Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 1.1. The biogeography of the Southern Ocean.
De Broyer C., Koubbi P., 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. 2-9.

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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 Antarctic 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)

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Printed by: Altitude Design, Rue Saint Josse, 15, B-1210, 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:

For the volume:

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.

1.1. The biogeography of the Southern Ocean

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1. Introduction

Biogeographic information is of fundamental importance in providing the necessary geospatial framework to the marine biodiversity knowledge and understanding, and for assessing its gaps. It is for example essential for discovering biodiversity hotspots, detecting impacts of environmental changes, monitoring biodiversity, and modelling future distributions. In the context of increasing human pressure, it appears a key resource for supporting conservation and sustainable management strategies and designing marine protected areas.

The Southern Ocean (SO) (Map 1), was the last discovered on Earth and some of its parts, far from the scientific stations and their supply-ship routes, remain unexplored. Its depths have only been sampled by a few dedicated exploratory campaigns.

Its biodiversity - adapted to extreme conditions of life - appears unique and at the same time vulnerable to effects of global change such as climate warming, UV exposure and ocean acidification. In places, the region is warming more rapidly than the global ocean average and the Southern Ocean acts as a sentinel in detecting the impact of environmental changes upon marine ecosystems. It is also well recognized that it plays a critical role in the global ocean circulation, biogeochemical cycles and climate by connecting the ocean basins and the upper and lower limbs of the ocean overturning circulation (Rintoul *et al.* 2009).

The extensive exploration and assessment of the Southern Ocean biodiversity by the Census of Antarctic Marine Life programme (CAML 2005-2010; see Chapter 1.2) and the intense compilation and validation efforts of biogeographic data by the SCAR Marine Biodiversity Information Network (www.biodiversity.aq ; see Chapter 2.1) and other Antarctic data centres provided a unique opportunity, a strong collaborative framework and the appropriate momentum to attempt to synthesise the current biogeography knowledge of the Southern Ocean. This new synthesis was able to draw 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.

2. Mapping the Southern Ocean biodiversity patterns

2.1. Historical background

Since James Cook's second voyage in 1772-1775, which allowed the first descriptions of Antarctic animals (the birds of South Georgia by Forster, from 1777), the naturalists onboard a number of pioneer Antarctic exploratory expeditions progressively revealed the composition of the unique Southern Ocean biodiversity (see Fogg 1992).
(Fig. 1)

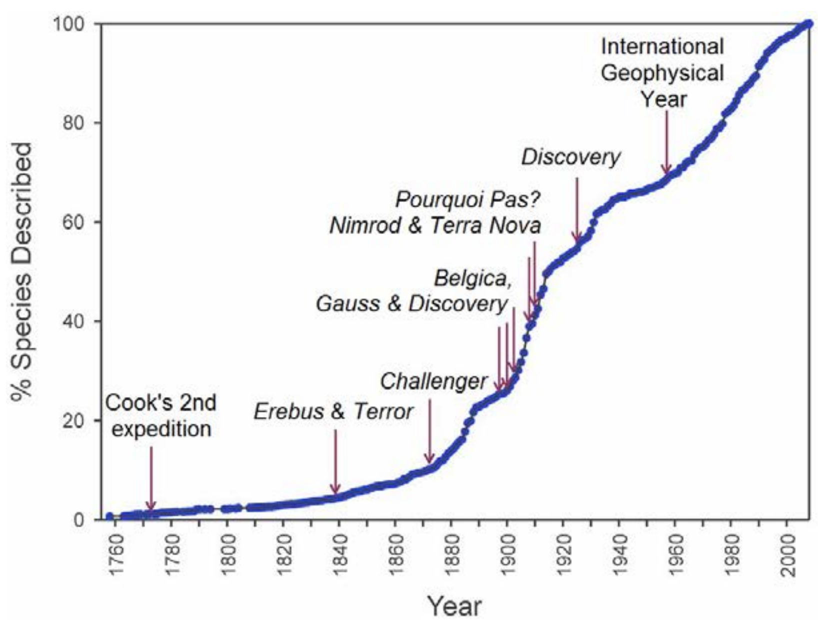


Figure 1 Rate of description of Southern Ocean species (from Griffiths 2010)

The very first attempt to characterise the Southern Ocean zoogeography may be that of Allen (1878), who, on the basis of mammal distribution, distinguished 8 main zoogeographical regions ("realms") on Earth. He named the last one the "Antarctic or South Circumpolar Realm" that was described as follows: *"The Antarctic Realm …embraces not only the Antarctic Zone, but a large part of the cold south-temperate… It will hence include not only the few small groups of Antarctic Islands, but also Tierra del Fuego and the Falkland Islands, …, while some of its characteristic forms also extend to New Zealand, and even Australia and the Cape of Good Hope. The only mammals that can be considered as strictly characteristic of this region are Pinnipeds and Cetaceans, of which several genera of each are almost wholly restricted to it."*

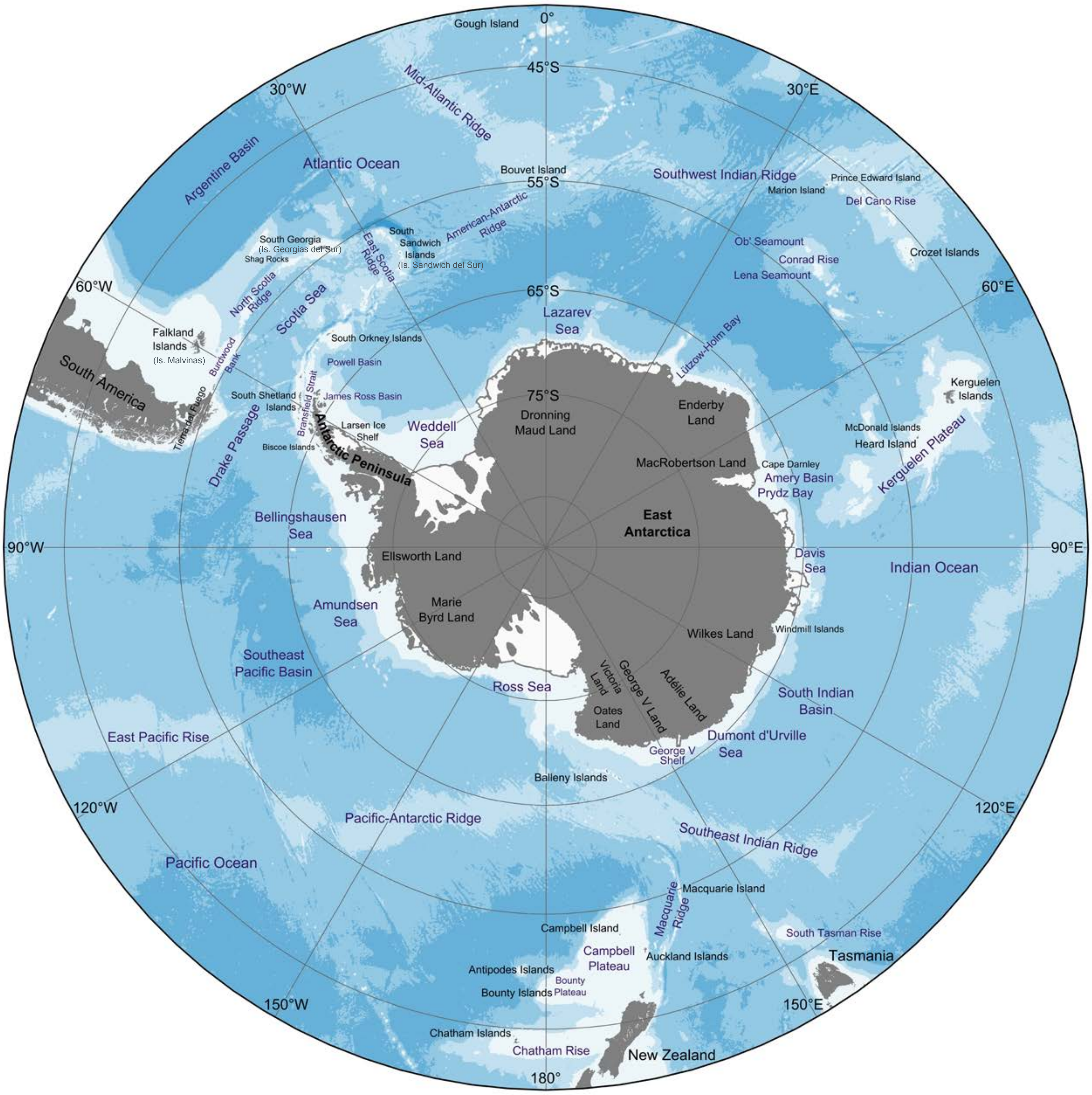
Few years later, in his "Principles of Zoogeography" (1884), Gill, relying mostly on fish data and records along the southern South American coasts, distinguished an "Antarctalian Realm" that *"may cover the antipodal ocean up the isocryme of 44°F"* [i.e. 6.7°C] and a "Notalian Realm", the south temperate realm, that *"may provisionally be said to extend from the southern isocryme of 68° to that of 44°"* [i.e. 20°C to 6.7°C]. It seems that Gill was the first to introduce an obvious reference to sea surface temperatures.

