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) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biodiversity.

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future biodiversity patterns and assessing the potential for species range shifts. The Biogeographic Atlas of the Southern Ocean provides a unique opportunity to access high-quality data, visualisations and interactive tools for a comprehensive understanding of the Southern Ocean biota.

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.

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 biodiversity information by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS) and the Marine Biodiversity Information Network (SCAR-MarBIN) as part of the World Register of Marine Species (WoRMS). The project was launched 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 Census of Antarctic Marine Life (CAML)

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq. Through maps, graphs and visualisations, it will be possible to explore biodiversity patterns in the Southern Ocean, from the pelagic to the benthic environment, and to gain insights into the underlying processes that drive these patterns. The atlas will be a valuable tool for researchers, conservationists and policymakers, and will contribute to the development of strategies for the sustainable management of biodiversity in the Southern Ocean.
THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN


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).

Edited by:
Claude De Broyer (Royal Belgian Institute of Natural Sciences, Brussels)
Philippe Koubbi (Université Pierre et Marie Curie, Paris)
Huw Griffiths (British Antarctic Survey, Cambridge)
Ben Raymond (Australian Antarctic Division, Hobart)
Cédric d’Udekem d’Acoz (Royal Belgian Institute of Natural Sciences, Brussels)
Anton Van de Putte (Royal Institute of Natural Sciences, Brussels)
Bruno Danis (Université Libre de Bruxelles, Brussels)
Bruno David (Université de Bourgogne, Dijon)
Susie Grant (British Antarctic Survey, Cambridge)
Julian Gutt (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven)
Christoph Held (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven)
Graham Hosie (Australian Antarctic Division, Hobart)
Falk Huettmann (University of Alaska, Fairbanks)
Alix Post (Geoscience Australia, Canberra)
Yan Ropert-Coudert (Institut Pluridisciplinaire Hubert Curien, Strasbourg)

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.

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, Belgium (www.altitude-design.be)

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

Cover pictures: amphipod crustacean (Epimeria rubriques 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:

For individual chapter:


This publication is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License.
Contents

PART 1. INTRODUCTION
1.1. The biogeography of the Southern Ocean (C. De Broyer, P. Koubbi)........................................................................................................................... 1
1.2. The Census of Antarctic Marine Life (CAML) (M. Stoddart)............................................................................................................................. 10

PART 2. METHODS
2.1. Data and mapping (A.P. Van de Putte, H.J. Griffiths, B. Raymond, B. Danis) .................................................................................................................. 13
2.2. Data distribution: Patterns and implications (H.J. Griffiths, A.P. Van de Putte, B. Danis) ................................................................. 16
2.3. Distribution modelling (S. Mormède, J.O. Irisson, B. Raymond) .................................................................................................................... 27

PART 3. EVOLUTIONARY SETTING
3.1. Evolutionary setting (A. Crame)............................................................................................................................................................... 31
3.2. Reconstructions of the Southern Ocean and Antarctic regions (L. Lawver, L.M. Gahagan, I. Dalziel)...................................................... 36
3.3. Palaeo-oceanography (Box) (R. Gersonde).................................................................................................................................................... 43

PART 4. ENVIRONMENTAL SETTING

PART 5. BIOGEOGRAPHIC PATTERNS OF BENTHOS
5.1. Macroalgae (C. Wiencke, C.D. Amsler, M.N. Clayton).................................................................................................................................................. 65
5.2. Benthic Foraminifera (A.J. Gooday, N. Rothe, S.S. Bowser, J. Pawlowski)............................................................................................................... 74
5.3. Antarctic free-living marine Nematodes (J. Ingels, F. Hauquier, M. Raes, A. Vanreusel)................................................................. 83
5.4. Southern Ocean Harpacticoida (Crustacea: Copepoda) (K.H. George) .................................................................................................................. 86
5.5. Porifera (D. Janussen, R.V. Downey)......................................................................................................................................................... 94
5.6. Benthic Hydroids (Cnidaria: Hydrozoa) (Á.L. Peña Cantero)........................................................................................................................................... 103
5.7. Styelasteridae (Cnidaria: Hydrozoa) (N. Bax, S. Cairns).............................................................................................................................................. 107
5.8. Antarctic Hexacorals (Cnidaria: Anthozoa: Hexacorallia) (E. Rodríguez, D.G. Fautin)............................................................. 113
5.9. Spuncula and Echiura (J.J. Saiz Salinas)....................................................................................................................................................... 117
5.10. Gastropoda (S. Schiaparelli, K. Linse)............................................................................................................................................................... 122
5.11. Bivalvia (K. Linse)....................................................................................................................................................................................... 126
5.12. Southern Ocean Octopuses (A.L. Allcock)................................................................................................................................................ 129
5.13. Polychaetes (M. Schüller, B. Ebbe)................................................................................................................................................................. 134
5.15. Benthic Ostracoda (S.M. Brandão, R.V. Dingle)....................................................................................................................................................... 142
5.16. Lophogastrida and Mysida (Crustacea: Malacostraca: Peracarida) of the Southern Ocean (V.V. Petryashov)............................................ 149
5.17. Biogeographic patterns of Southern Ocean benthic Amphipods (C. De Broyer, A. Jazdzewska)................................................... 155
5.18. Antarctic and sub-Antarctic Isopod Crustaceans (Peracarida: Malacostraca) (S. Kaiser)............................................................ 166
5.19. Tanaidacea (M. Błażewicz-Paszkowycz)......................................................................................................................................................... 173
5.20. Southern Ocean Cumacea (U. Mühlenhardt-Siegel)........................................................................................................................................... 181
5.22. Shrimps (Crustacea: Decapoda) (Z. Basher, M.J. Costello)........................................................................................................................... 190
5.23. Bryozoa (D.K.A. Barnes, R.V. Downey)...................................................................................................................................................... 195
5.25. Southern Ocean Crinoids (M. Éléaume, L.G. Hemery, M. Roux, N. Améziane).......................................................................................... 208
5.26. Echinoids (T. Sauvède, B. Pierrat, B. David)..................................................................................................................................................... 213
5.27. Ascidian fauna south of the Sub-Tropical Front (C. Primo, E. Vázquez).......................................................................................... 221
5.28. Classification and spatially explicit illustration of Antarctic macrobenthic assemblages: A feasibility study (J. Gutt, D.K.A. Barnes, S.J. Lockhart).................................................................................................................................................. 229
5.29. Southern Ocean benthic deep-sea biodiversity and biogeography (A. Brandt, A.P. Van de Putte, H.J. Griffiths)............................................ 233
6.5. Southern Ocean Squid (P.G.K. Rodhouse, H.J. Griffiths, J. Xavier) ........................................................................... 284
6.6. Southern Ocean pelagic Copepods (J.H.M. Kouwenberg, C. Razoulès, N. Desreumaux) ........................................... 290
6.7. Halocyprid Ostracods of the Southern Ocean (M.V. Angel, K. Blachowiak-Samolyk) .................................................. 297
6.8. Amphipoda: Hyperidea (W. Zeidler, C. De Broyer) ............................................................................................... 303
6.10. Sea-ice Metazoa (K.M. Swadling) ..................................................................................................................... 321

