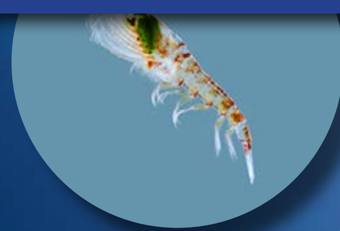
Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 10.1. BENTHIC REGIONAL CLASSIFICATION.

Douglass L.L., Beaver D., Raymond B., Constable A.J., Brandt A., Post A., Kaiser S., Grantham H.S., Nicoll R.A., 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. 414-417.



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Claude DE BROYER & Philippe KOUBBI (chief editors)

with Huw GRIFFITHS, Ben RAYMOND, Cédric d'UDEKEM d'ACOZ, Anton VAN DE PUTTE, Bruno DANIS, Bruno DAVID, Susie GRANT, Julian GUTT, Christoph HELD, Graham HOSIE, Falk HUETTMANN, Alexandra POST & Yan ROPERT-COUDERT

SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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

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

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Published by:

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

Publication funded by:

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

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

Publication supported by:

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

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

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

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

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

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

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

Online dynamic version :

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

Recommended citation:

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.

10.1. Benthic Regional Classification

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1. Introduction

Regional classification analyses aim to identify biogeographic patterns, by spatially subdividing an area such that assemblage compositions can be expected to be similar within each region relative to adjacent regions. Here we outline a regional classification of the Southern Ocean benthos, intended for general use in spatial planning and management. Full details are provided by Douglass *et al*. (in press).

Ideally, regional classification analyses would be mostly based on biological data. However, on a circum-Antarctic scale, such data are limited especially within the Amundsen Sea, eastern Antarctica, below 1500 m and under ice shelves (chapter 5.29, Brandt *et al.* 2007, Griffiths 2010, Gutt *et al.* 2013). Where biological data are insufficient, environmental data combined with an appropriate classification method can be used and guided by what is known about the regions ecology and biogeography (Pressey & Bottrill 2009, Delegations of Australia & France 2011). In these cases, the method used should enhance the biological relevance of the results. Where the relationships between the distribution of benthos and abiotic factors can be reasonably inferred, they can be manually incorporated to delineate regions rather than relying on an automated unsupervised (purely data-driven) classification (e.g. clustering, Whiteway *et al.* 2007). For instance, the continental shelf usually supports distinct species assemblages when compared to the deeper ocean (Brandt *et al*. 2007, Kaiser *et al*. 2011, Koubbi *et al*. 2011).

Marine habitat conditions, and thus the abundance and distribution of taxa, are largely driven by physical and chemical processes, including those that affect the connectivity between similar habitats. Two main environmental drivers are depth and geomorphology (Barry *et al.* 2003, Beaman & Harris 2005, Post *et al.* 2010, Kaiser *et al.* 2011, Koubbi *et al.* 2011). Other important drivers include seabed temperature, icebergs and sea ice cover, sea-surface productivity and ocean currents (Gutt 2001, Gili *et al.* 2006, Gutt 2007, Hall & Thatje 2011). Refer to chapter 4 for more detail of these environmental drivers and their influence on Southern Ocean taxa.

The biogeography of species and the genetic connectivity between subpopulations is strongly linked to the ability of individuals to move or disperse away from their parents. Divergent evolution of similar taxa can occur from reduced connectivity. The distance between suitable habitats, steep environmental clines and geomorphic features can be barriers that constrain this dispersal ability. For benthic organisms, long-distance dispersal is confined by transport during pelagic larval stages and the passive oceanic transport of adults or via turbidites termed rafting (Bradbury & Snelgrove 2001). Habitats will support different species assemblages where the distance between them is greater than the dispersal ability of species. Strong circum-Antarctic currents will facilitate the transport of some species but the probability of travelling long distances will be constrained by biotic interactions (e.g. predation, parasitism and starvation), especially for species with non-feeding larvae. The benthic assemblages of the Southern Ocean have a higher proportion of species with either brooding or non-feeding larval development relative to those species with feeding pelagic larvae (Thatje *et al.* 2005). Furthermore, some widely dispersive species have shown strong genetic variation suggesting higher heterogeneity at a finer spatial scale (Wilson *et al.* 2007, Hoffman *et al.* 2010, Arango *et al.* 2011). Steep ecoclines, geomorphic barriers and oceanography can also cause ecological and genetic differentiation. For example, genetic differentiation is suggested to be linked to seabed temperature changes even over short distances (Arango *et al.* 2011), and the inhibition of adult migration by geomorphic features (Shaw *et al.* 2004). Depth-related factors, habitat fragmentation and oceanography such as frontal systems can be barriers to gene flow (Grebmeier & Barry 1991, Thornhill *et al.* 2008, Matschiner *et al.* 2009, Hoffman *et al.* 2010, White *et al.* 2010). The ecological dynamics of populations can be spatially restricted where gene flow is hindered.