At the end of the 19th century, the important results of the *Challenger* voyage in 1872-1876 were published, describing parts of the fauna of Kerguelen, Heard, Crozet and Prince Edward Islands. The results of the German Polar Expedition to South Georgia in 1882-83, in particular Pfeffer 1890, were also available. This allowed Ortmann (1896) in his influential "Grundzüge der Marinen Tiergeographie" to attempt a first generalisation of the SO fauna distribution patterns. For the benthos of the "littoral life zone" (which limit was set at the depth to which daylight is able to penetrate, which was "*about 400 m*") he distinguished an "Antarctic Region" (without stipulating its precise northern limits) with "*numerous local faunas*", which comprised: 1. A supposed coastal circumpolar fauna (fairly unknown); 2. A "Chilean-Patagonian" fauna, which may likely include South Georgia, South Orkney and South Shetland Islands; 3. A (South African) "Cape" fauna; 4. An "Australian-New Zealand" fauna. An Antarctic Region was also recognised for the "pelagic life zone", which was divided in two sub-regions: the "Antarctic-circumpolar sub-region" under sea ice influence, and the "Notal-circumpolar subregion". He did not define precisely "notal" (see Baur 1896), but in a footnote he referred to the (loose) concept originally introduced by Gill (1884). The term "notal" was subsequently used inconsistently by some Russian workers but was unambigously rejected by Hedgpeth (1970).

Taking advantage of a new wealth of faunistic data collected by the Antarctic "heroic age" expeditions at the turn of the century (*Belgica, Valdivia, Southern Cross, Gauss, Antarctic, Discovery*, *Scotia*, *Français, Pourquoi Pas*, *Terra Nova,…*), Ekman (1935, 1953), in his seminal "Zoogeography of the Sea", was the first to summarise Southern Ocean distributions in a comprehensive biogeographic scheme. Relying on both the hydrographic framework (in particular the sea surface temperatures) and mostly echinoderm and fish records, he divided the Southern Ocean shelf and slope fauna (<1000 m) into two main regions: an Antarctic Region and an Antiboreal Region, the latter corresponding to the Sub-Antarctic Region of subsequent authors such as Hedgpeth (1969). The Antarctic Region, with a suggested northern limit at the Antarctic Convergence, was subdivided into two sub-regions (or provinces): the "Low Antarctic", which includes South Georgia and the Shag Rocks Bank, and the "High Antarctic" which includes the rest of the region. The High Antarctic was in turn subdivided into a "West Antarctic" sub-region (Weddell Sea, Peninsula and Scotia Arc islands) and the "East Antarctic" including the Ross Sea and the regions lying south of Australia.

His Antiboreal Region comprised a South American well-defined sub-region, several isolated oceanic islands and a possible Kerguelen sub-region. The South American sub-region includes south Chile from about 40-42°S, Tierra del Fuego, and the Patagonian shelf, which northern limit "*may possibly be put as far north as Rio de la Plata mouth"* (36°S), although Norman (1937), relying on the fish fauna, placed the boundary of his "Patagonian Region" at 42°S. Ekman noted the great similarity of the Falkland fauna with the Patagonian fauna. He grouped among the Antiboreal oceanic islands: Gough Island, Prince Edward and Marion Islands, Crozet Islands, Auckland and Campbell Islands (noting nevertheless their close affinities with New Zealand) and Macquarie Island, recognizing, however, that their fauna was still poorly known and that they do not form a homogeneous faunal region. Kerguelen Islands (grouped with Heard and McDonald Islands) is considered a transitional, mixed region with strong endemism (about 50%) as well as strong affinities both with the Antarctic but even stronger with cold temperate regions.

A general scheme for the littoral regions of the southern cold temperate and Antarctic zones was proposed by Knox (1960), based on wide information about oceanographic conditions and distribution patterns of shallow-water organisms. His occurrence dataset of macroalgae and several animal groups was limited to distribution data obtained to the lower depth limit of algal growth, which may restrict the comparison with previous and following studies taking also into account the deeper shelf benthos. After characterising the littoral zonation patterns of an array of species typical of the various southern regions considered (Table 1), Knox (1960) distinguished an Antarctic Region with two provinces: the Antarctic Province, which includes Bouvet and Heard Islands as well as the South Sandwich Islands, and the South Georgia Province, considered a very distinctive biogeographic unit. Within the Antarctic Province, two sub-provinces are further recognized: the Scotian sub-province comprising Antarctic Peninsula and the Scotia Arc, while the Ross Sea and

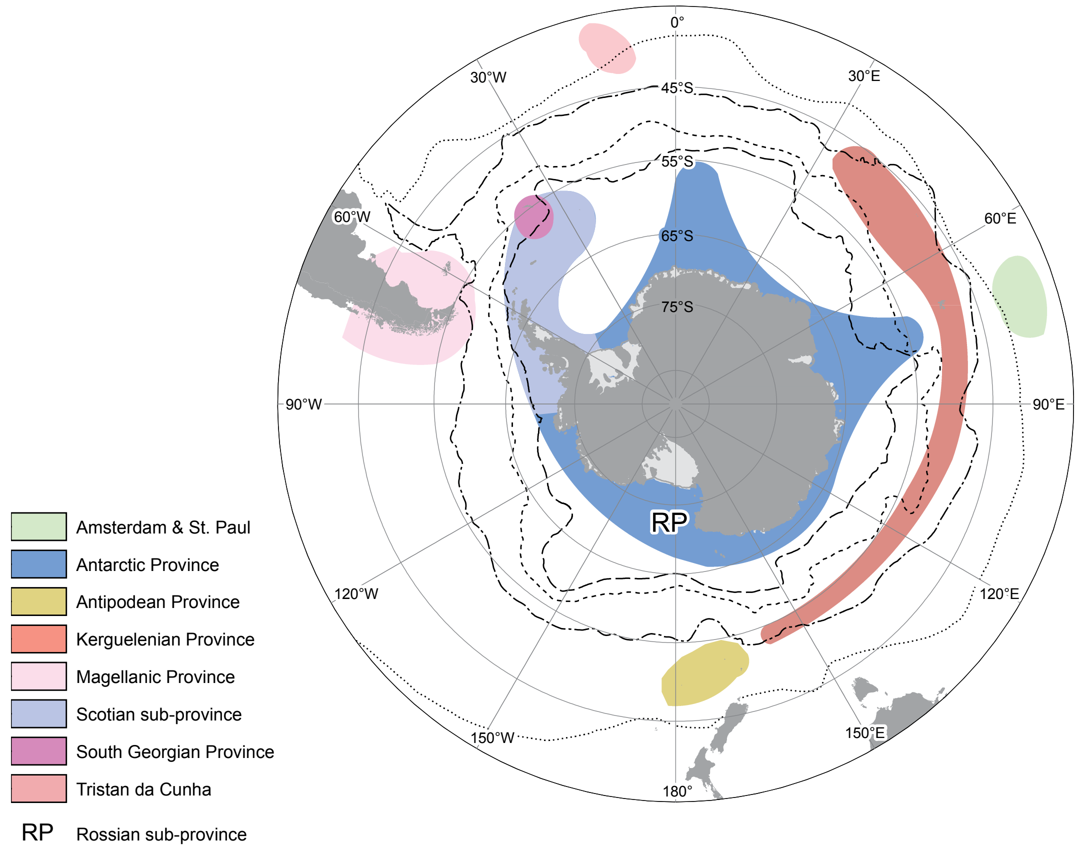


Introduction Map 1 General map of the Southern Ocean.