PART 7. BIOGEOGRAPHIC PATTERNS OF FISH ................................................................. 327

PART 8. BIOGEOGRAPHIC PATTERNS OF BIRDS AND MAMMALS .......................................................... 363

PART 9. CHANGES AND CONSERVATION IN THE SOUTHERN OCEAN ........................................................................ 389
9.1. Climate change and predictions on pelagic biodiversity components (F. Huettmann, M.S. Schmid) ......................... 390
9.2. Past, present and future state of pelagic habitats in the Antarctic Ocean (D. Reygondeau, F. Huettmann) ................ 497
9.4. Conservation and management (S.M. Grant, P. Koubbi, P. Penhale) ................................................................. 408

PART 10. PATTERNS AND PROCESSES OF SOUTHERN OCEAN BIOGEOGRAPHY ................................................................................................. 413
10.2. Pelagic regionalisation (B. Raymond) .................................................................................................................. 418
10.3. Near surface zooplankton communities (G. Hosie, S. Mormède, J. Kitchener, K. Takahashi, B. Raymond) .............. 422
10.4. Bipolarity (L. Allicock, H.J. Griffiths) .................................................................................................................. 431
10.5. Phylogeography (C. Held) .................................................................................................................................... 437
10.7. Phylogeographic patterns of the Southern Ocean Crinoids (Crinoidea: Echinodermata) (M. Eléaume, L.G. Hemery, N. Améziane) ........................................................................................................ 448

PART 11. THE DYNAMIC BIOGEOGRAPHIC ATLAS PROJECT ................................................................................................. 465
(B. Danis, C. De Broyer, P. Koubbi, A.P. Van de Putte)

PART 12. CONCLUSIONS : PRESENT AND FUTURE OF SOUTHERN OCEAN BIOGEOGRAPHY ......................................................................................... 469

APPENDICES .......................................................................................................................................................... 477
Appendix 1: Nematoda (Chap. 5.3)
Appendix 2: Tanaidacea (Chap. 5.19)
Appendix 3: Asteroidea (Chap. 5.24)
Appendix 4: Ascidiae (Chap. 5.27)
Appendix 5: Fish (Chap. 7)
Preface

Famous lines from the diary of explorer Robert F. Scott, 17 January, 1912: “Great God! This is an awful place, and terrible enough for us to have labored to it without the reward of priority. Now for the run home, and a desperate struggle.” Scott and his companions would starve, freeze, and die ten weeks later in an Antarctic blizzard, disheartened by the knowledge that Roald Amundsen had reached the South Pole a month before them. A century later, we know in much greater detail the gigantic ferocity of Antarctica. But, as the Biogeographic Atlas of the Southern Ocean proves, we also know the unpredicted diversity and fecundity of the waters around it, and that rewards of priority from Antarctic exploration are far from exhaustion.

Still, Antarctica does not yield secrets easily. To modernize our knowledge of the diversity and distribution of its marine life required five years of field work and then three years of analysis by about 140 researchers from all the other six continents. About equally men and women, they looked from the sea birds and the sea surface to the sea floor as deep as six thousand meters and into the sediments. They looked on and under the ice. They looked from the microplankton to the macroalgae, from the sponges and corals to the molluscs and the crustaceans, from the sea spiders and sea stars to the seals and the fish. They looked at animals living off heat and gases coming from the crust beneath the ocean as well as those that bask in the seasonal sun above and enjoy its photosynthesis. They looked at the uniquely Antarctic and the cosmopolitan.

