5 [2]	8 [2]	0	2	17 (88%)
Ceriantharia	1 [0]	0 [0]	0	0	1 (?)
Corallimorpharia	0 [0]	1 [0]	2	2	5 (20%)
Scleractinia	7 [2]	7 [2]	20	6	42 (38%)
Zoanthidea	1 [0]	4 [0]	0	1	6 (83%)
TOTAL	43 [27]	62 [27]	42	13	187 (71%)

3.4. Corallimorpharia (Map 8)

Five species of mushroom anemones have been documented in the Southern Ocean, *Corallimorphus profundus* Moseley, 1877*, C. rigidus* Moseley, 1877, *C. niwa* Fautin, 2011a, *Corynactis carnea* Studer, 1879, and *Corynactis chilensis* Carlgren, 1941. Most specimens of *Corallimorphus* are from deep waters, although some records are from water shallower than 100 m in the Southern Ocean (Fautin 2011b). *Corallimorphus rigidus* and *C. profundus* are widely distributed, occurring also in the northern hemisphere, and extending south of the Polar Front; *C. profundus* is circumpolar, inhabiting shallower depths in the Antarctic than in the Sub-Antarctic Region (continental shelf *vs.* bathyal depths). *Corallimorphus niwa* is a sub-Antarctic species found around New Zealand. In the Southern Ocean, specimens of *Corynactis* have been reported to about 50 m off both coasts of South America to north of the Sub-Tropical Front.

3.5. Scleractinia (Map 9)

Of the 42 species of stony corals in the Southern Ocean (Cairns 1982, Cairns *et al.* 2005), four are of uncertain identity (Cairns 1982). They display three biogeographic patterns: some are confined to the Antarctic Region; some are confined to the Sub-Antarctic Region; and some are cosmopolitan or widespread, only barely reaching the Sub-Antarctic Region (Table 1). Twenty-six species (20 SBA-O + 6 ANT-SBA-O; 62%) are cosmopolitan; 14 species (7 ANT + 7 SBA; 33%) are endemic to either the Antarctic or the Sub-Antarctic Region, whereas two species (<5%) are endemic to both the Antarctic and Sub-Antarctic Regions.

3.6. Zoanthidea (Map 10)

Six nominal species of mat anemones are documented in the Southern Ocean; only *Parazoanthus antarcticus* (Carlgren, 1927) (Antarctic Peninsula, 290 m) occurs in the Antarctic Region (Fautin 2011b). Four records of zoanthid specimens identified only as *Parazoanthus* sp. (Arntz & Brey 2001, 2003, 2005, Fütterer *et al.* 2003) are from West Antarctica (Antarctic Peninsula and eastern Weddell Sea area, 306–3925 m). Five named species are restricted to shallow waters in the Sub-Antarctic Region around South America: *Parazoanthus fuegiensis* Carlgren, 1899 (also Carlgren 1927; Magellan Strait), *P. elongatus* McMurrich, 1904 (southern Chile, 20–25 m), *Epizoanthus fiordicus* Sinniger & Häussermann, 2009 (southern Chile, 28 m), *Mesozoanthus fossii* Sinniger & Häussermann, 2009 (southern Chile, 25–29 m), and *Epizoanthus patagonicus* Carlgren, 1899 (Argentinean Patagonia, 20–197 m), the only species to extend north of the Sub-Tropical Front.

3.7. General remarks

Of the three orders that have been well studied, the percentage of species in the Southern Ocean relative to the total number of species worldwide is lower for Scleractinia (2.5%) than for Corallimorpharia and Actiniaria (about 11% each). We note some complementarity (Fautin 1989) in the distribution of members of the three hexacoral orders for which there are data.