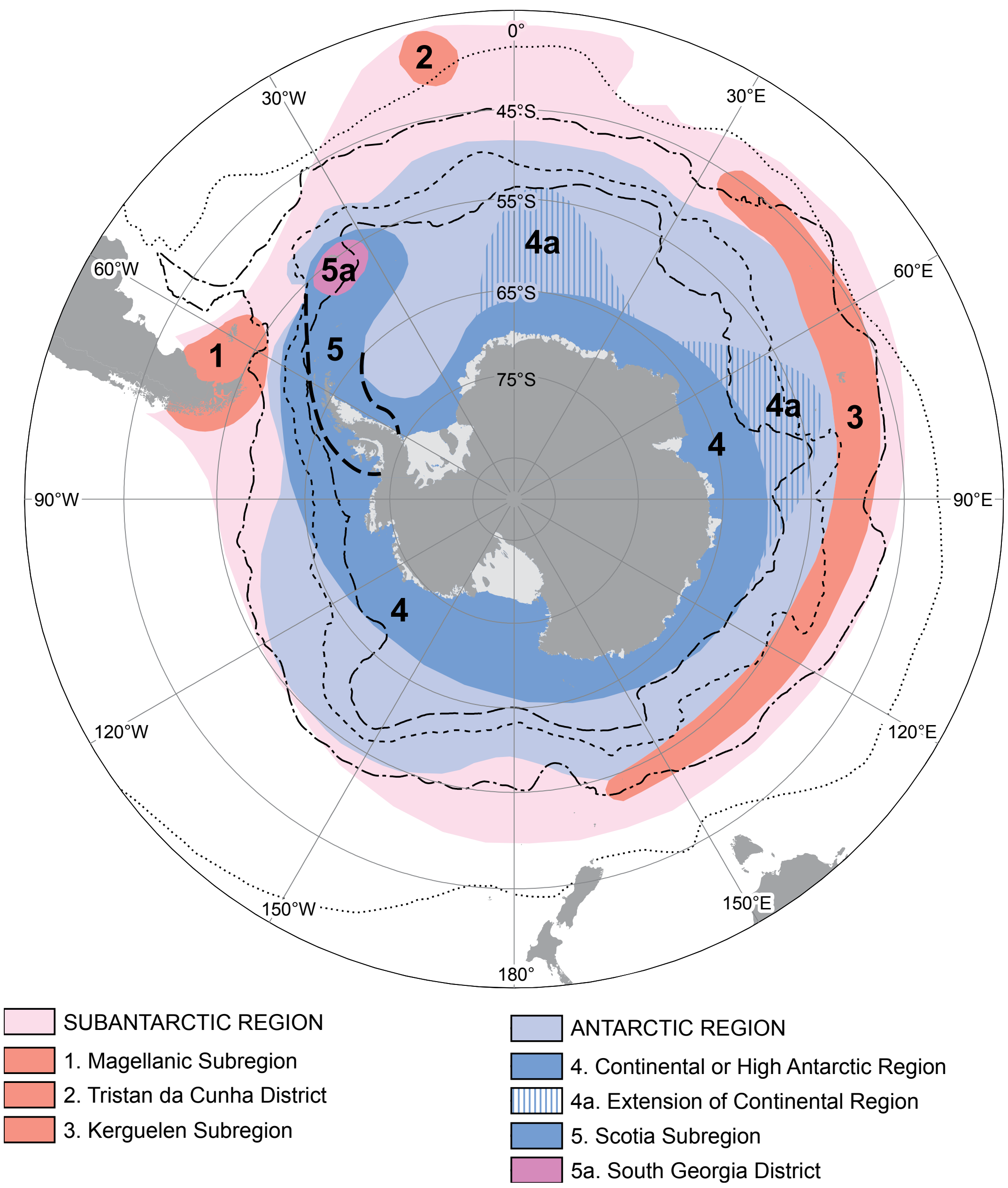
The place-names used in the Atlas are based on the following gazetteers: SCAR Composite Gazetteer: https://data.aad.gov.au/aadc/gaz/scar/ , GEBCO Gazetteer of undersea feature names: http://www.ngdc.noaa.gov/gazetteer/ , and USGS: United States Board of Geographic Names: http://geonames.usgs.gov/antarctic/

Table 1 Characteristics of the water masses of the southern temperate and Antarctic regions with the corresponding biogeographic provinces (from Knox 1960)

Characteristic temperature range	Characteristic salinity range	WATER MASS	BIOGEOGRAPHIC PROVINCE			
			New Zealand sector	South Australian sector	South American sector	South African sector
Winter: 3 to 11,5°C Summer: 5,5 to 14,5°C	34,0 to 34,5‰	Subantarctic cold temperate	Antipodean	Kerguelenian	Magellanic	Kerguelenian
Mean range: 1.3 to 3.7°C		Transitional zone			Georgian	
Winter: -1,8 to 0,5°C Summer: -1,0 to 3,5°C	33,0 to 34,0‰	Antarctic	Rossian sub-P.	Antarctic	Scotian sub-P.	Antarctic



Introduction Map 2 Biogeographic division of the littoral zone of the southern cold temperate and Antarctic regions according to Knox (1960).



Introduction Map 3 Biogeographic divisions of the Southern Ocean according to Hedgpeth (1969).

adjacent regions are considered to be a separate Rossian sub-province. In the sub-Antarctic or cold temperate regions, the Kerguelenian Province is formed by the scattered islands of Prince Edward and Marion, Crozet, Kerguelen and Macquarie, and the Subantarctic islands near New Zealand are considered the Antipodean Province. The southernmost part of South America and the Falkland Islands constitutes the Magellanic Province (Map 2).

Summarising the early works on Antarctic zoogeography done by ichthyologists (in particular Regan 1914 and Nybelin 1947) and relying on his more recent findings, Andriashev (1965) proposed a scheme based on coastal fishes, comprising an Antarctic Region with a Glacial Sub-Region and a Kerguelen Sub-Region. The Glacial Sub-Region comprised a South Georgian Province (South Georgia, South Sandwich Islands and Bouvet Island) and a Continental Province, which was in turn subdivided into an East Antarctic District (including the coasts from the eastern Ross Sea to the western Weddell Sea) and a West Antarctic District (Antarctic Peninsula, South Shetland and South Orkney Islands). His Kerguelen Sub-Region included Marion Island, the Crozet Islands, Kerguelen and Heard Islands, and Macquarie Island. At the difference of previous biogeographic schemes, Andriashev did not retain the sub-Antarctic islands into a Sub-Antarctic Region but kept them in a large Antarctic Region. This view was subsequently supported by DeWitt (1971).

Although recognising that biogeographical regionalisation should ideally be carried out on the basis of distribution patterns of whole communities of organisms and should not be based only on data from any one group, Kussakin (1967) proposed a biogeography of Antarctic and sub-Antarctic waters based on his extensive studies on isopods and tanaids. These brooding peracarid crustaceans have poor dispersal capabilities and thus can be useful biogeographical indicators. Relying on endemism data and records down to 2000 m depth, and using Preston's index to calculate affinities between localities, his zonation scheme retained three main regions: the Antarctic, Kerguelen and Patagonian Regions. The Antarctic Region comprised an East Antarctic Province extending from the eastern Weddell Sea to Eights Coast (at about 100°W), a Graham or West Antarctic Province (Bellingshausen Sea, Antarctic Peninsula, South Shetland and South Orkney Islands), and a South Georgia Province (South Georgia, Shag Rocks, South Sandwich Islands, and possibly Bouvet Island). The Kerguelen Region included a Macquarie Province, a Kerguelen Province (with Kerguelen and Heard Islands) and a Marion Province (with Marion, Prince Edward and Crozet Islands). The Patagonian Region comprised a Magellan Province (south Chile from 40-42°S, south Argentina from 40°S, Tierra de Fuego and Falkland Islands), an Arauca Province (central Chile) and an Argentinian Province (from 40°S to north of Rio de la Plata).