To perceive the patterns and processes emerging from studying more than one million records of about ten thousand species, the fourteen editors of the Atlas organized knowledge on the evolutionary and environmental settings, and finally prepared the way for a gratifying chapter that synthesizes knowledge on the realms and regions of the Southern Ocean. Wizardly cartographers present the information in colorful maps that allow us to understand at a glance the grand carousel that whirls around Antarctica.

Meanwhile, wizardly geneticists using molecular clocks allow us to explore deep time as well as space. We learn about Antarctic ancestors, their kinships, and how past changes in the Southern Oceans may have sent species such as octopods venturing forth into the Pacific, Indian, and Atlantic oceans.

We also learn modesty, as do all who encounter high latitudes. We learn of regions still little explored, such as the sea named for Amundsen below the South Pacific, and taxa, such as the sea squirts (tunicates) and roundworms (nematodes). We also learn of threats to the life of the Southern Ocean, from fishing, tourism, pollution, and climate change, and proposals for new marine protected areas matching the richness of our hard-won knowledge.

This magnificent scholarly achievement comes to us because of organizations as well as individuals. The Census of Antarctic Marine Life (CAML) program of the global Census of Marine Life (2000-2010) fostered many expeditions that have provided observations, and the Scientific Committee on Antarctic Research Marine Biodiversity Information Network (SCAR-MarBIN) has carefully filtered and archived the data and made them accessible. Founded in 1958, SCAR initiates, develops, and coordinates research in the Antarctic region, and adds to its lustrous history with this volume. National organizations such as the such as the Australian Antarctic Division and the Royal Belgian Institute of Natural Sciences in turn make possible cooperative international efforts such as CAML and SCAR-MarBIN.

Finally, only the truly visionary and persistent succeed in Antarctica, and here we salute Claude De Broyer and Philippe Koubbi, chief editors. They together with their 140 co-authors prove conclusively that the Southern Ocean is not monotonously blank but a shining, stirring, diving world of anemone and albatross, jelly and whale, revealing Earth’s history and nature and still rich with rewards for the hard labor of future explorers.

Jesse H. Ausubel
Co-Founder, Census of Marine Life
Director, Program for the Human Environment, The Rockefeller University
Foreword

Many people unfamiliar with the Southern Ocean regard this ice-bound region as still largely unexplored biologically. This is far from the truth, for the study of the diversity and distribution of organisms in the Southern Ocean has a long and distinguished history. James Cook got close to the Antarctic continent in 1774 aboard HMS Resolution, although he never saw it. His reports of the abundant wildlife led to an explosion of commercial sealing activity, but sadly none of this contributed much to a wider understanding of Southern Ocean biology as the knowledge gained was of powerful commercial interest and largely remained within the community of fishermen to whom it was valuable economically.

Some Antarctic marine species were, however, described as early as the 19th century, reflecting how even the earliest voyages of exploration contributed something to science. The initial exploration of Antarctica was dominated by political, geographical and economic considerations, but even so many of the expeditions undertook biological collections and observations. These were typically fairly limited in scope and often undertaken by participants whose primary role was elsewhere. This early work was dominated by collection of shallow-water benthos and fish, although Bellinghausen did undertake some plankton tows.

Although these early collections were valuable, we can trace the dedicated scientific investigation of the Southern Ocean fauna and flora to the seminal voyages of HMS Challenger (1872-1876), which penetrated to the Antarctic Circle off Queen Maud Land in the Southern Indian Ocean whilst sailing eastwards in 1874. The concept of a purely scientific voyage was novel at that time and although the equipment and approach were perhaps somewhat conservative, this voyage revolutionised our understanding of the biology and chemistry of the oceans. Working up the material took a great many years, but in the end some fifty volumes of scientific findings were published, all beautifully illustrated, and these remain an important scientific resource to this day.

During the Heroic Era of Antarctic exploration, many national expeditions included biologists in their complement and these added incrementally to our knowledge. For some expeditions science was a minor component, whereas for others it was integral to the enterprise as a whole. The next significant contribution to our knowledge of Southern Ocean marine diversity, however, came from the Discovery Investigations. Fieldwork was initiated in 1925, based at South Georgia, and the work was intended to provide an understanding of the biology of the great whales on which the whaling industry depended. In doing so, these extensive voyages of biological oceanography covered the entire Southern Ocean and provided the single greatest advance in our understanding of the system since the voyage of HMS Challenger.

The legacy of this important early work can be seen in the sharp increase in the rate of description of new marine species from the Southern Ocean during the early half of the 20th century. At this time ecology as a discipline was developing rapidly, and the attention of many biologists was moving away from the documentation of new species to understanding how species interacted with each other and with their environment. Although the description of new taxa continued to be important in museums, university researchers were busy exploring this new field of ecology and the rate of description of new Antarctic taxa slowed markedly.

The later decades of the 20th century were a time when Antarctic science started to flourish and many new young researchers starting their careers in Antarctic research at this time rapidly became aware of the importance of this early work. When I started my first Antarctic work in 1970, I decided to explore aspects of the biology and physiology of the ciddane decapod Chorismus antarcticus in the shallow waters of South Georgia. In those early days there was no easy way to identify Antarctic marine invertebrates, and so to be certain I was working on the animal I thought I was, I had to find a copy of the original description by Georg Johann Pfeffer, from specimens collected by the German South Georgia expedition which was based at Moltke Harbour for the first International Polar Year in 1862/63.

