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▶ CHAPTER 5.11. BIVALVIA.

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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).

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5.11. Bivalvia

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1. Introduction

Bivalvia, commonly known as bivalves, is a diverse class of molluscs (seashells) that occurs in marine and freshwater environments. Bivalves have two laterally compressed two shells connected by a hinge but some radiated groups produced secondarily tube-like structures that encase the body. They include well-known groups like clams, mussels, oysters and scallops. In the fossil record, bivalves were found for the first time in Lower Cambrian deposits (~543–511 Ma) but significant taxonomic and ecological diversification did not take place until the Lower Ordovician (~487–472 Ma) (Waller 1998). Since then bivalve diversification carried on until today and despite taxon losses in the end-Permian and end-Cretaceous became a dominant group in most marine ecosystems. The total number of living species is estimated around 9200 (Huber 2010).

The first bivalve fossils in Antarctic are reported from Late Cambrian deposits in the Ellsworth Mountains and Northern Victoria Land (Stilwell & Long 2011) and bivalves belong to the dominant groups in patchy fossil record of Antarctica (Beu 2009). The past biogeographic affinities of the fossil molluscan faunas, including bivalves, have been studied (Beu 2009 and references therein). Amongst the Antarctic Cretaceous fauna, only the bivalve genus *Malletia*, a deposit feeder, is represented today. Following the K-T boundary (65 Ma) the bivalve composition and richness changed significantly. The currently known Early Palaeocene fauna of Seymour Island (northern Antarctica Peninsula), comprises 18 species of bivalves belonging to 13 families (Beu 2009). Two of these genera (*Nucula* and *Thyasira*) are still extant, as are 6 families (Nuculidae, Nuculanidae, Malletiidae, Limidae, Thyasiridae, Hiatellidae). During the Early Eocene (50 Ma) patterns of fossil richness in the La Meseta Formation from Seymour Island show a strong Eocene radiation of the bivalve fauna. Beu's revision (2009) lists 57 species and 41 genera , with the dominant families being nuculanid, malletiid mytilid, mactrid and venerid bivalves. Only 12 of these genera are still represented in the Southern Ocean, most of the remaining genera occur at present in the seas north of the Polar Front. During the early Cenozoic, when seawater temperatures cooled down, an ice cap covered most of the Antarctic continent and the continental shelf, bivalve fauna underwent further compositional shifts and extinction events. Taxa, which are typically adapted to warmer, temperate waters, such as ostreids, mactrids and venerids, disappeared from the Southern Ocean while other taxa like philobryids radiated extensively (Crame 1999). Pliocene fossils (5.3 to 1.8 Ma) from Cockburn Island comprise three bivalve species of which two (*Adamussium colbecki* and *Laternula elliptica*), are still extant and circum-Antarctic in distribution (Stilwell 2002). The analysis of Cenozoic radiation of the genus *Limopsis* in the Southern Hemisphere showed the disappearance of the temperate shallow-water clade after climate cooling followed by subsequent re-colonisation of Antarctic shelf by members of the deep-water clade (Whittle *et al.* 2011).

In the Southern Ocean scientific work on Recent bivalves started with the HMS Adventure and Beagle expedition to southern South America and the Antarctic Peninsula (King & Broderip 1832). The large species *Laternula elliptica* collected at the South Shetland Islands was one of the first high Antarctic species to be described. To date 160 bivalves have been listed from the Southern Ocean, which the bulk being described following the era of international Antarctic exploration and discovery in the late nineteenth and early twentieth centuries (Clarke *et al.* 2007). Over the last two decades the number of new discovered and described species has significantly increased again following a) the recent international expeditions especially those previously unknown areas like the deep, southern Bellingshausen and Amundsen seas (Linse 2004, Brandt *et al.* 2007, Aldea & Troncoso 2008, Zelaya 2005, 2010), and b) ecological and behaviour observations (Passos *et al* 2006). Currently ongoing molecular phylogenetic and population genetic work is likely to identify new and cryptic bivalve species as indicated for *Lissarca notorcadensis* (Linse *et al.* 2007).

The current bivalve taxonomic diversity comprises 33 families of which the Philobryidae are most numerous (20 species, 3 genera) followed by the Cuspidariidae (13/3) and Sareptidae (12/2). Limopsidae are also diverse with 10 species in 1 genus (Clarke *et al.* 2007).