2.2. The Antarctic Map Folio Series (1967-1978) and beyond

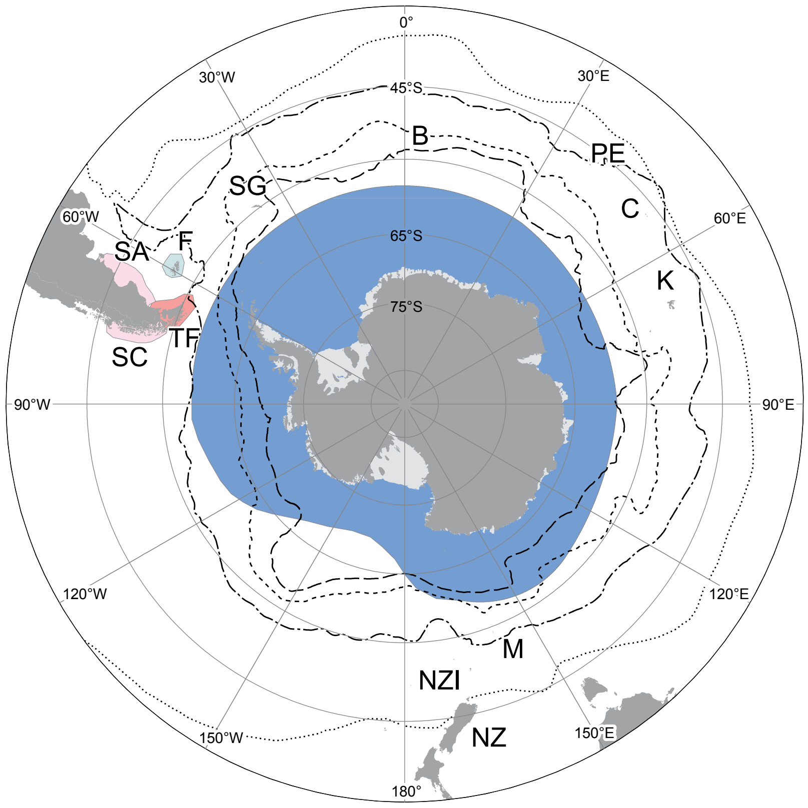
The first comprehensive effort to systematically map the distribution of the Southern Ocean biota is due to the "Antarctic Map Folio Series" published by the American Geographical Society (1967-1978). At the same period, the "Biology of the Antarctic Seas" monographs (1964-1995, in the Antarctic Research Series, published by the American Geophysical Society) substantially contributed to document the Antarctic and sub-Antarctic biodiversity and its distribution. Five Antarctic Map Folios were devoted to marine biodiversity: the biogeography of macroalgae was covered by Balech *et al.* (1968), the invertebrates by Bushnell & Hedgpeth (1969), the fish by DeWitt (1971), the birds by Watson *et al.* (1971), and the mammals by Brown *et al.* (1974).

Resulting from these efforts, Hedgpeth (1969, 1970) biogeographic synthesis was the first modern attempt to establish the SO biological regionalisa-

tion on the basis of a largely documented and diverse dataset – the occurrence records of 17 benthic and 4 pelagic invertebrate taxonomic groups. Hedgpeth recognised two main Antarctic and Sub-Antarctic Regions. The Antarctic Region extended south of the Antarctic Convergence (as suggested initially by Ekman and essentially valid for plankton) and divided into a Continental or High Antarctic Sub-Region (with an extension to Bouvet Island and a second one to Heard Island), and a Scotia Sub-Region (Peninsula and Scotia Arc Islands) with a separate district (or sub-province) for South Georgia. The Sub-Antarctic Region included a Magellanic sub-Region, a large Kerguelen Sub-Region and a separate district for Tristan da Cunha and Gough Islands (Map 3).

Hedgpeth's biogeographic scheme, which was very close to Knox (1960)'s proposal for littoral regions, was widely accepted by subsequent workers analysing patterns at the level of the whole benthic fauna (e.g., White 1984; Arntz *et al.* 1997; Clarke & Johnston 2003) or at the level of particular taxa.

Soon after Hedgpeth's contributions (1969, 1970, 1971), Dell (1972) published a comprehensive analysis of the Antarctic benthos, and critically reviewed the previous biogeographic schemes. He supported in general Hedgpeth's scheme, but at the same time drew attention to the difficulties to properly define and delineate biogeographic provinces valid for many different organisms, bathymetric regions, or isolated islands. His view of the East Antarctic sub-region, including part of the Weddell and Bellingshausen Seas, is similar to Kussakin's view. In contrast to the findings of Hedgpeth and Knox, he considered Heard Island – located south of the Antarctic Convergence - as essentially sub-Antarctic, like Kerguelen and Macquarie Islands.



Introduction Map 4 The Antarctic and sub-Antarctic biogeographic regions according to Briggs & Bowen (2012). South American Provinces: SC : Southern Chile, TF : Tierra del Fuego, SA : Southern Argentina, and F : Falkland Islands. Sub-Antarctic Provinces: SG: South Georgia, B: Bouvet Island, PE: Prince Edward Islands, C: Crozet Islands, K: Kerguelen Islands, and M: Macquarie Island. Antipodes Province: NZI (Auckland, Antipodes, Campbell and Bounty Islands), NZ: New Zealand Province. The blue area indicates the cold Antarctic Region.

From a detailed analysis of the benthic Amphipoda (450 spp., 2151 records) and the Polychaeta (558 spp., 4476 records), Knox & Lowry (1977) attempted a biogeographic synthesis of the Antarctic shelf benthos (<500 m). Their affinity matrix differentiated 4 distinct areas in the Southern Ocean: 1. The Sub-Antarctic area, which includes the Auckland and Campbell Islands, Macquarie Island, Kerguelen and Heard Islands, and the Prince Edward Islands; 2. The East Antarctic area, which includes the Ross Sea, the Adélie Coast and the Davis Sea; 3. The Scotia area, which includes South Georgia and the islands of the Scotia Arc, plus the South Shetland Islands and the islands along the western coast of the Antarctic Peninsula; 4: The Magellanic area, composed of the southern tip of South America, the Falkland Islands and the Burdwood Bank.

Briggs (1974, 1995) established a system of coastal and shelf provinces for the world ocean, which was largely based on fish distributions and defined by their degree of endemism (of >10%). For the Southern Ocean the system was recently reviewed by Briggs & Bowen (2012) relying in particular on the new inputs provided by Linse *et al.* (2006), Clarke *et al.* (2007) and Griffiths *et al.* (2009). They distinguished in their "Cold-Temperate and Polar Southern Hemisphere" zone, 4 regions and 13 provinces as follows: 1. South American Region, with 4 provinces: Southern Chile, Tierra del Fuego, Southern Argentina, Falkland Islands; 2. New Zealand–Australian Region, with 3 provinces: Tasmania, New Zealand, Antipodes; 3. Sub-Antarctic Region, with 6 provinces: South Georgia, Bouvet, Crozet, Prince Edward, Kerguelen, Macquarie; 4. Antarctic Region considered a single entity, without provincial subdivision, following the suggestion by Griffiths *et al.* (2009) (Map 4).

This selective "historical" review, focusing mostly on benthos, showed the difficulties in adopting consistent concepts, methodology and terminology for establishing biogeographical subdivisions, but this has been a recurrent topic in biogeography (see the review of the biogeographic province concept by Lomolino *et al.* 2010).

Since Ekman (1953), all workers agreed on a latitudinal division between the southern part of the SO, the Antarctic zone located south of the Polar Front (or Antarctic Convergence), and a sub-Antarctic zone located north of the Polar Front, but with different northern limits and components according to the data used. Within the Antarctic zone, most authors recognised for the benthos a continental ("high Antarctic") biogeographic unit around the continent and a longitudinal division into a "West Antarctic" part, including the Peninsula and (some of) the Scotia Arc Islands, and an "East Antarctic" part, of various extent but always including the Ross Sea. South Georgia is generally considered a distinct biogeographic unit, within the Antarctic zone. Within the sub-Antarctic zone, the southernmost South American shelf is always clearly individualised (with however different northern limits), and the various oceanic islands were grouped in different ways according to the taxa investigated and the level of their knowledge. Several authors identified the West Wind Drift (now Antarctic Circumpolar Current) as the main potential dispersal factor for the sub-Antarctic fauna, which may explain the faunal links between South America and the eastward sub-Antarctic islands or between New Zealand and South America.