In the late 20th century many funding agencies became less interested in funding primary taxonomy, but the documentation of Antarctic marine diversity remained important for many national Antarctic programmes. The next important phase in the study of Southern Ocean diversity and biogeography was the support of Antarctic marine biology by the Scientific Committee on Antarctic Research (SCAR), and in particular the EASIZ (Ecology of the Antarctic Sea Ice Zone) programme which ran for ten years from 1994. Whilst this international programme was focussed primarily on ecology, it also stimulated a considerable volume of primary taxonomic work and prompted the first comprehensive assessments of marine diversity for all of Antarctica. Whilst these assessments were valuable in themselves, they were also important in directing attention at gaps in our knowledge. In particular they identified how little was known of the fauna of the continental slope and the deep-sea around Antarctica. Other important features of the EASIZ programme were the emphasis placed on understanding the relationship between marine organisms and the oceanographic environment within which they lived, and also the evolutionary context in respect of the climatic and tectonic history of the Southern Ocean.

After the EASIZ programme had drawn to a close, the ANDEEP (Antarctic Deep-Sea Biodiversity) programme undertook a series of cruises directed specifically at improving our knowledge of the Antarctic deep-sea fauna. At about this time another significant development was the initiative, under the auspices of SCAR and hosted by Royal Belgian Institute of Natural Sciences, of an interactive database for Antarctic marine diversity, MarBIN (Marine Biodiversity Information Network). As science becomes ever more reliant on information being available on-line, SCAR-MarBIN has been instrumental in improving the quality of marine diversity data for Antarctica, and in disseminating this information to those who need it. The Southern Ocean is now part of the global information network, and no longer an isolated region of the world.

These important developments meant that when the Census of Antarctic Marine Life (CAML) was initiated, and fieldwork undertaken in conjunction with the second International Polar Year (2007/08), the stage was set for a major step forward in our knowledge and understanding of Southern Ocean marine diversity. This volume shows the extent to which this opportunity has been taken and the potential realised. CAML has delivered the single largest step in our knowledge of Antarctic marine diversity and biogeography since the first half of the 20th century. The Biogeographic Atlas has sections devoted to every major taxonomic group, with detailed maps of distribution, as well as chapters documenting the environmental background and evolutionary history, and synthetic analyses. This is a magnificent achievement and testament to the vision of those who planned and developed the programme. It will undoubtedly remain an important resource for many years to come.

Andrew Clarke
Emeritus fellow
British Antarctic Survey, Cambridge
Anthony Press, Antarctic Climate and Ecosystem Cooperative Research Centre, Private Bag 80, Hobart, Tasmania 7001, Australia. E-mail: tony.press@acecrc.org.au

Carmen Primo, National Centre for Marine Conservation and Resource Sustainability, Australian Maritime College, University of Tasmania, Locked Bag 1370, Launceston, Tasmania 7250, Australia. E-mail: c.primo@amc.utas.edu.au

Patrice Pruvost, Museum national d'Histoire naturelle, UMR CNRS 7208 BOREA, CP 26, 43 rue Cuvier, F-75231 Paris Cedex 5, France. E-mail: pruvost@mnhn.fr

Maarten Raes, Marine Biology Department, Ghent University, Krijgslaan 281 (S8), B-9000 Ghent, Belgium. E-mail: maartenraes@yahoo.com

David Ram, CCAMLR, 137 Harrington Street, Hobart, Tasmania 7000, Australia. E-mail: david@ccamlr.org

Ben Raymond, Australian Antarctic Division, Department of Sustainability, Environment, Water, Population and Communities, Channel Highway, Kingston, Tasmania 7050, Australia. E-mail: ben.raymond@aad.gov.au

Antarctic Climate & Ecosystems Cooperative Research Centre, University of Tasmania, Private Bag 90, Hobart, Tasmania 7001, Australia

Claude Razoules, UPMC Université Paris VI, UMS 2348, Observatoire Océanologique, 50650 Banyuls-sur-Mer, France. E-mail: razoules@libertysurf.fr

Gabriel Reygondeau, Université Paris VI, Laboratoire d'océanographie de Villefranche, 181 Chemin du Lazaret, F-06230 Villefranche-sur-Mer, France. E-mail: gabriel.reygondeau@gmail.com

Estefania Rodríguez, Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA. E-mail: erodriguez@amnh.org

Alex D. Rogers, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK. E-mail: alex.rogers@zoo.ox.ac.uk

Yan Ropert-Couëtoud, Université de Strasbourg, CNRS, UMR7178, Institut Pluridisciplinaire Hubert Curien, 23 rue Bœqueuil, F-67087 Strasbourg, France. E-mail: yan.ropert-couëtoud@iphc.cnrs.fr ; docyaounde@gmail.com

Nina Rothe, National Oceanography Centre Southampton, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK. E-mail: nr3@noc.soton.ac.uk

Dirk Welsford, Wildlife Conservation and Fisheries Program, Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia. E-mail: dirk.welsford@aad.gov.au

Mark Westneat, Department of Zoology and Biodiversity Synthesis Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA. E-mail: mwestneat@fieldmuseum.org

Rowan J. Whittle, British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK. E-mail: rowan.jwhittle@bas.ac.uk