Data concerning distribution of Antipatharia, Ceriantharia, and Zoanthidea are few in the Southern Ocean, many species being known from single sites. Both limited sampling and limited taxonomic expertise confound any analysis. Members of order Antipatharia are restricted to deep waters (which is typical of the taxon); species in the Sub-Antarctic Region are restricted to either the surroundings of the Auckland Island area or the east Pacific coast, and occur in shallower water than those in the Antarctic Region. That species seem to have small ranges (most of the Antarctic ones are restricted to West Antarctica, only three being circumpolar) may be an artefact of poor knowledge. Zoanthids are more or less restricted to shallow waters of the Sub-Antarctic Region; like antipatharians, they occur shallow in the Sub-Antarctic Region and deeper in the Antarctic Region. However, the only zoanthid species known from the Antarctic Region is apparently circumpolar.

The distribution patterns of antipatharians and zoanthids might be related to their ecology. Many zoanthids are epizoic. The availability of substrate in the Antarctic Region is considered a key factor regulating benthic communities (Lovell & Trego 2003), which are highly structured; competition for substrate is important (Dayton 1990). Their restricted distributions could be because of their larvae: the only antipatharian species to have been studied, which live in shallow water, have lecithotrophic crawling larvae with low dispersal capacities (Grigg 1965, Miller 1998). The relatively small size of antipatharian polyps might be adapted to exploit small particles of organic matter that are available year round in “food banks” (Mincks *et al.* 2005), and thereby favor members of this order in deeper Antarctic waters.

Continental shelves in the Antarctic Region are dominated by solitary scleractinians and sea anemones. However, whereas about 15% of Southern Ocean scleractinian species are widespread (6 species ANT-SBA-O), only 2% (2 species ANT-SBA-O) of actiniarian species recorded in the Antarctic Region extend north of the Sub-Antarctic Region (Table 1). This difference is more remarkable in the proportion of Southern Ocean species reported only north of the Polar Front (SBA-O + ANT-SBA-O species): almost 70% of scleractinians but only 19% of actiniarians. The predominance of widely distributed or cosmopolitan species of members of Corallimorpharia resembles the pattern of Scleractinia; this is maybe because members of these two orders are closely related phylogenetically (Daly *et al.* 2007, Daly & Fautin 2007). However, in contrast with Scleractinia, no corallimorpharian species seem to have diversified in the Southern Ocean — two of the five known species occur in northern latitudes and only those two barely reach the Antarctic Region.

There is no clear explanation for differences in distribution of Southern Ocean scleractinians and actiniarians. It is unlikely to be the calcified skeleton, which actiniarians lack and scleractinians have, even though the cold and deep waters of the Southern Ocean are undersaturated with calcium carbonate, because corallimorpharians, with a distribution resembling that of scleractinians, lack one as well. Dispersal could account for these differences, but, although reproductive and larval biology of Southern Ocean hexacorals has not been well studied, among actiniarians are external and internal brooders, gonochores and hermaphrodites, and broadcast spawners, so reproductive/sexual pattern may not be important in explaining their differential success.