2.3. The last decades: time of biodiversity

Probably triggered by the application of the Rio Convention on Biological Diversity (1992) and the threats of environmental change impacts, the last two decades have seen a strong resurgence of interest for biodiversity issues and the development of macroecological approaches. An important number of biogeographic studies of Antarctic taxa were published, some quite recently in connection with the Atlas project and the development of online, open-access biodiversity databases, such as SCAR-MarBIN/ANTABIF and OBIS (www.iobis.org). We may cite the following examples, limited to contributions dealing with the whole SO benthic fauna of selected taxonomic groups: sponges : Downey *et al.* (2012) ; hydrozoans: Peña Cantero & Garcia Carroscosa (1999); sea-anemones: Rodriguez *et al.* (2007) ; cephalopods: Collins & Rodhouse (2006); gastropods and bivalves : Linse *et al.* (2006), Clarke *et al.* (2007) ; pycnogonids : Munilla & Soler Membrives (2009), Griffiths *et al.* (2011) ; crustaceans : De Broyer *et al.* (2003); mysids : Petryashov (2007); amphipods : De Broyer & Jazdzeswki (1996), De Broyer *et al.* (2007) ; isopods : Brandt (1992, 1999); decapods : Gorny (1999), Boschi & Lavio (2005); bryozoans : Barnes & Griffiths (2008), Hayward (1995) ; ophiuroids: Martín-Ledo & López-González (2014); echinoids : David *et al.* (2005); ascidians: Primo & Vasquez (2007). This renewed interest in biodiversity patterns was noticeable also in plankton, fish (e.g. Gon & Heemstra 1990) or top predators studies. For the zooplankton, the SCAR "Continuous Plankton Recorder (CPR) Survey" (see Chapter 10.3) recently published the "Zooplankton Atlas of the Southern Ocean" (Mc Leod *et al.* 2010).

We will not try to summarize here the various findings of these recent contributions as most of their authors were invited to write a synthesis chapter in this Atlas.

Other recent studies on spatial patterns were oriented toward particular ecosystems, or regions of the Southern Ocean, e.g., Brandt *et al.* (2009) and Kaiser *et al.* (2011) on bathymetric distribution of benthos, Barnes *et al.* (2006) and Hogg *et al.* (2011) on South Georgia biodiversity, Arntz *et al.* (2006) on Bouvet island, Barnes *et al.* (2008) on South Orkney archipelago biodiversity, or Koubbi *et al.* (2011) on the d'Urville Sea demersal and pelagic fish fauna, to cite just a few.

Some more general overviews of patterns and processes of the SO biodiversity distribution were provided by Clarke (2008); Griffiths (2010); Convey *et al.* (2012, 2014); and Kaiser *et al.* (2013). In addition, Griffiths *et al.* (2009) attempted to generalise the SO benthic biogeography.

The first insights to the Southern Ocean deep sea biogeography were given by Brandt *et al.* (2007a, b, 2012) reporting the significant results of the ANDEEP campaigns in the deep basins of the Weddell and Scotia Seas. These investigations revealed high level of unknown abyssal biodiversity and showed that bathymetric and biogeographic trends varied between taxa. They also indicated that the Antarctic abyssal fauna has stronger links with other oceanic abyssal basins (particularly in the Atlantic) than with the Antarctic shelf fauna, but this is mainly valid for taxa with good dispersal capabilities. On the contrary, the poor dispersers include many species with high apparent SO endemism.

2.4. Ecosystem biogeography or the macroecological approach

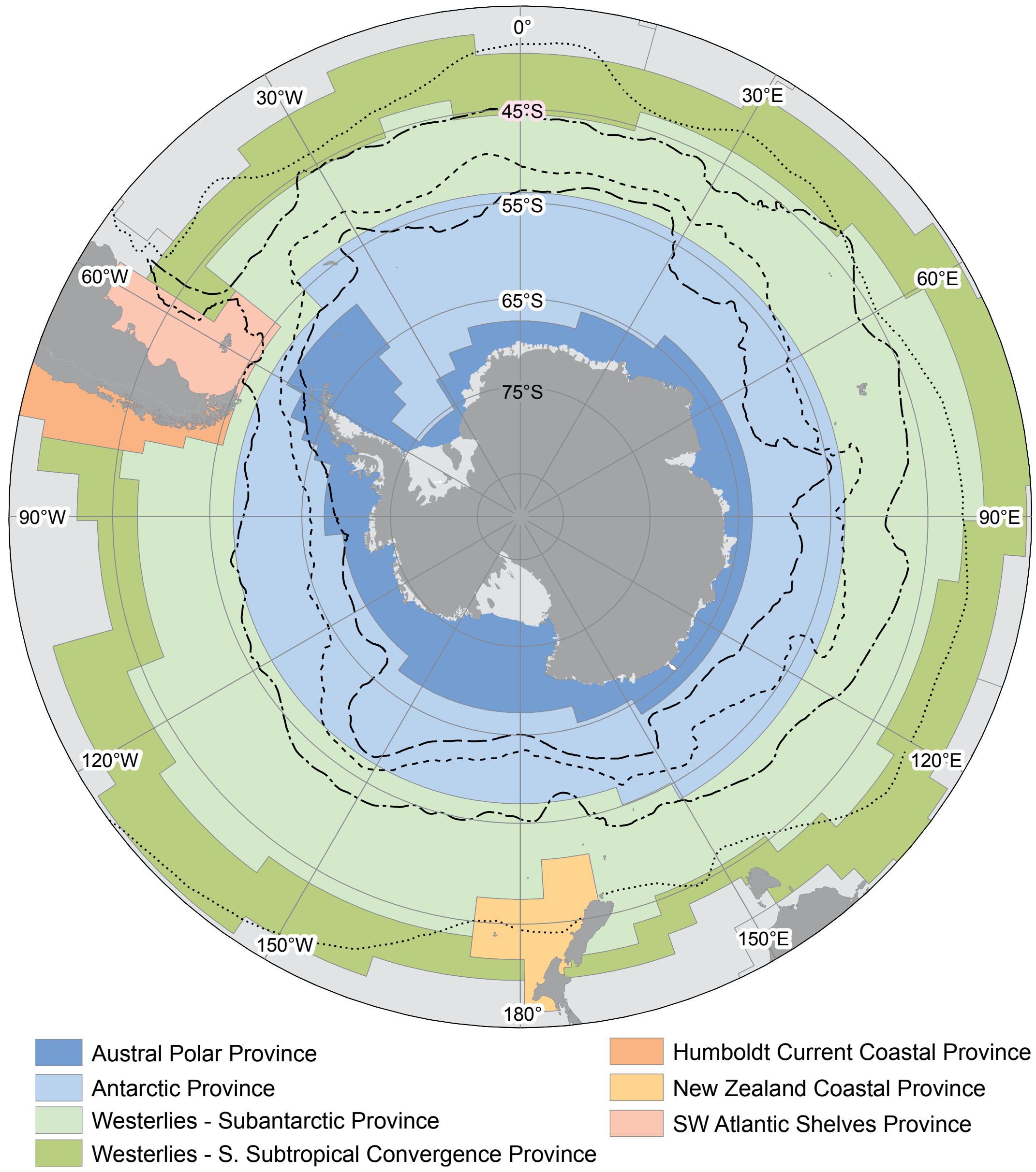
Departing from the classical faunistic and floristic approach of biogeography, i.e. the "compositionist" approach, there were recent attempts to establish biogeographic classifications by reference to the characteristics of regional marine ecosystems, shaped by hydrographic features, oceanographic and bio-geochemical processes (i.e. the "functionalistic" approach).