Christian Wienecke, Department Seaweed Biology, Section Functional Ecology, Alfred Wegener Institute for Polar and Marine Research, D-27570 Bremerhaven, Germany. E-mail: christian.wienecke@awi.de

Eric J. Woehler, School of Zoology, Centenary Building, Sandy Bay Campus, University of Tasmania, Private Bag 50, Hobart, Tasmania 7001, Australia. E-mail: eric.woehler@utas.edu.au

Oscar Schofield, Coastal Ocean Observation Lab, Institute of Marine & Coastal Sciences, Rutgers University, New Brunswick, NJ 08901, USA. E-mail: oscar@sorine.rutgers.edu

Myriam Schüller, Animal Ecology, Evolution & Biodiversity, Ruhr-Universität Bochum, Universitätsstraße 150, D-44780 Bochum, Germany. E-mail: myriam.schuller@freenet.de

Anna Soler-Membrives, Unidad de Zoología, Facultad de Bicónceres, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Centre d'Estudis del Vallés (Barcelona), Spain. E-mail: anna.soler@ub.cat

Michael Stoddart, Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, Tasmania 7001, Australia. E-mail: michael.stoddart@utas.edu.au

Kerrie M. Swadling, Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, Tasmania 7001, Australia. E-mail: k.swadling@utas.edu.au

Kunio Takahashi, National Institute of Polar Research, 10-3, Midori-cho, Tachikawa-shi, 190-8518, Tokyo, Japan. E-mail: takahashi.kunio@nipr.ac.jp

Sven Thätje, National Oceanography Centre Southampton, School of Ocean and Earth Science, University of Southampton, European Way, Southampton SO14 3ZH, UK. E-mail: svth@noc.soton.ac.uk

Laurenie Trudelle, LOCEAN, UPMC/CNRS/IRD/Muséum National d'Histoire Naturelle, Université Pierre et Marie Curie, Tour 45-55, 4 place Jussieu, BP 100, F-75252 Paris Cedex 05, France. E-mail: laureenie.trudelle@locean-lapl.ufr.fr

Marino Vecchi, Institute for Environmental Protection and Research (ISPRA) c/o Institute of Marine Sciences (ISMAR), National Research Council, Viale Benedetto XV, 9, I-16132 Genoa, Italy. E-mail: marino.vecchi@ispri.beniculturali.it

Carole Valle, Université d'Artsis, Laboratoire d'Océanologie et de Géosciences, UMR 8187, 32 rue Foch, F-62930 Wimereux, France. E-mail: carole.valle@univ-littoral.fr

Anton F. Van de Putte, Royal Belgian Institute for Natural Sciences, Operational Directorate Natural Environment, Vautierstraat 29, B-1000 Brussels, Belgium. E-mail: antonarctica@gmail.com

Ann Vannuesel, Marine Biology Department, Ghent University, Krijgslaan 281 (S8), B-9000 Ghent, Belgium. E-mail: ann.vannuesel@ugent.be

Elena Vázquez, Departamento de Ecología y Biología Animal, Facultade de Ciencias do Mar, Universidade de Vigo, E-36310 Vigo, Spain. E-mail: astero@uvigo.es

Stéphanie Vigetta, Laboratoire d'Océanographie de Villefranche, UMR CNRS 7093, BP 28, F-06230 Villefranche-sur-Mer, France. E-mail: vigetta@sbs-utlf.fr

Victoria Wadley, Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia. E-mail: victoria.wadley@aad.gov.au

Harold J. Walker Jr, Scripps Institution of Oceanography, University of California, San Diego 0208, La Jolla, California 92093-0208, USA. E-mail: hjwalker@scripps.edu

Gregory J. Watkins-Colwell, Yale Peabody Museum of Natural History, 170 Whitney Avenue, Box 209118 New Haven CT 06520, USA. E-mail: gregory.watkins-colwell@yale.edu

Mark Westneat, Department of Zoology and Biodiversity Synthesis Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA. E-mail: mwestneat@fieldmuseum.org

Rowan J. Whittle, British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK. E-mail: rowan.jwhittle@bas.ac.uk

Richard Wienecke, Department Seaweed Biology, Section Functional Ecology, Alfred Wegener Institute for Polar and Marine Research, D-27570 Bremerhaven, Germany. E-mail: christian.wienecke@awi.de

Eric J. Woehler, School of Zoology, Centenary Building, Sandy Bay Campus, University of Tasmania, Private Bag 50, Hobart, Tasmania 7001, Australia. E-mail: eric.woehler@utas.edu.au

José C. Xavier, British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK. E-mail: jxavier@bas.ac.uk

Wolfgang Zeidler, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia. E-mail: wolfgang.zeidler@samuseum.sa.gov.au
Acknowledgements

The Editors express their appreciation for the invaluable support received from the following reviewers:

Shane T. Ahyong (Sydney, Australia), Roger Bamber (London, United Kingdom), Nina Bednarsek (Nova Gorica, Slovenia), Marthin N. Bester (Pretoria, South Africa), Damien Cardinal (Paris, France), Andrew Clarke (Cambridge, United Kingdom), Martin Collins (Stanley, Falkland Islands), Jordi Corbera (Argentina, Spain), Astrid Cornils (Bremerhaven, Germany), Vonda Cummings (Wellington, New Zealand), Bruno Danis (Brussels, Belgium), Hans-Uwe Dahms (Seoul, Korea), Claude De Broyer (Brussels, Belgium), Maria Cristina Gambi (Naples, Italy), Sammy De Grave (Oxford, United Kingdom), Cédric d’Udekem d’Acoz (Brussels, Belgium), Rolf Gradinger (Fairbanks, AK, USA), Ofir Gon (Grahamstown, South Africa), Claudio A. González-Wevar (Santiago, Chile), Ken Halanych (Auburn, AL, USA), Charlotte Havermans (Brussels, Belgium), Bruce W. Hayward (Auckland, New Zealand), Max H. Hommersand (Chapel Hill, NC, USA), Tammy Horton (Southampton, United Kingdom), Graham Hosie (Hobart, Australia), Grant R.W. Humphries (Dunedin, New Zealand), Brian Hunt (Vancouver, BC, Canada), Christopher D. Jones (La Jolla, CA, USA), Stefanie Kaiser (Southampton, United Kingdom), Karl-Hermann Kock (Hamburg, Germany), Philippe Koubbi (Paris, France), Krzysztof Jaźdżewski (Łódź, Poland), Phil Leat (Cambridge, United Kingdom), Florian Leese (Bochum, Germany), Anne-Nina Lötz (Wellington, New Zealand), Fabien Lombard (Villefranche-sur-Mer, France), Enrique Macpherson (Girona, Spain), Christopher Mah (Washington, DC, USA), Wojciech Majewski (Warsaw, Poland), Valdim O. Mokievsky (Moscow, Russia), Françoise Monniot (Paris, France), Lenka Nealova (London, United Kingdom), Marco Oliverio (Rome, Italy), Krzysztof Pabis (Łódź, Poland), David L. Pawson (Washington, DC, USA), Uwe Piatkowski (Kiel, Germany), Gary Poore (Melbourne, Australia), Alix Post (Canberra, Australia), Stefania Puce (Ancona, Italy), Philip R. Pugh (Southampton, United Kingdom), Keith Reid (Hobart, Tasmania), Robin Ross (Santa Barbara, CA, USA), Daniel Roccatagliata (Buenos Aires, Argentina), Stefano Schiaparelli (Genova, Italy), Volker Siegel (Hamburg, Germany), Sven Thalje (Southampton, United Kingdom), Jesús Troncoso (Vigo, Spain), Barbara Wienecke (Hobart, Australia), Jason D. Whittington (Oslo, Norway), Andrew Wright (Hobart, Australia), Moriaki Yashihara (Reston, VA, USA), Katharina Zacher (Bremerhaven, Germany), Diego Zelaya (Buenos Aires, Argentina).

The Editors thank all the SCAR-MarBIN / ANTABIF data providers and the taxonomic editors of the Register of Antarctic Marine Species. We also thank the scientific observers on commercial fishing vessels, and the officers, crew and scientists on research vessels involved in the collection of data used in this Atlas. Without their dedication and support this Biogeographic Atlas would never have been possible.

The Editors gratefully acknowledge the financial support received from the A.P. Sloan Foundation, New York (Census of Marine Life), the Total Foundation, Paris, and the Cosmos Prize Foundation, Tokyo.
PART 1. INTRODUCTION
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 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 Antarctic regions considered (Table 1), Knox (1960) distinguished an Antarctic Region that may cover the antipodal ocean up to 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°F” [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 made available. This allowed Ortmann (1896) in his book “Grundriß 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 (farly 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 unambiguously 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 (Belpica, Valdivia, Scotia, Crozet, Tierra del Fuego, and the Patagonian shelf, which northern limit “may possibly be put as far north as the Plata mouth” 36°S, although Norman (1937), 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 Antitropical 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 Antitropical 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 the 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 Antitropical 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 on 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 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 Scitian sub-province comprising Antarctic Peninsula and the Scotia Arc, while the Ross Sea and...
**Introduction Map 1** General map of the Southern Ocean.


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

<table>
<thead>
<tr>
<th>Characteristic temperature range</th>
<th>Characteristic salinity range</th>
<th>WATER MASS</th>
<th>New Zealand sector</th>
<th>South Australian sector</th>
<th>South American sector</th>
<th>South African sector</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter: 3 to 11.5°C &lt;br&gt; Summer: 5.5 to 14.5°C</td>
<td>34.0 to 34.5‰</td>
<td>Subantarctic cold temperate</td>
<td>Antipodean</td>
<td>Kerguelenian</td>
<td>Magellanic</td>
<td>Kerguelenian</td>
</tr>
<tr>
<td>Mean range: 3.3 to 3.7°C</td>
<td></td>
<td>Transitional zone</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter: -1.8 to 0.5°C &lt;br&gt; Summer: -1.0 to 3.5°C</td>
<td>33.0 to 34.0‰</td>
<td>Antarctic</td>
<td>Russian sub-P</td>
<td>Antarctic</td>
<td>Scottish sub-P</td>
<td>Antarctic</td>
</tr>
</tbody>
</table>
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 Magellanian 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 naupliids. 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 (Bellinghausen 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 Arauco 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 provinces: the Antarctic Region, which comprises the Antarctic Peninsula and the Scotia Arc 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 Bwood Bank.