The Recent Southern Ocean bivalve species share prominent characteristics with other Southern Ocean shelled molluscs (chitons, gastropods and scaphopods): more than half of the species are less than 10 mm in maximum size and more than 90% of the species have very thin and fragile shells. Most bivalve species brood their young or have lecithotrophic larvae with a reduced free-living stage while meropelagic, planktotrophic larvae are rare (Hain 1990). The brooding mode is likely to limit active larval/juvenile dispersal and to favour the separation of populations and consequent speciation processes (Pearse *et al.* 2008). Adult bivalves are often characterised by minimised vagility; many species are infaunal or epifaunal and collect food as deposit- or suspension feeders rather than being able to actively search for food sources. An exception is the pectinid *Adamussium colbecki* which can swim as well as attached itself to substrate by a byssus (Bailey *et al.* 2005).

Photo 1 *Yoldia eightsii* (Jay, 1839), King George Island. Image: Dirk Schories © Universität Rostock.

2. Bivalve bathymetry

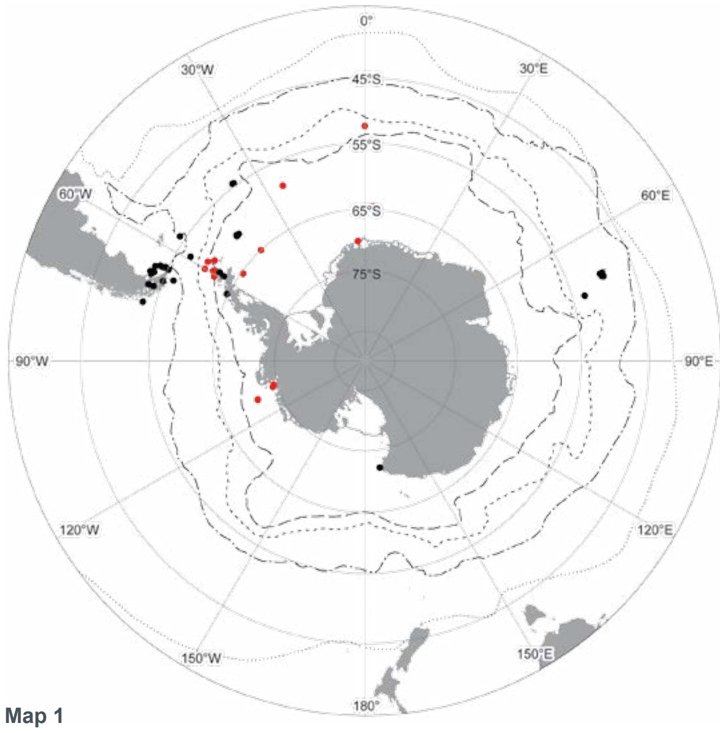
Recently the bathymetric distributions of Antarctic bivalves have been reviewed by Brandt *et al.* (2009), analysing the distribution records of 160 bivalves from 0 to 5000 m. The characteristic phenomenon of the Antarctic benthos, eurybathy, is a common feature among bivalve species. The discovered pattern showed the highest species richness on the shelf with constantly dropping species numbers on the upper slope (roughly around 1000 m) and then more or less constant species numbers in bathyal and abyssal depths. In the shallow, nearshore waters of 0–100 m, bivalve richness was lower with about 60 species than on the shelf where up more than 80 species occurred. Almost 50% of the Antarctic bivalve species occurred on the shelf and upper slope. Below 1200 m depth the species richness dropped to around 20 species per depth interval and continued at this number of species down to 5000 m. Only 9 species (*Axinulus* sp., *Cardiomya* sp., *Cuspidaria* sp., *Silicula* sp. *Vesicomya sirenkoi*, 4 species of *Yoldiella*) have been found in deeper depth. The Condylocardiidae, Erycinidae, Gaimardiidae, Hiatellidae and Nuculidae were examples for families with a narrow, shelf bound depth range. Most analysed families occurred from the shelf to the upper slope, e.g. Astartidae, Kelliidae and Philobryidae. The Arcidae, Cuspidariidae, Limidae, Limopsidae, Mytilidae, Propeamussiidae, Sareptiidae and Thyasiridae occurred from the shelf to abyssal depth. Since Brandt *et al.* (2009), *Calyptogena*-like vesicomyid bivalves have been discovered in seepage habitats on the shelf and upper slope (Domack *et al.* 2005, see Rogers & Linse this volume) and more records of this group are likely with the discovery of venting in the South Sandwich fore-arc. A representative for a shallow-water bivalve with a narrow depth distribution from the intertidal to mid shelf depth is *Lissarca miliaris* while *Vesicomya sirenkoi* is a typical deep sea species with a wide eurybathic range of more than >4000 m (Map 1).