For cosmopolitan species that are distributed across wide spatial ranges, a regional classification may falsely subdivide their distribution. However, the focus of such a classification, especially one intended for conservation planning purposes, is to identify general patterns of assemblages and areas associated with species that have restricted ranges or are endemic. Furthermore, there is increasing evidence from molecular studies that widely distributed Antarctic shelf and deep-sea assemblages contain species complexes with each species having a more restricted range. For example, isopods (Held 2003, Held & Wägele 2005, Leese *et al.* 2008), crinoids (Wilson *et al.* 2007), and ophiuroids (Hunter & Halanych 2008).

2. Methods

The study area for the analysis was bounded by the Antarctic ice shelf and the outer boundary of the area administered by the Commission for the Conservation of Antarctic Marine Living Resources which approximates the position of the polar front (Grant *et al.* 2006).The data used are listed in Table 1, and Douglass *et al*. (in press) discusses the analysis methods used in more detail.

The regionalisation was based on the hierarchical classification of Last *et al*. (2010) and includes the identification of ecoregions, bathomes and environmental types. Ecoregions are the broadest spatial unit which, in a similar manner to the East Antarctic marine protected area planning process (Delegations of Australia & France 2011), were delineated by accounting for patterns of endemism, recent biogeographic research, and the influence of environmental drivers as potential barriers to dispersal. Bathomes are depth ranges based on the depth strata of known species distributions. Geomorphic features classify the seabed according to its surface attributes, which are shaped by geological, sedimentary and oceanographic processes. These features influence the types of benthic organisms that can live there (Harris & Baker, 2012). Environmental types are the finest level of the spatial hierarchy, and refer to each unique combination resulting from nesting geomorphic features within bathomes for each ecoregion. This nesting avoids the potential for false within-class homogeneity that can arise if such features are not modified by depth (Williams *et al.* 2009). Ecoregions, bathomes and geomorphic features were defined according to the processing steps described below.

Table 1 Circumpolar datasets used within the classification. See Chapter 4 for further details.

Data	Source
Depth	Smith & Sandwell (2010)
Geomorphology	O'Brien *et al.* (2009)
Seafloor temperature	Clarke *et al.* (2009)
Sea-surface chlorophyll	Feldman & McClain (2010)
Sea ice concentration	Spreen *et al.* (2008)
Frontal systems	Sokolov & Rintoul (2009)