Briggs (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, 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, with a longitudinal 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.obis.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: Feña Cantero & Garcia Carrossa (1999); sea-ancestors: Rodriguez et al. (2007); cephalopods: Collins & Rodhouse (2006); gastropods and bivalves: Linse et al. (2006), Clarke et al. (2007); isopods: Brandt (1992, 1999); decapods: Gorny (1999), Bosch & 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 noted in different areas, especially 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” (McLeod 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 Southern Ocean biodiversity, Ant; 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, giving the first insights into 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 ability. 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 bi-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 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/Bellinghausen Sea; 229. Ross Sea. Scotia Sea province: 219. South Sandwich Islands; 220. South Georgia; 221. South Sandwich 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. Chileense. (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 includes 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 southwestern 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." Aimed 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 biogeographical classification of coastal and shelf seas (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) subdivided into 21 ecoregions, mostly based upon the data of SE (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. Wattling et al. (2013) proposed a deep-sea biogeographic classification for the shallow benthal 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 benthal, 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 benthal and 14 abyssal provinces, which are "to be considered as hypothetically", and "need to be tested with species distribution data" (Maps 7, 8).

3. The Biogeographic Atlas project

Taking advantage of an unprecedented amount, available, 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 biogeographic 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 guidance 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 significant representation of Southern Ocean biodiversity, illustrated by more than 800 selected distribution maps. The Atlas covered the Southern Ocean at large, south of the Sub-Tropical Frontier, 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 literature (since the very beginning of Antarctic research), and 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 taxonomic 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 & Danss 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 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 fulfill 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.
In 2000 the Alfred P. Sloan Foundation in New York launched a Census of Marine Life, an ambitious ten-year-long international project that was to examine the world’s oceans and log the occurrence and demise of marine species. Its principal objective was to assess the state of marine biodiversity at the start of the 21st century to enable predictions to be made about what species might inhabit oceans in the future. By supporting scientific coordination, rather than putting money in the water, the foundation leveraged over USD 650 million in total outlays. The Census ran until a final meeting in October 2010 in the Royal Society in London at which outcomes from the six ocean realms under study were presented. In total, some 2700 scientists from 60 nations participated in the Census, undertaking 540 research expeditions and producing over 2600 publications. A quarter of a million new species have been identified and recorded and there remain about three times that number waiting to be processed.

The ocean realm “Ice Ocean; Arctic and Antarctic” was the responsibility of two projects – Arctic Ocean Diversity (ArcOD) for the north of the globe, and the Census of Antarctic Marine Life (CAML) for the south. Both projects worked closely together and engaged in a number of joint initiatives. CAML started its activities mid-way through the Census, in 2005, following a decision to hold a third International Polar Year (IPY) in 2007–2009. The Scientific Committee on Antarctic Research (SCAR) accepted a proposal from its Life Sciences committee that CAML should go ahead as one of fifteen biological projects to be undertaken in Antarctica during the IPY; in the event CAML turned out to be the largest of them. The Alfred P. Sloan Foundation provided a grant of USD 1.4 million from 2005 until 2010 to SCAR for purposes of scientific co-ordination of CAML. SCAR contracted with the Australian Antarctic Division based in Hobart, Australia, to co-ordinate and manage the project, and appointed an international Steering Committee to oversee it and report back on progress. The Steering Committee met for the first time in Bremerhaven in October 2004 to write a scientific justification for Foundation support and in early 2005 Dr. Victoria Wedley was appointed as Project Manager. Working with Professor Michael Stoddart, Chief Scientist of Australia’s Antarctic research program, CAML’s Administrator, an initial workshop was held in Genoa, Italy, in May 2005. At this meeting decisions were made about final publications.

The main source of funds for CAML came from the National Antarctic Programs of a number of countries who, with a commitment to support the IPY, agreed to provide ship-time and research staff to work on CAML projects. France, Japan, New Zealand, Australia, UK, USA and a consortium of Latin-American countries provided research voyages dedicated to CAML; many other countries provided periods of ship-time for CAML work (Map 1). A conservative estimate of the value of National Antarctic program support to CAML is over USD 60 million, through their support of infrastructure and personnel. Thirty countries and fifty institutions participated on, and following, eighteen research voyages that delivered CAML data. The Washington Declaration on the International Polar Year and Polar Science, made at Baltimore, USA, in April 2009 urged “states, national and international scientific bodies, and other interested parties to cooperate to deliver a lasting legacy from the IPY, and to support appropriate infrastructures to achieve this…” and called upon “states, organisations, scientists, and other stakeholders to continue to engage with young people to cultivate the next generation of polar scientists, and to communicate with the general public to develop an awareness of the importance of polar research for life in all regions of the world.” In both respects CAML achieved considerable success and can be confident it has materially advanced understanding of the biodiversity of the high latitude Southern Ocean.

CAML quickly established a series of scientific goals, as follows:

1. Undertake an inventory of plankton, nekton and sea-ice associated biota
2. Undertake an inventory of benthic fauna under disintegrating ice shelves and abyssal plains
3. Undertake an inventory of phycological communities at all levels of biological organisation from viruses to vertebrates
4. Assess critical habitats for Antarctic top predators
5. Develop a coordinated network of interoperable databases for all Antarctic marine biodiversity data.