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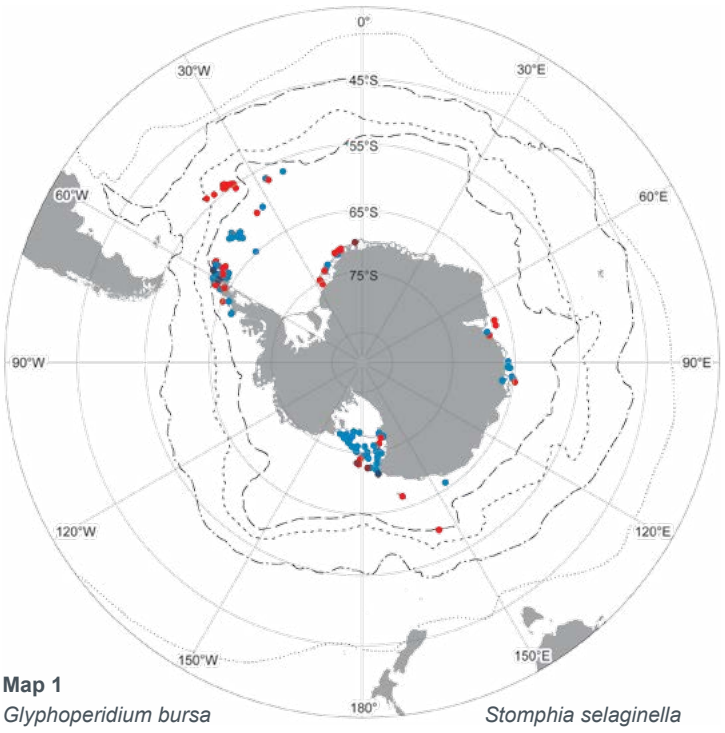
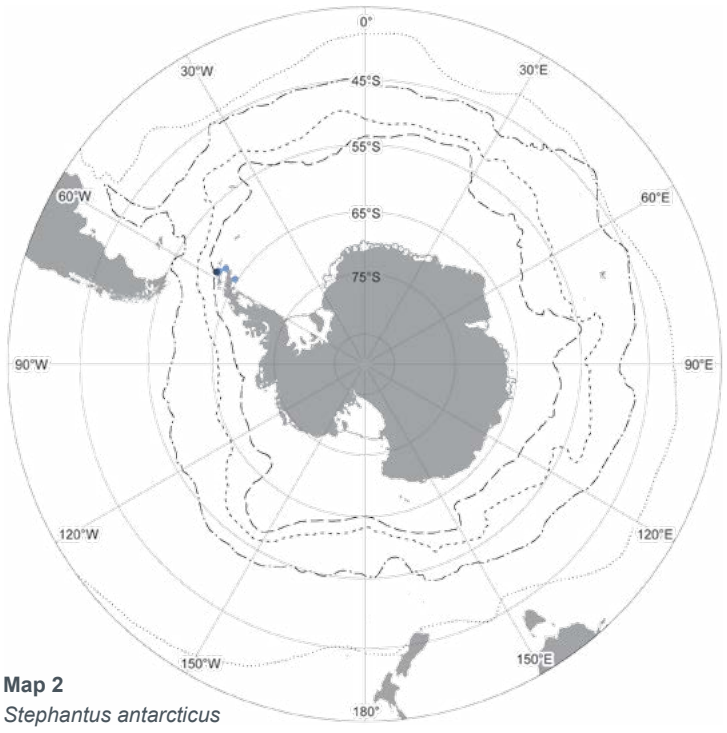


Map 1

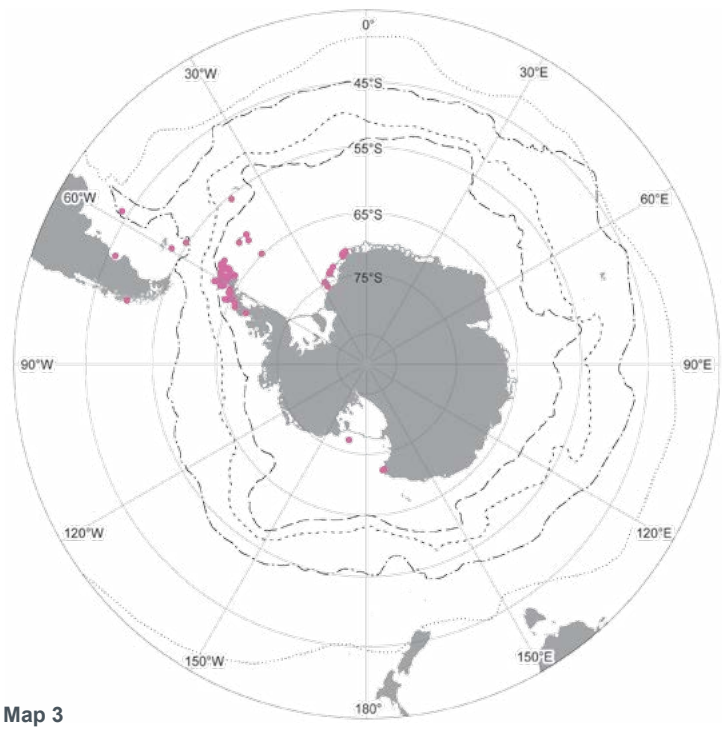
Glyphoperidium bursa
- 0-999 m
- >1000 m