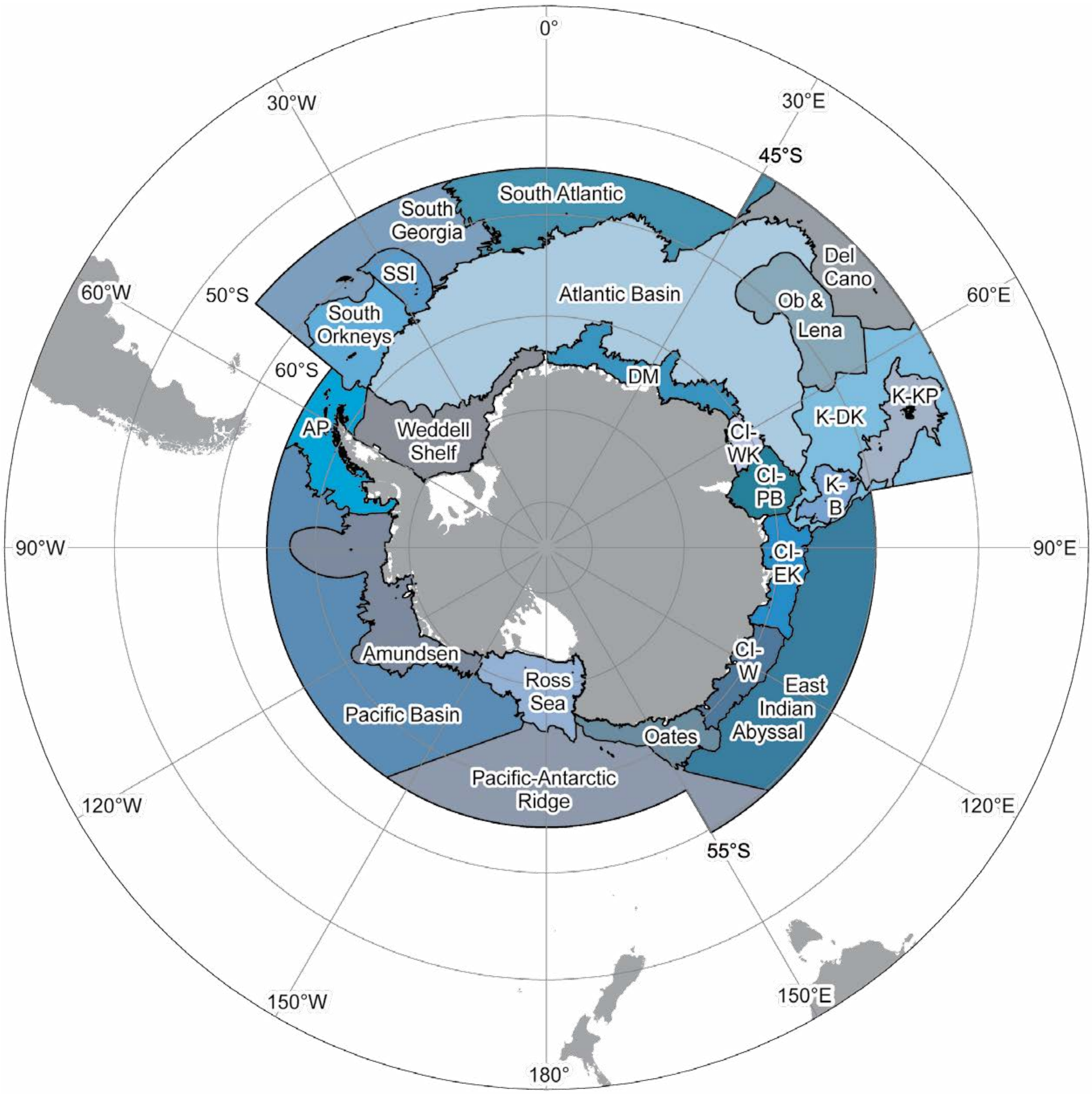
2.1. Benthic ecoregions

We initially separated the distinct environment of the Antarctic continental shelf and slope from the deeper ocean using the 4000 m contour. Bathomes were applied later to further account for the depth distribution of species. Where possible, previously defined regions, which occur primarily on the Antarctic continental shelf and slope, were reviewed and incorporated (especially Grant *et al.* 2006, Linse *et al.* 2006, Clarke *et al.* 2007, Spalding *et al.* 2007, Griffiths *et al.* 2009, Constable *et al.* 2010). These boundaries were maintained if levels of endemism greater than 10% were reported by Linse *et al.* (2006) or Griffiths *et al.* (2009). Where appropriate, previously defined boundaries were altered to better reflect bathomes and geomorphic features.

Ecoregion boundaries within the deeper ocean were defined by considering the effects of environmental drivers on patterns of biodiversity. It is assumed that the spatial separation of similar habitat types increases the likelihood that these habitats support genetically dissimilar species due to isolation. Therefore, for areas without previously defined ecoregions, we identified ecoregion boundaries by dividing areas of similar habitat types (predominantly bathomes and geomorphic features) that were separated by more than 200 km (Palumbi 2004, Halpern *et al.* 2006). All data layers were then used to corroborate or refute the validity of these regions.