In addition CAML participated strongly in the Barcode of Life Data System (BOLD). Over 11,500 sequences (over 15,000 more than 2,330 species) from the range of common eukaryotic and prokaryotic species in 18 phyla have already been completed, providing a solid basis for future research.

A key element in CAML’s success as a project was its close association with SCAR’s Marine Biodiversity Information Network (SCAR-MarinBin; www.scarmarbin.be), a data portal initiated by the Royal Belgian Institute of Natural Sciences in Brussels, implemented by the Belgian Biodiversity Platform and supported financially by the Belgian Science Policy Office. It was accepted by SCAR as the main repository for marine biodiversity data in 2005. SCAR-MarinBin became CAML’s database. SCAR-MarinBin has recently transmigrated into an Antarctic Biodiversity Information facility (AntaBIF), financially supported by a number of countries with ongoing interests in Antarctic marine biodiversity. SCAR-MarinBin established data protocols and developed a suite of analytical tools for interrogating the data. A register of Antarctic marine species currently carries information on over 25,000 taxa (De Broyer et al. 2013), and almost 3 million occurrence data records (http://www.marinespecies.org/amps/, www.biodiversity.aq). The mass of data is growing since then, with data quality assured by an international editorial panel. Many successful ventures are springing from this central data portal, including a dynamic Antarctic field guides system (http://afg.biodiversity.aq), the Biogeographic Atlas of the Southern Ocean. CAML (http://atlas.biodiversity.aq) or the Micropolar Antarctic Resource System (http://mars.biodiversity.aq). CAML succeeded in drawing together over 200 distributed databases for inclusion in SCAR-MarinBin, and captured publications dating from the very beginning of Antarctic exploration. It catalogued the largest collection of marine biodiversity data in Russia, at the Zoological Institute of St Petersburg, adding almost 300 publications and about 1.7 million data items relating to over 15,000 taxa occurrences. This is only one example of data that might otherwise be lost or inaccessible, which are now preserved for permanent access by the scientific community.

A significant legacy of CAML is a series of special publications that have appeared over recent years, stemming from CAML’s association with national Antarctic programs, e.g. “BIOPEREAL Expedition in the Scotia Sea” (Linse 2008), “Antarctic Biology in the 21st Century” (Fukuchi et al. 2010), “Cooperative East Antarctic Marine Census CEAMARC” (Hosie et al. 2011), “Diversity and Change in the Southern Ocean Ecosystems” (Schiaparelli & Hopcroft 2011).

Many other papers appeared in the normal scientific literature, including in several special IPY and CoML publications (e.g. Bathmann et al. 2010, Gupta et al. 2010, Danis et al. 2013, Schiaparelli et al. 2013). Together these publications carry almost 161 papers on Antarctic marine biodiversity.

The need to understand the marine diversity of the high latitude Southern Ocean didn’t stop with CAML. Knowing what there is, and the environmental conditions that support the biome is still needed for the successful conservation management of the region, and for understanding the consequences of climate change. SCAR has initiated two new major Scientific Research Programs (SRP): the “Status of the Antarctic Ecosystem” (AntEco), and “Antarctic Thresholds – Ecosystem Resilience and Adaptations” (AnT-ERA). These complementary programs are successors to the long-running SRP Evolution and Biodiversity of Antarctica (EBA), of which CAML was a part. Ant-Eco seeks to “understand the patterns of biodiversity across the marine environments, as well as the terrestrial, limnological and glacial marine environments within the Antarctic, sub-Antarctic and Southern Ocean regions.” AnT-ERA will examine “the current biological processes in all Antarctic ecosystems, to define their thresholds and thereby determine resistance and resilience to change.” CAML has contributed much groundwork to these new programs, ensuring a solid base for future studies.

When SCAR’s Steering Committee met for the first time in Bremerhaven in 2004 few people could have imagined how CAML would grow and capture the imagination of countless people around the world. Through the highly efficient media arm of the Census of Marine Life, CAML scientists gained much international exposure for their work and reached out to the general public about the need for an awareness of what cannot be seen beneath the sea’s surface. The Washington Declaration asked no more of us, and we delivered. We are still delivering, with the Biogeographic Atlas being our latest initiative.
CAML Map 1: Tracks of selected CAML-dedicated cruises

Acknowledgments
Huw Griffiths (BAS, Cambridge) and Anton Van de Putte (RBINS, Brussels) prepared the map. This is CAML contribution # 89.

References


THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope
Biogeographic information of fundamental importance for identifying marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, evaluating biodiversity 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 biodiversity 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 biodiversity.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN) 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) since 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. 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 by the Scientific Committee on Antarctic Research (SCAR), 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 Josie, Falk Huettmann, Alexandra Post & Yan Ropert-Couderc.

The Atlas is focused on the design and implementation of marine protected areas, particularly in areas of high vulnerability to climate change, non-invasive technologies, and outreach. Its aim is to understand biotic and abiotic factors operating within an evolutionary framework, including species interactions, and their responses to environmental change, as well as new insights provided by molecular and biogeographic approaches, and test various 3D models and models of biodiversity for conservation.

The Atlas will be a dynamic online version of the Biogeographic Atlas hosted on www.biodiversity.aq, providing high-quality information on the biogeography of species and communities. It will be a key tool to assess the potential impacts of climate change on biodiversity, to inform biodiversity and biogeography conservation strategies, and to provide a sound basis for sustainable management strategies of marine ecosystems.