3. Bivalve endemism

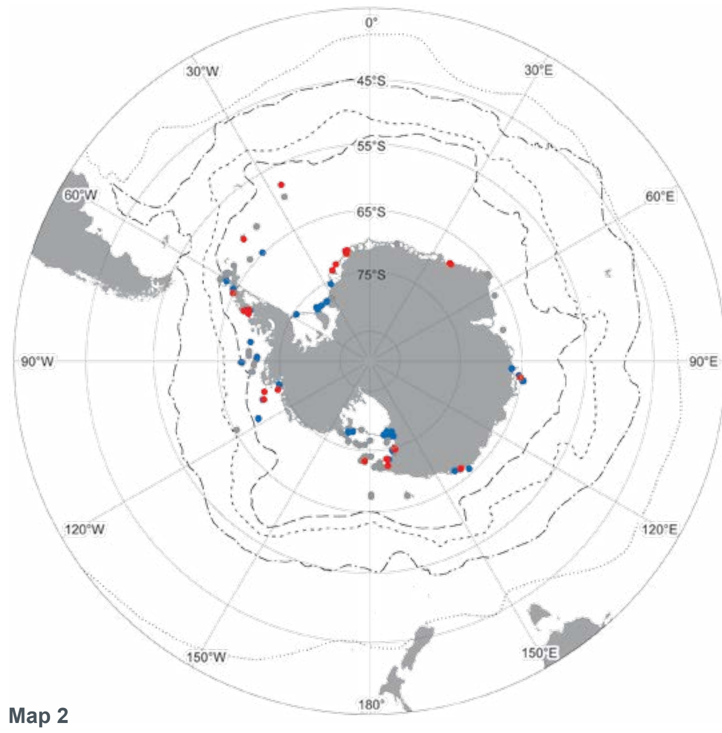
The species level of endemism for bivalves within the Southern Ocean is approximately 57% (Linse *et al.* 2006). At generic and familial levels this is reduced to 4.3% and 0% respectively, indicating that in the cold Antarctic environment adaptive radiation influenced species but not higher taxon level. While most Antarctic genera and families can be found at both poles, no bipolar bivalve species are known to date. Comparison of regional endemism within and outside the Southern Ocean showed the patterns, that several sub-Antarctic areas have had endemism rates of 13.2–22.6 %, while areas near the continent had low of rates (0–4.2%). A representative Antarctic endemic bivalve is the scallop *Adamussium colbecki*, which is the only species of the globally distributed and diverse family Pectinidae in the Southern Ocean (Map 2).

4. Antarctic bivalve biogeography

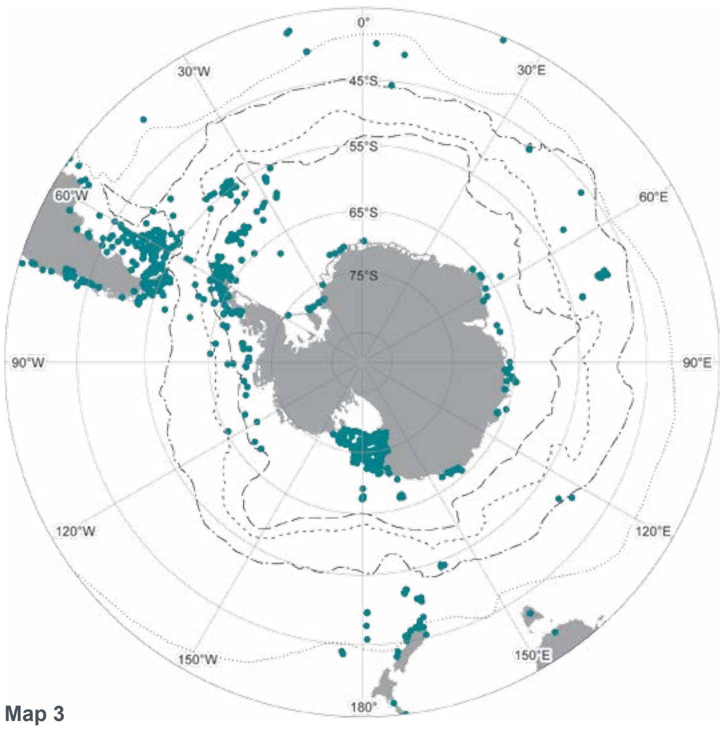
The patterns on the distributions of bivalves in the Southern Ocean area have been studied since the early nineteenth century followed by a comprehensive analysis had by Dell (1969, 1972) (Map 3), which was recently updated by Linse *et al.* (2006) and Griffiths *et al.* (2009) (Map 4). The last two studies analysed 27 areas in the Southern Ocean and adjacent regions and 379 bivalve species, highlighting the very poor knowledge of the Admundsen and southern Bellingshausen seas as well as of the Southern Ocean deep sea. Therefore they examined shelf (0–1000 m depth) patterns only, but gave full taxon lists for shelf only and all depth and in most areas the recorded species numbers differed little. Bivalve species richness differed between shelf and all depths at the South Georgia, the South Shetland Islands and in