The "ecological geography of the sea". Longhurst (2007) proposed a new "ecological geography of the sea" based on regional oceanographic characteristics and on pelagic bio-geochemical data obtained from satellite imagery and *in situ* data. This classification, mostly applicable to the pelagic realm, identified seven biogeochemical provinces south of the Sub-Tropical Front, among the 50 provinces in 4 major biomes (Polar, Westerlies, Trades and Coastal) detected in the global ocean.

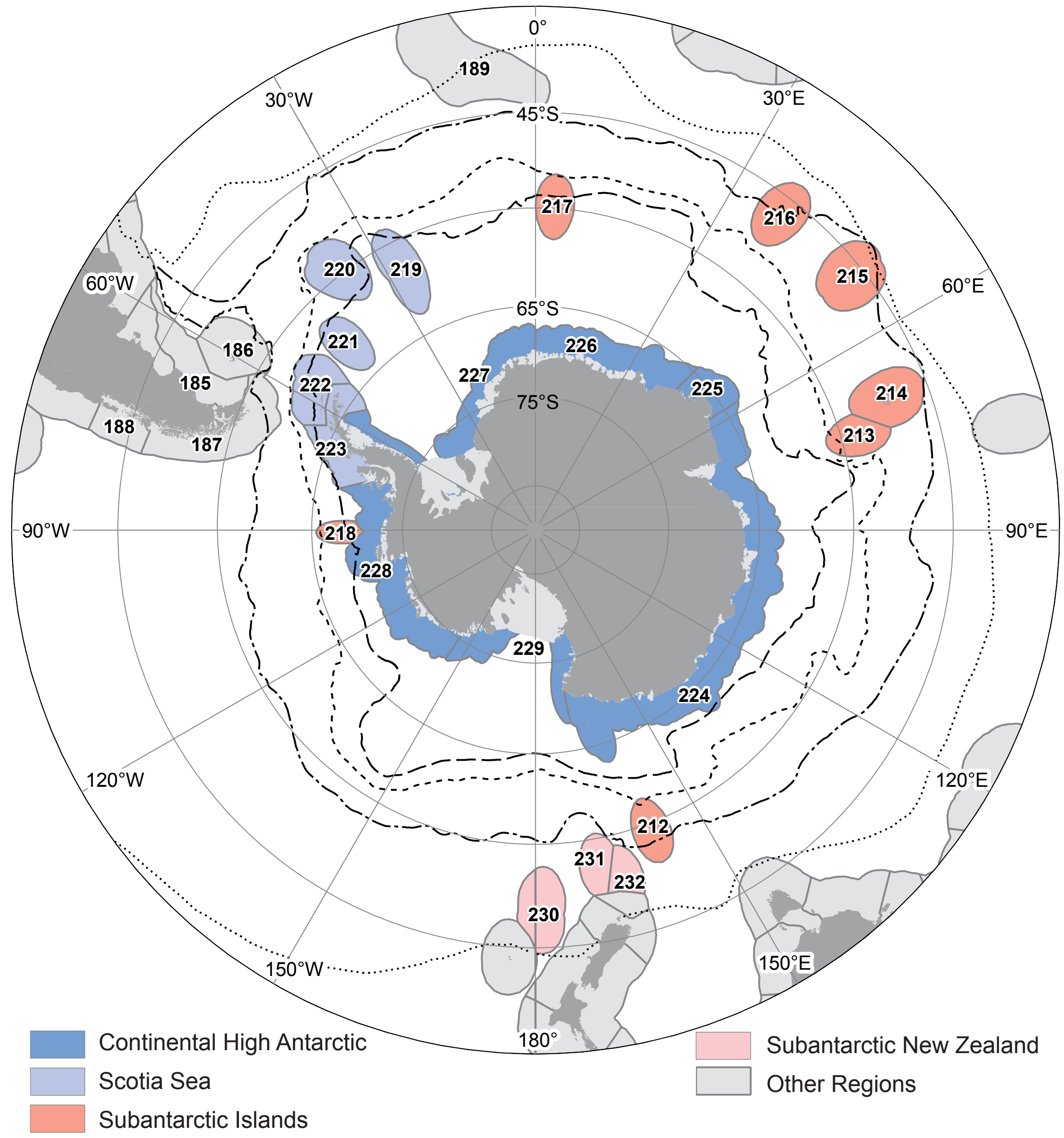
Within the "Polar Biome", two provinces have been defined south of the Polar Front. The "Austral Polar Province" comprises the seasonally ice-covered sea from the coasts of the continent to the level of the Antarctic Divergence at 60-65°S and includes the Antarctic Peninsula as well as the Scotia Arc islands of South Orkney, South Sandwich and South Georgia. The "Antarctic Province" is an annular province lying between the Antarctic Divergence and the Polar Front at about 55°S, which is synonymous with the southern branch of the Antarctic Circumpolar Current (ACC). The Bouvet, Kerguelen and Heard islands are attributed to this province.

North to the Polar Biome lies the "Antarctic Westerly Winds Biome", which includes the "Sub-Antarctic Water Ring Province" that is formed by the northern flow of the circumpolar ACC lying between the Sub-Tropical Front and the Polar Front and covering the Sub-Antarctic Zone and the Polar Frontal Zone. It is circled to the north by the "South Sub-Tropical Convergence Province" that covers the entire Sub-Tropical Convergence Zone at about 35-45°S, marking the boundary between waters of sub-Tropical and sub-Antarctic origin. The Patagonian shelf and the Falkland plateau are parts of the "Southwest Atlantic Shelves Province" within the "Atlantic Coastal Biome". This province extends from the latitude of Mar del Plata (38°S) to the tip of Tierra del Fuego at 55°S. On the Pacific side, the south Chilean waters are included in the "Humboldt Current Coastal Province" within the "Pacific Coastal Biome". The sub-Antarctic islands of New Zealand on the Campbell and Bounty plateaus are part of the "New Zealand Coastal Province" within the same "Pacific Coastal Biome" (Map 5).

The Large Marine Ecosystems of the World. With a perspective to support the application of practical management issues for the marine ecosystem goods and services, the system of "Large Marine Ecosystems" (LME) (http://www.lme.noaa.gov) was conceived by a number of regional experts to classify relatively large marine regions (on the order of 200,000 km2 or greater), characterized by distinct bathymetry, hydrography, productivity, and trophic relationships. Based on these four ecological criteria, 64 LME's have been delineated around the



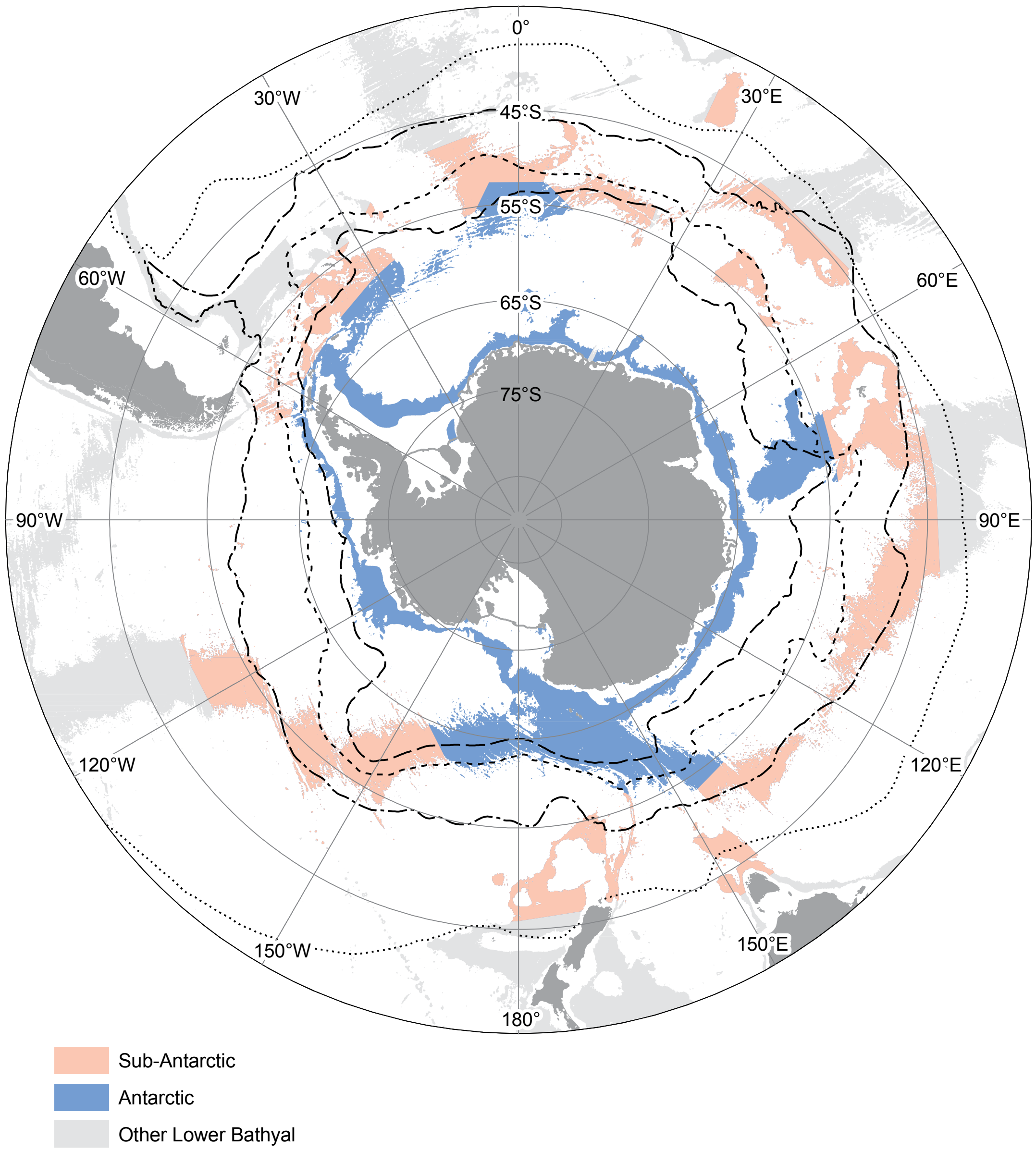
Introduction Map 5 The biogeochemical provinces of the Southern Ocean according to Longhurst (2007).