2.2. Bathomes

Bathomes are broad-scale depth classes based on the depths at which there are expected to be rapid transitions in assemblage composition. We identified those depths based on available depth-species relationship studies within the Southern Ocean. Studies included but were not limited to the research of Williams & de la Mare (1995), Munilla León (2001), Peña Cantero (2004), Beaman & Harris (2005), Brandt *et al.* (2009), Duhamel & Hautecoeur (2009), Kruse *et al.* (2009), Barnes & Kuklinski (2010), and Post *et al.* (2010).



AP: Antarctic Peninsula
CI-EK: Central Indian - East Kerguelen Subregion
CI-PB: Central Indian - Prydz Bay Subregion
CI-W: Central Indian - Wilkes Subregion
CI-WK: Central Indian - West Kerguelen Subregion
DM: Dronning Maud
K-B: Kerguelen - Banzare Bank Subregion
K-DK: Kerguelen - Deep Kerguelen Subregion
K-KP: Kerguelen - Kerguelen Plateau Subregion
SSI: South Sandwich Islands

Map 1 The benthic ecoregions identified within the Southern Ocean.

2.3. Geomorphic features

The geomorphic features used are described in chapter 4. We converted the mapped line 'canyon axes' (O'Brien *et al.* 2009), to areas by applying a 5 km buffer around the axes to capture both the canyon and its surrounding zone of influence. Since depth modification of geomorphology is captured by the hierarchical classification analysis, 'wave affected banks' and 'shelf banks' were reclassified as 'banks'.

3. Discussion

We identified 23 benthic ecoregions and 9 bathomes (Map 1, Table 2). The existing geomorphology mapping identified 30 geomorphic feature types. These three datasets were combined within a hierarchical framework to identify finer scale environmental types. The spatial dataset and supplementary details of the results are provided (see Douglass *et al.* in press). The nine bathome depth ranges identified were:

1. 0–100 m
2. 100–200 m
3. 200–500 m
4. 500–1000 m
5. 1000–1500 m
6. 1500–2000 m
7. 2000–3000 m
8. 3000–4500 m
9. 4500 m+

Many of the broad patterns of the data incorporated within the analysis are reflected in the ecoregion boundaries. Generally, ecoregion boundaries most closely resemble depth, geomorphology and seabed temperature. Productivity and ice cover tend to show a stronger within-ecoregion variation. In the shallower shelf and slope regions of the Southern Ocean, where survey effort is higher, biological data of species distributions (in the form of past biogeographical studies) were the key drivers of ecoregion delineation. Therefore, our results broadly reflect Spalding *et al.* (2007); Constable *et al.* (2010) and Clarke *et al.* (2007). Within the deeper environments of the Southern Ocean, the distribution of rare and mostly isolated shallow habitats often associated with seamounts, seamount ridges, plateaus and islands were the primary drivers of the classification. Mid-ocean ridges and large plateaus that separate deeper habitats were also important.

The classification described here provides a whole of Southern Ocean context for patterns found in previous studies. It differs from most other recent benthic biogeographic studies (examples include Linse *et al.* 2006 and Spalding *et al.* 2007) by incorporating the deeper environments as well as shallower shelf and island regions. The classification presented here incorporates known or inferred relationships between the benthic biology and the physical environment and their influence on barriers to dispersal. Furthermore, it offers a classification of the seabed habitats contained within

Table 2 Benthic Ecoregions and their features.