Stomphia selaginella
- 0-999 m
- >1000 m



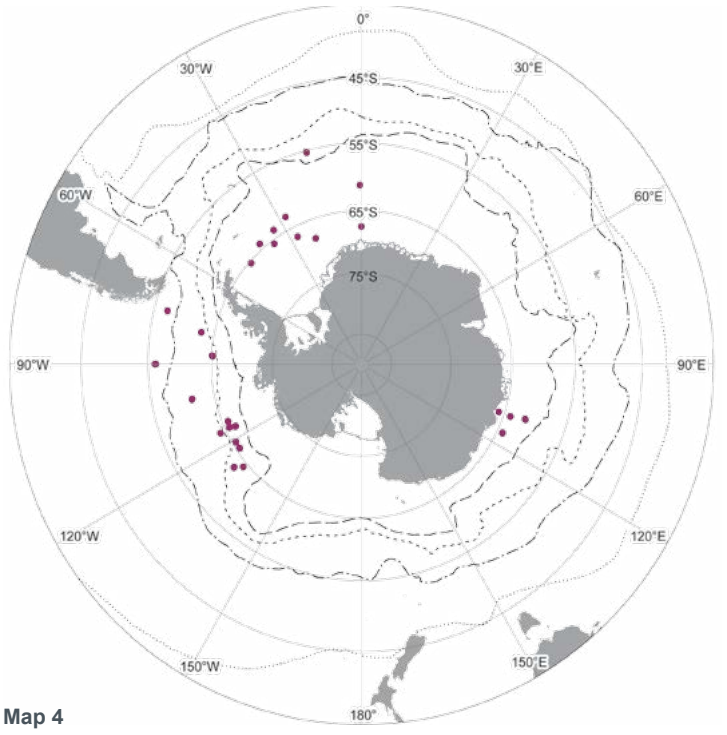
Map 2

Stephantus antarcticus
- 0-999 m
- >1000 m



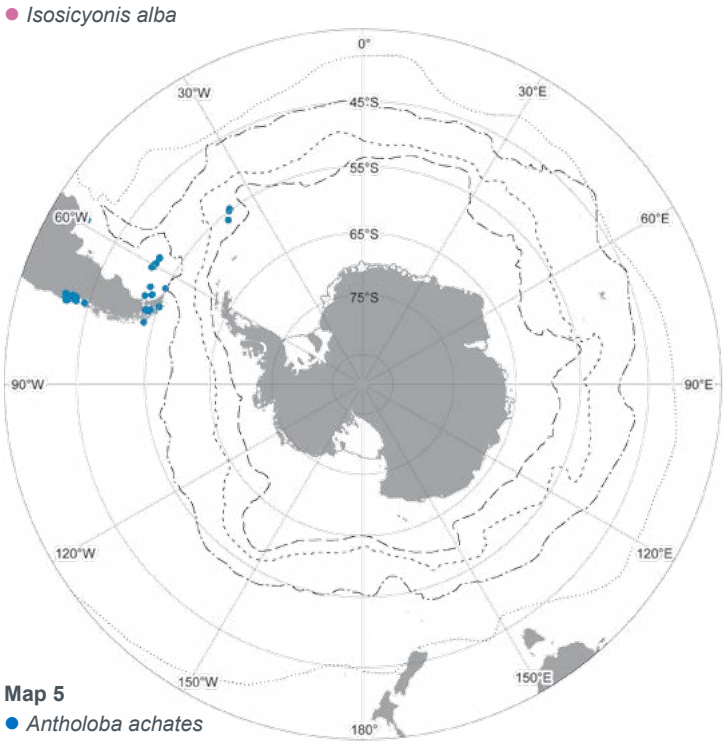
Map 3

- *Isosicyonis alba*



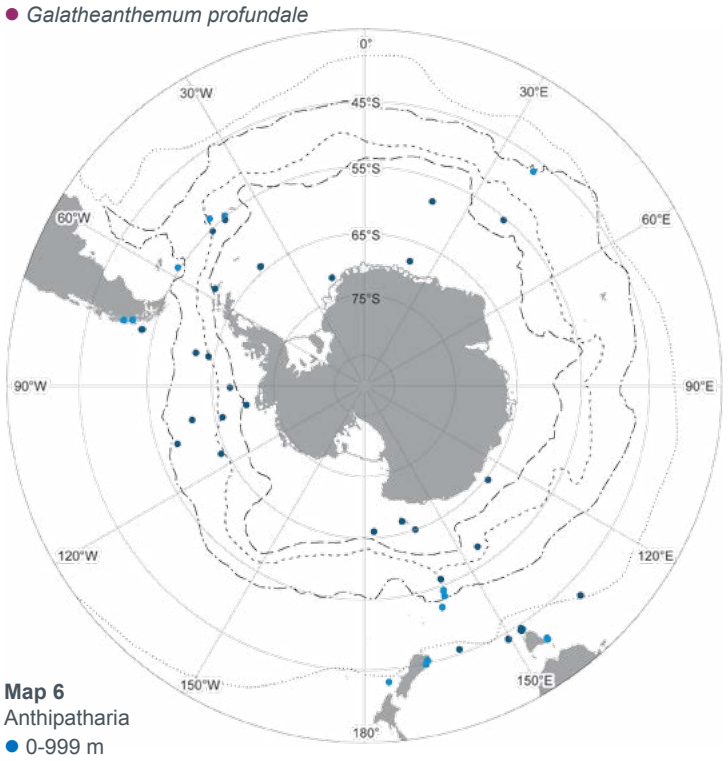
Map 4

- *Galatheanthemum profundale*



Map 5

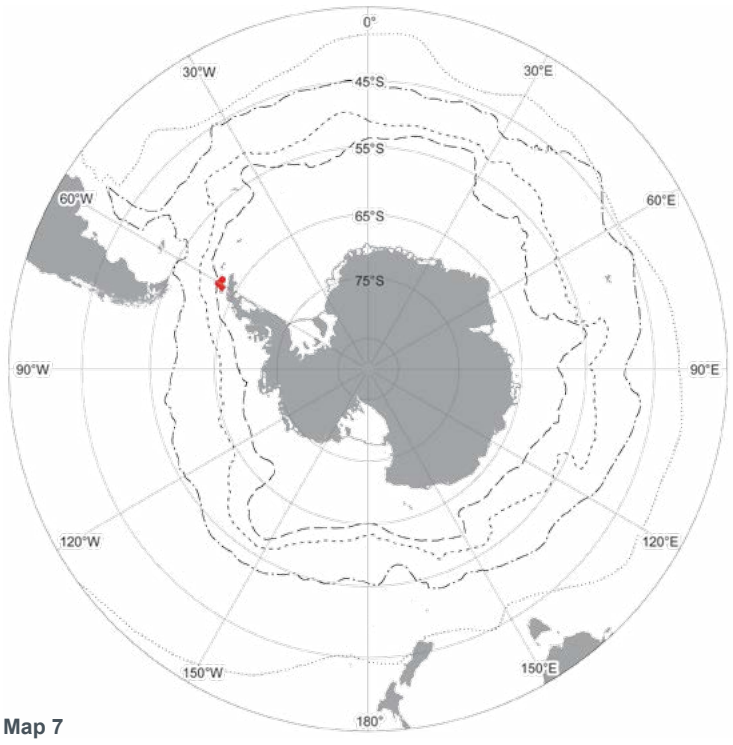
- *Antholoba achates*



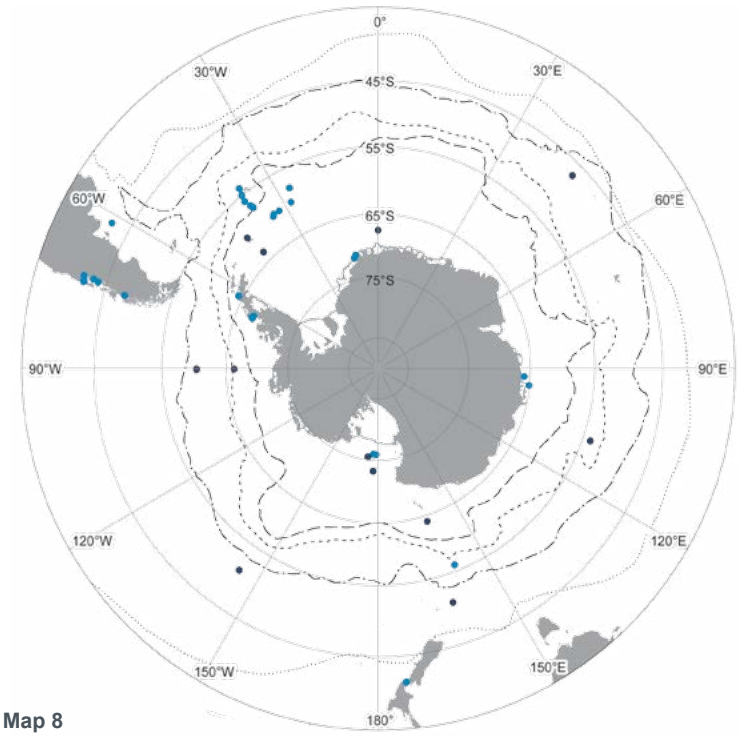
Map 6

Anthipatharia
- 0-999 m
- >1000 m