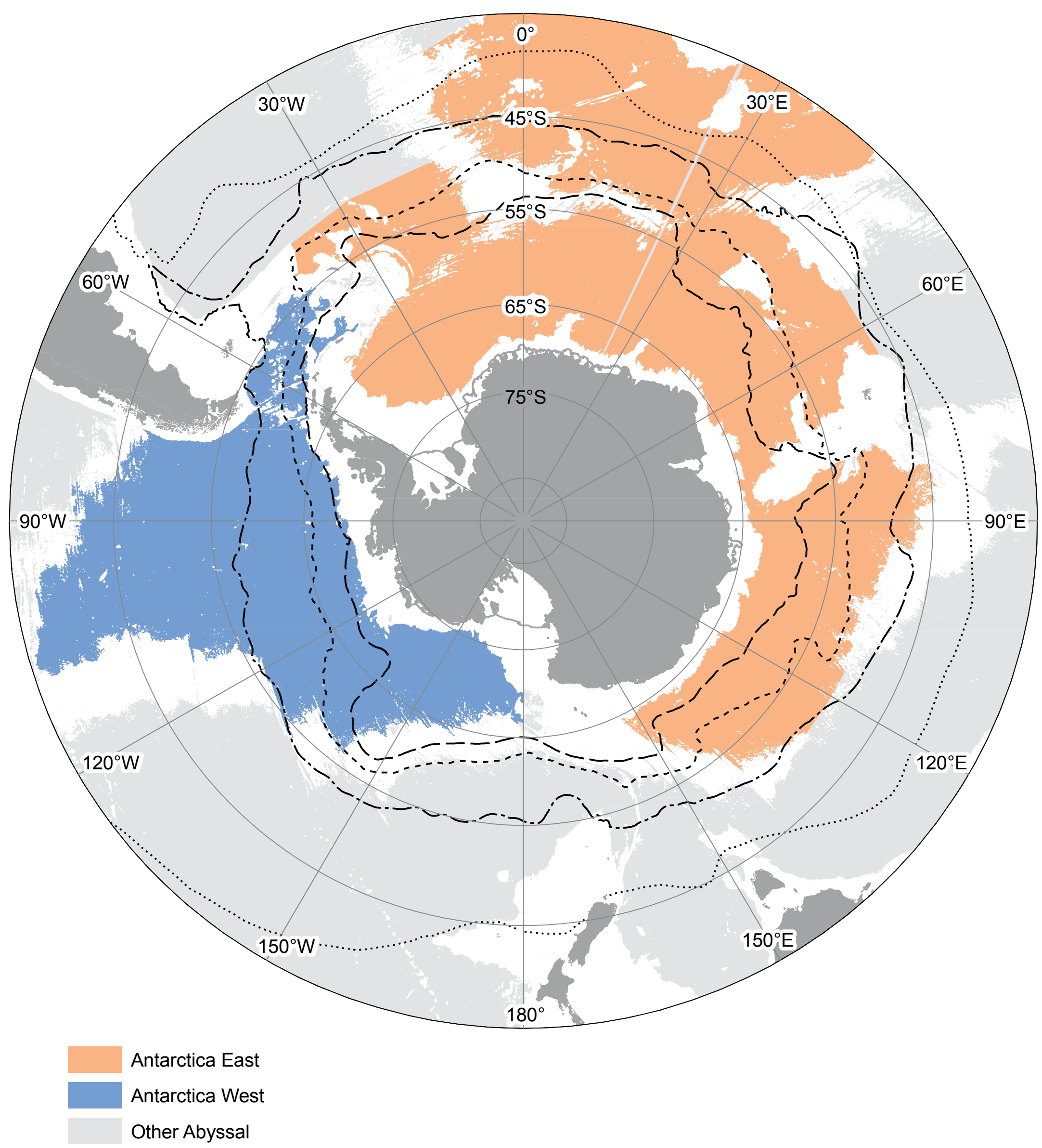


Introduction Map 6 The Southern Ocean marine ecoregions according to Spalding *et al.* (2007).The numbering of ecoregions followed the "MEOW" nomenclature.

Southern Ocean realm: Continental High Antarctic province: 224. East Antarctic Wilkes Land; 225. East Antarctic Enderby Land; 226. East Antarctic Dronning Maud Land; 227. Weddell Sea; 228. Amundsen/Bellingshausen Sea; 229. Ross Sea. **Scotia Sea province**: 219. South Sandwich Islands; 220. South Georgia; 221. South Orkneys Islands; 222. South Shetland Islands; 223. Antarctic Peninsula. **Sub-Antarctic Islands province:** 212. Macquarie Island; 213. Heard and McDonald Islands; 214. Kerguelen Islands; 215. Crozet Islands; 216. Prince Edward Islands; 217. Bouvet Island; 218. Peter I Island. **Sub-Antarctic New Zealand province**: 230. Bounty and Antipodes Islands. 231. Campbell Island; 232. Auckland Island.**Temperate South America realm: Magellanic province:** 185. Patagonian Shelf; 186. Falklands/Malvinas; 187. Channels and Fjords of Southern Chile; 188. Chiloense. (map source: http://www.worldwildlife.org/science/ecoregions/marine/item1266.html)

Introduction Map 7 The bathyal provinces (801 to 3500 m) of the Southern Ocean according to Watling *et al.* (2013). The Antarctic Province encompasses all the slope and ridge areas around the Antarctic continent connected by Circumpolar Deep Water. The Sub-Antarctic Province extends northward around the Southern Ocean, encompassing a 10–20° of latitude band from 40–45°S to 55–60°S; defined by the extent of 1–2°C Circumpolar Deep Water.





Introduction Map 8 The abyssal provinces (>3500 m) of the Southern Ocean according to Watling *et al.* (2013). The Antarctica East Province include the areas where very cold bottom water flows into the adjacent basins (Cape, Agulhas, Natal, Crozet, and South Indian Basins). The Antarctica West Province includes the Amundsen Plain in the region from the Ross Sea to the Antarctic Peninsula and north to the Antarctic-Pacific Ridge and the Southeast Pacific Basin.

ocean coastal margins. The Antarctic LME (# 61) includes the shelf around the continent (with the Peninsula) to a depth of 1000 m. The Patagonian Shelf (LME # 14) extends from the southernmost tip of South America to north of the mouth of Rio de la Plata and includes the Falkland Islands.