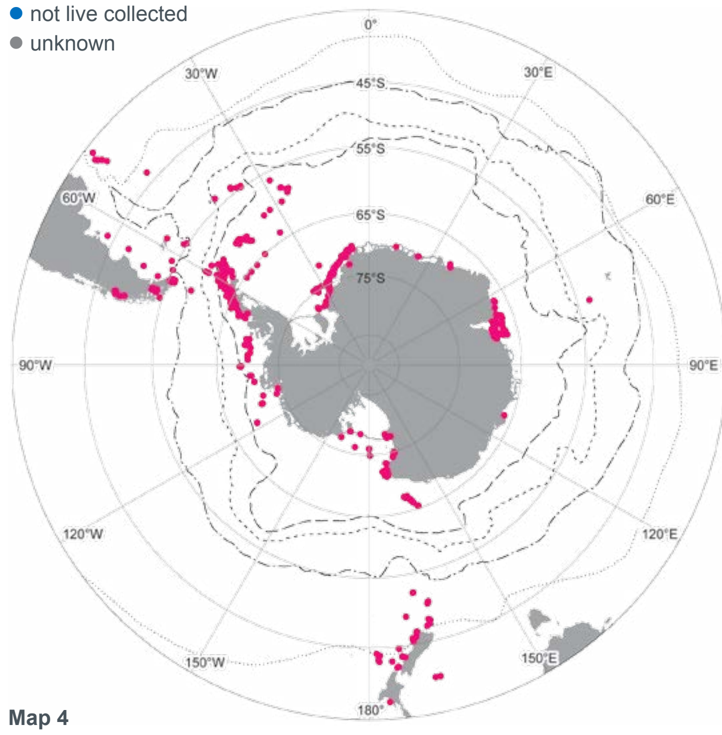
Map 1
● *Lissarca miliaris*
● *Vesicomya sirenkoi*



Map 2
Adamussium colbecki
● live collected
● not live collected
● unknown



Map 3
● Bivalve records until 1969



Map 4
● Bivalve records after 1969

Bivalvia Maps 1–4 Map 1. Recent distribution of the shallow-water bivalve *Lissarca miliaris* and the eurybathic *Vesicomya sirenkoi.* Map 2. Recent distribution of the Antarctic endemic scallop *Adamussium colbecki.* Map 3. Bivalve species records at the time of Dell (1969). Map 4. Bivalve species records since of Dell (1969) up to March 2012.

the Weddell Sea. Typically larger (shelf) areas, e.g. the Weddell Sea, Ross Sea, Tierra del Fuego and East Antarctic - Wilkes Land were richest, followed by the larger islands (Falkland Islands, South Georgia and Kerguelen Islands). The small and most isolated islands, such as Peter I Island and the Heard Islands exhibited the lowest richness. The three richest areas of our study areas were the Weddell Sea (80 species / 39 genera / 27 families), South Georgia (59/37/25) and the South Shetland Islands (58/32/23). Two areas of East Antarctica (Dronning Maud Land, Enderby Land) were impoverished in bivalve taxa. Areas identified as having the highest taxonomic diversity ('hotspots') differed depending on the taxonomic level of the analysis. For example South Georgia patterns of richness were moderate at species level but high at generic and familial levels.

Analysis of species richness in families and genera bivalves revealed that most were encompassed by just five overall patterns:

1) the Weddell and Ross Seas as centres of taxon richness, with richness decreasing towards the Scotia Arc, Antarctic Peninsula region and East Antarctica, and lowest in the sub-Antarctic, Magellanic and other areas like in the Cuspidariidae and its genus *Cuspidaria*,

2) a richness centre spanning the Weddell Sea to Magellanic areas, through the Scotia Arc comprising the Philobryidae,

3) a high Southern Ocean richness coupled with low richness in the sub-Antarctic and other northern areas in the Limidae and Montacutidae, and the genera *Mysella*, *Limatula* and *Yoldiella*,