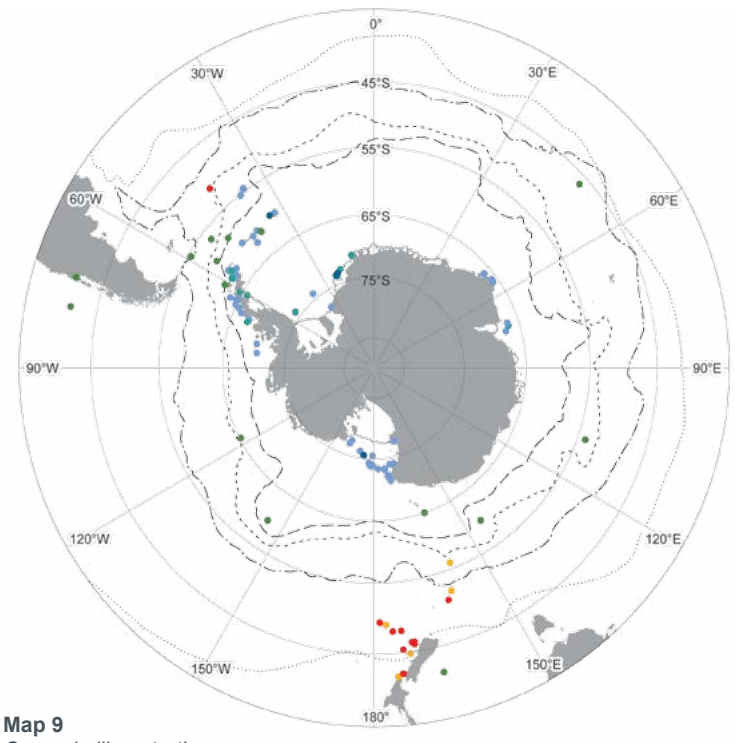
Hexacorallia Maps 1–6 Antarctic and sub-Antarctic records of representative species of order Actiniaria, and records of order Antipatharia. Map 1. Examples of Antarctic endemic circumpolar actiniarians: *Glyphoperidium bursa* Roule, 1909, and *Stomphia selaginella* (Stephenson, 1918). Map 2. Example of deep-sea endemic Antarctic actiniarian: *Stephanthus antarcticus* Rodríguez & López-González, 2003. Map 3. Example of endemic circumpolar Antarctic and sub-Antarctic distributed actiniarian: *Isosicyonis alba* (Studer, 1879). Map 4. Example of cosmopolitan deep-sea species extending to Antarctica: *Galatheanthemum profundale* Carlgren, 1956. Map 5. Example of shallow-water actiniarian distributed both in Antarctica and Southern Patagonia: *Antholoba achates* Drayton in Dana, 1846**.** Map 6. Antarctic and sub-Antarctic records of Antipatharia.