The "Marine Ecoregions of the World". Aiming at supporting global and regional strategies for the conservation and sustainable use of marine resources, the "Marine Ecoregions of the World" (MEOW) system consists of a bioregionalisation of coastal and shelf areas (Spalding *et al*. 2007). MEOW is a nested system of 12 realms, 62 provinces and 232 ecoregions, based on "*taxonomic configurations influenced by evolutionary history, patterns of dispersal, and isolation*". The Southern Ocean is classified as one realm comprising 4 provinces (Continental High Antarctic, Scotia Sea, Sub-Antarctic Islands, Sub-Antarctic New Zealand) sub-divided into 21 ecoregions, mostly based upon Linse *et al.* (2006) results (Map 6).

The deep ocean floor. As largely confirmed by the ANDEEP results (see supra), the SO deep sea fauna clearly exhibits different composition and distribution patterns than the coastal and shelf faunas. Watling *et al.* (2013) proposed a deep-sea biogeographic classification for the lower bathyal and abyssal benthos of the global ocean. After reviewing existing classifications and data, they conducted a comprehensive analysis of high-resolution data of depths, water mass characteristics (temperature, salinity and dissolved oxygen) and particulate organic flux to the seafloor, encompassing two large bathymetric zones: the lower bathyal, set at 801–3500 m, and the abyssal, 3501–6500 m. Due to the limitation of available biotic data, these physical and chemical proxies were selected as potential good predictors of the distributions of deep-sea floor organisms. This process resulted in the delineation of 14 lower bathyal and 14 abyssal provinces, which are "*to be considered as hypothetical*", and "*need to be tested with species distribution data*" (Maps 7, 8).

3. The Biogeographic Atlas project

Taking advantage of an unprecedented amount, availability, diversity, and quality of biogeographic data, and of new conceptual and methodological developments in biogeography, the Atlas contributors have attempted to establish a benchmark of the Antarctic and sub-Antarctic biogeography knowledge, covering a large number of species and assemblages from the phyto- and zooplankton, macroalgae and zoobenthos, nekton, and birds and mammals top predators. More than 140 contributors (biogeographers, taxonomists, ecologists, molecular biologists, IT experts, environmental dataset providers, modellers, and GIS experts) contributed to the Atlas, under the aegis of SCAR.

This Biogeographic Atlas is based on the analysis of more than 1.07 million occurrence records of 9064 validated species from ~434,000 distinct sampling stations. It presents a collection of 66 syntheses describing the distribution patterns and processes of a significative representation of Southern Ocean organisms, illustrated by more than 800 selected distribution maps. The Atlas covered the Southern Ocean at large, south of the Sub-Tropical Front, but focused in particular to the Southern Ocean *s.s.*, the Antarctic region, south of the Antarctic Polar Front. Most analyses and syntheses relied on data south of 40°S; however, some few studies were limited to the Southern Ocean *s.s.*

Preceding the analysis and synthesis phases, the first and fundamental step of the Atlas project was to compile and database all occurrence records available from the literature (since the very beginning of Antarctic exploration), from museum collections, as well as from CAML and other recent Antarctic sampling campaigns. This required facing problems of data discovery, data quality assessment, correct interpretation and standardisation, and, vitally, required significant validation effort by numerous experts. It is important here to emphasize the key role of basic descriptive taxonomy in gaining these results. Despite being often disregarded by funding agencies, morphology-based taxonomical identification remains an essential step in biodiversity studies, and has to be supported in conjunction with molecular taxonomy in an integrative approach (see De Broyer & Danis 2011).

This wealth of expert-validated data has been made publicly available on the SCAR-MarBIN/ANTABIF portal (www.biodiversity.aq), allowing further improvements and additions, as well as multiple uses and applications, including in particular the predictive modelling of biogeographic distributions in face of the potential impacts of environmental changes.

This "Biogeographic Atlas of the Southern Ocean" is primarily intended to fulfil the needs of biogeographic information for science, conservation, monitoring and sustainable management of the Southern Ocean, in the context of environmental changes and increasing human pressure.

In addition to this printed version, a digital dynamic version of this Atlas with further functionalities is developed on the www.biodiversity.aq portal.

Acknowledgments

We are grateful to Huw Griffiths (BAS, Cambridge) and Ben Raymond (AAD, Hobart) for the preparation of the maps. This is CAML contribution # 88.

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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.

Huw GRIFFITHS is a marine Biogeographer at the British Antarctic Survey. He created and manages SOMBASE, the Southern Ocean Mollusc Database. His interests include large-scale biogeographic and ecological patterns in space and time. His focus has been on molluscs, bryozoans, sponges and pycnogonids as model groups to investigate trends at high southern latitudes.

Cédric d'UDEKEM d'ACOZ is a research scientist at the Royal Belgian Institute of Natural Sciences, Brussels. His main research interests are systematics of amphipod crustaceans, especially of polar species and taxonomy of decapod crustaceans. He took part to 2 scientific expeditions to Antarctica on board of the *Polarstern* and to several sampling campaigns in Norway and Svalbard.

Bruno DANIS is an Associate Professor at the Université Libre de Bruxelles, where his research focuses on polar biodiversity. Former coordinator of the scarmarbin. be and antabif.be projects, he is a leading member of several international committees, such as OBIS or the SCAR Expert Group on Antarctic Biodiversity Informatics. He has published papers in various fields, including ecotoxicology, physiology, biodiversity informatics, polar biodiversity or information science.

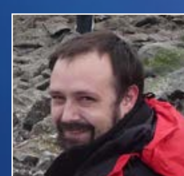
Susie GRANT is a marine biogeographer at the British Antarctic Survey. Her work is focused on the design and implementation of marine protected areas, particularly through the use of biogeographic information in systematic conservation planning.

Christoph HELD is a Senior Research Scientist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven. He is a specialist in molecular systematics and phylogeography of Antarctic crustaceans, especially isopods.

Falk HUETTMANN is a 'digital naturalist' he works on three poles (Arctic, Antarctic and Hindu-Kush Himalaya) and elsewhere (marine, terrestrial and atmosphere). He is based with the university of Alaska-Fairbank (UAF) and focuses primarily on effective conservation questions engaging predictions and open access data.

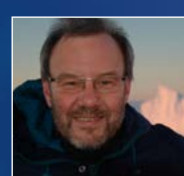
Philippe KOUBBI is professor at the University Pierre et Marie Curie (Paris, France) and a specialist in Antarctic fish ecology and biogeography. He is the Principal Investigator of projects supported by IPEV, the French Polar Institute. As a French representative to the CCAMLR Scientific Committee, his main input is on the proposal of Marine Protected Areas. His other field of research is on the ecoregionalisation of the high seas.

Ben RAYMOND is a computational ecologist and exploratory data analyst, working across a variety of Southern Ocean, Antarctic, and wider research projects. His areas of interest include ecosystem modelling, regionalisation and marine protected area selection, risk assessment, animal tracking, seabird ecology, complex systems, and remote sensed data analyses.



Anton VAN DE PUTTE works at the Royal Belgian Institute for Natural Sciences (Brussels, Belgium). He is an expert in the ecology and evolution of Antarctic fish and is currently the Science Officer for the Antarctic Biodiveristy Portal www. biodiversity.aq. This portal provides free and open access to Antarctic Marine and terrestrial biodiversity of the Antarctic and the Southern Ocean.

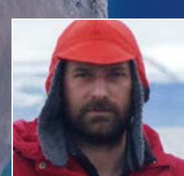
Bruno DAVID is CNRS director of research at the laboratory BIOGÉOSCIENCES, University of Burgundy. His works focus on evolution of living forms, with and more specifically on sea urchins. He authored a book and edited an extensive database on Antarctic echinoids. He is currently President of the scientific council of the Muséum National d'Histoire Naturelle (Paris), and Deputy Director at the CNRS Institute for Ecology and Environment.



Julian GUTT is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board Polarstern. He is member of the SCAR committees ACCE and AnT-ERA (as chief officer). Main focii of his work are: biodiversity, ecosystem functioning and services, response of marine systems to climate change, non-invasive technologies, and outreach.

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.