Benthic Ecoregion	Features
Amundsen	The productive shelf and polynyas of the Amundsen and Bellingshausen seas. The oceanic shallow environments of Peter I Island, de Gerlache Seamounts and the Marie Byrd Seamount group.
Antarctic Peninsula	The shallow, productive shelf of the west Antarctic Peninsula with a low duration of sea ice cover and warm seabeds relative to other Antarctic shelf areas. The island ecosystems of the South Shetland Islands.
Atlantic Basin	The very deep and very cold rugose ocean floor and abyssal plain of the South Atlantic Ocean Basin and Weddell Sea.
Central Indian - East Kerguelen Subregion	Central Indian region of East Antarctica that is influenced by the Kerguelen Plateau including downstream productivity from frontal activity across the Kerguelen Plateau (Delegations of Australia and France 2011).
Central Indian - Prydz Bay Subregion	Central Indian region of East Antarctica that contains the cold, productive waters of Prydz Bay and the Prydz Gyre which oceanographically separates the east Kerguelen and west Kerguelen Central Indian subregions (Delegations of Australia and France 2011).
Central Indian - West Kerguelen Subregion	Central Indian region of East Antarctica that is not influenced by the Kerguelen Plateau nor the Weddell Gyre (Delegations of Australia and France 2011).
Central Indian - Wilkes Subregion	Central Indian region of East Antarctica that is oceanographically separated from the Central Indian-East Kerguelen subregion (Nicol *et al.* 2000, Delegations of Australia and France 2011).
Del Cano	The shallow, warm seabeds in the Subantarctic Frontal Zone including the South West Indian Ridge seamounts, the Del Cano Rise and the Crozet and Prince Edward Islands.
Dronning Maud	Maud Rise and associated open ocean polynya, Astrid Ridge, Gunnerus Ridge and the canyons offshore Dronning Maud Land. Easternmost extent of the Weddell Gyre.
East Indian Abyssal	The very deep and cold seabeds of the rugose ocean floor and abyssal plains of the South Indian Ocean Basin.
Kerguelen - Banzare Bank Subregion	Shallower (mostly depths between 1000 m to 3000 m), warmer seabeds of the Banzare Bank, south of the frontal activity of the Fawn Trough.
Kerguelen - Deep Kerguelen Subregion	Deep (mostly depths greater than 3000 m) ocean surrounding the Kerguelen Plateau and Banzare Bank.
Kerguelen - Kerguelen Plateau Subregion	Shallower (mostly depths between 200 m to 3000 m), warmer seabeds of the Kerguelen Plateau, north of the frontal activity of the Fawn Trough.
Oates	Oceanographically separated from the Central Indian - Wilkes subregion with wind and sea ice vectors diverging at its western border (Delegations of Australia and France 2011). The eastern border is adjacent to the Ross Sea region (Clarke *et al.* 2007, Spalding *et al.* 2007, Ainley *et al.* 2010).
Ob and Lena	Shallow, warm seabeds in the Polar Frontal Zone, including the Ob and Lena banks and the seamounts to their east.
Pacific Basin	The very deep rugose ocean floor and abyssal plains of the South Pacific Ocean Basin which is warmer than other deep ocean basin regions of the Southern Ocean.
Pacific-Antarctic Ridge	The Pacific-Antarctic Ridge region with large extents of shallower environments of depths less than 2000 m.
Ross Sea	Very cold seabed and high sea ice duration of the productive Ross Sea.
South Atlantic	Shallower environments of the Mid Atlantic Ridge and associated seamounts.
South Georgia	Productive, shallow environments in the Polar Frontal Zone including the island ecosystems of South Georgia Island and the seamounts of the North Scotia Ridge.
South Orkney Islands	The island ecosystems of the South Orkney Islands and the seamounts and plateaus of the South Scotia Arc, many of which underlie the Southern Antarctic Circumpolar Current Frontal Zone.
South Sandwich Islands	Highly productive island ecosystems of the South Sandwich Islands and the deeper waters of the South Sandwich Trench.
Weddell Shelf	Very cold seabed and high sea ice duration of the productive Weddell shelf, usually rather deep, ~ 500 m, at places even 1000 m depth.

each ecoregion. This new circum-Antarctic map of environmental types can be used to support spatial management aimed at conserving benthic biodiversity across the whole of the Southern Ocean.

Acknowledgments

This is CAML contribution #148.

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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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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.

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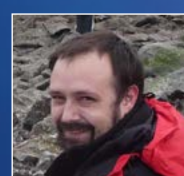

Anton VAN DE PUTTE works at the Royal Belgian Institute for Natural Sciences (Brussels, Belgium). He is an expert in the ecology and evolution of Antarctic fish and is currently the Science Officer for the Antarctic Biodiveristy Portal www. biodiversity.aq. This portal provides free and open access to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

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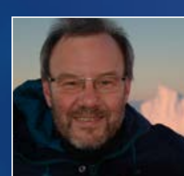
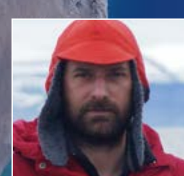


Julian GUTT is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board Polarstern. He is member 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.