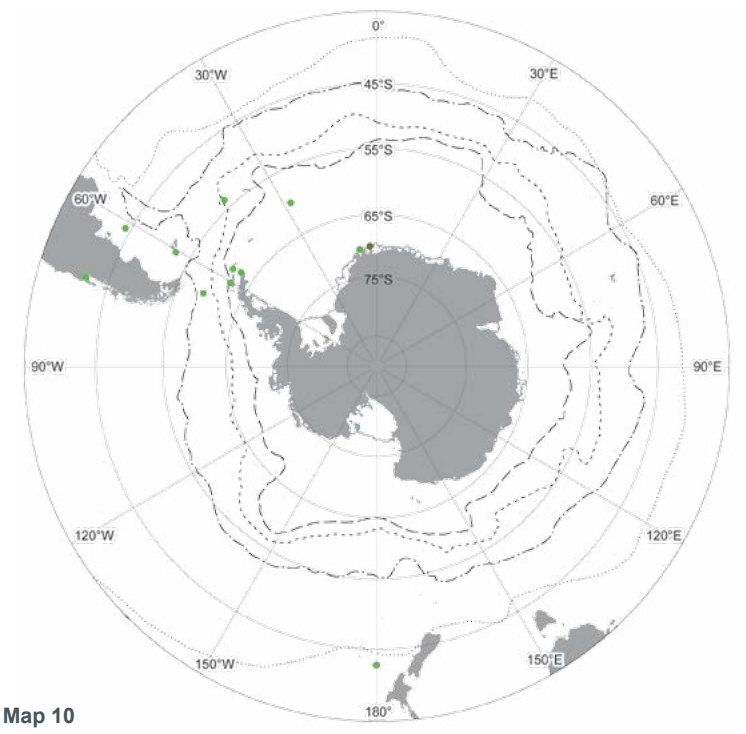
Map 7
● Ceriantharia



Map 8
Corallimorpharia
● 0-999 m
● >1000 m



Map 9
Caryophyllia antartica
● 0-999 m
● >1000 m
Flabellum apertum apertum
● 0-999 m
● >1000 m
Fungiacyathus marenzelleri
● 0-999 m
● >1000 m



Map 10
Zoanthidea
● 0-999 m
● >1000 m

Hexacorallia Maps 7–10 Known distribution of ceriantharians, corallimorpharians, scleractinians (selected species), and zoanthideans in the Southern Ocean. Map 7. Antarctic and sub-Antarctic records of Ceriantharia. Map 8. Antarctic and sub-Antarctic records of Corallimorpharia. Map 9. Antarctic and sub-Antarctic records of representative species of order Scleractinia: *Caryophyllia antarctica* Marenzeller, 1904 (endemic circumpolar Antarctic scleractinian); *Flabellum apertum apertum* Moseley, 1876 (sub-Antarctic endemic circumpolar scleractinian); *Fungiacyathus marenzelleri* (Vaughan, 1906) (cosmopolitan scleractinian extending to Antarctica). Map 10. Antarctic and sub-Antarctic records of Zoanthidea.

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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

Claude DE BROYER is a marine biologist at the Royal Belgian Institute of Natural Sciences in Brussels. His research interests cover structural and ecofunctional biodiversity and biogeography of crustaceans, and polar and deep sea benthic ecology. Active promoter of CAML and ANDEEP, he is the initiator of the SCAR Marine Biodiversity Information Network (SCAR-MarBIN). He took part to 19 polar expeditions.

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Graham HOSIE is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and biogeography of plankton species and communities, notably their response to environmental changes. He has participated in 17 marine science voyages to Antarctica.

Alexandra POST is a marine geoscientist, with expertise in benthic habitat mapping, sedimentology and geomorphic characterisation of the seafloor. She has worked at Geoscience Australia since 2002, with a primary focus on understanding seafloor processes and habitats on the East Antarctic margin. Most recently she has led work to understand the biophysical environment beneath the Amery Ice Shelf, and to characterise the habitats on the George V Shelf and slope following the successful CAML voyages in that region.

Yan ROPERT COUDERT spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.