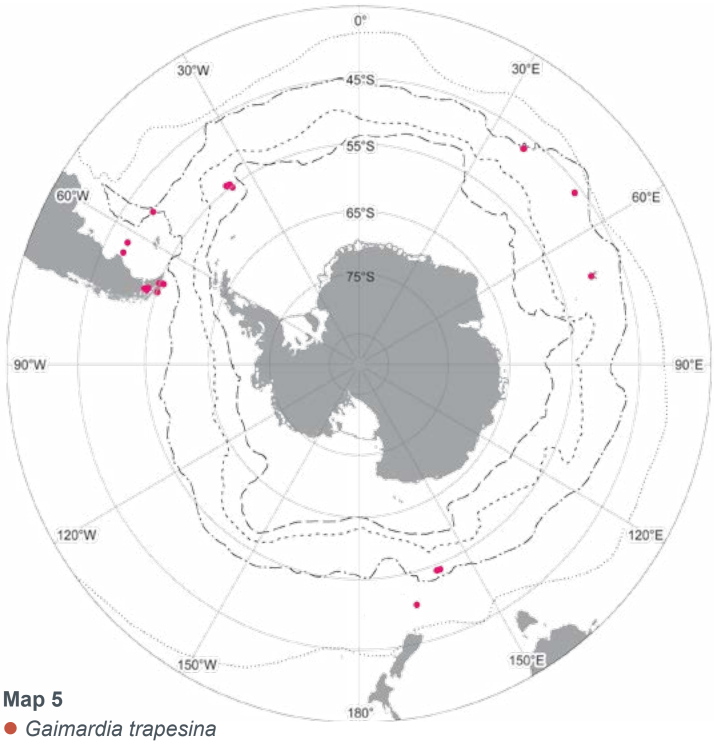
4) conversely, the forth distribution type was a high richness north of the PF and low richness south of it like shown by the families Pectinidae, Nuculidae, Mytilidae, Gaimardiidae and Condylocardiidae and

5) a centre of richness in the Weddell Sea like the Limopsidae, and the genera *Philobrya* and *Limopsis.*

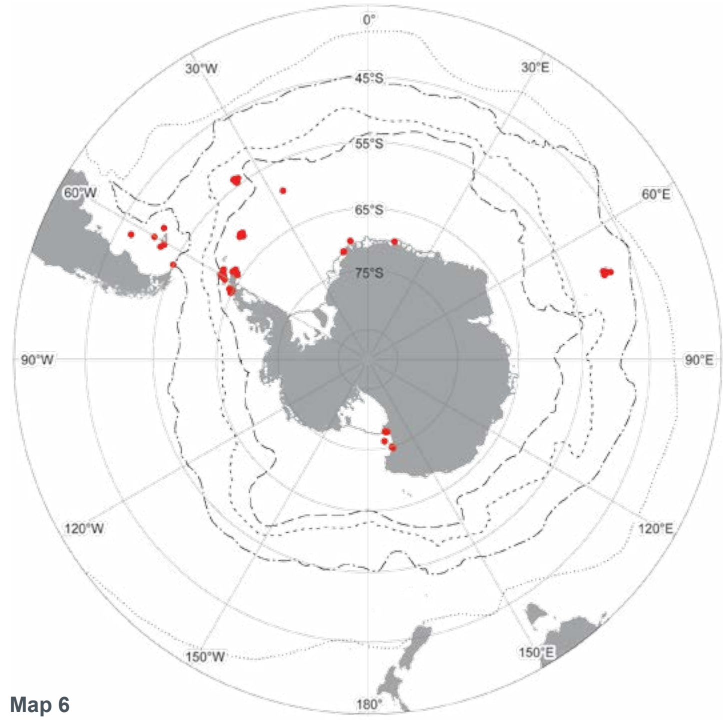
Latitudinal ranges in Antarctic bivalves showed a wide range with a large number of species (14–18) ranging over 35 degree, spanning from the high Antarctic to cold temperate latitudes (Clarke *et al.* 2007). Longitudinal range distributions analysed in the same study were dominated by species with very limited ranges, but this might be the result of most taxa being represented by few samples. Indeed it is striking that only a few taxa have latitudinal ranges approaching circumpolar.

At species level, the epifaunal bivalve *Gaimardia trapesina* is a representative for a species with a sub-Antarctic distribution (Map 5) , *Yoldia eightsii* (Photo 1) and *Limopsis marionensis* for a circum-Antarctic distribution also reaching the Magellan region (Maps 6–7) and *Cuspidaria multicostata* for a species with a restricted range (Map 8).

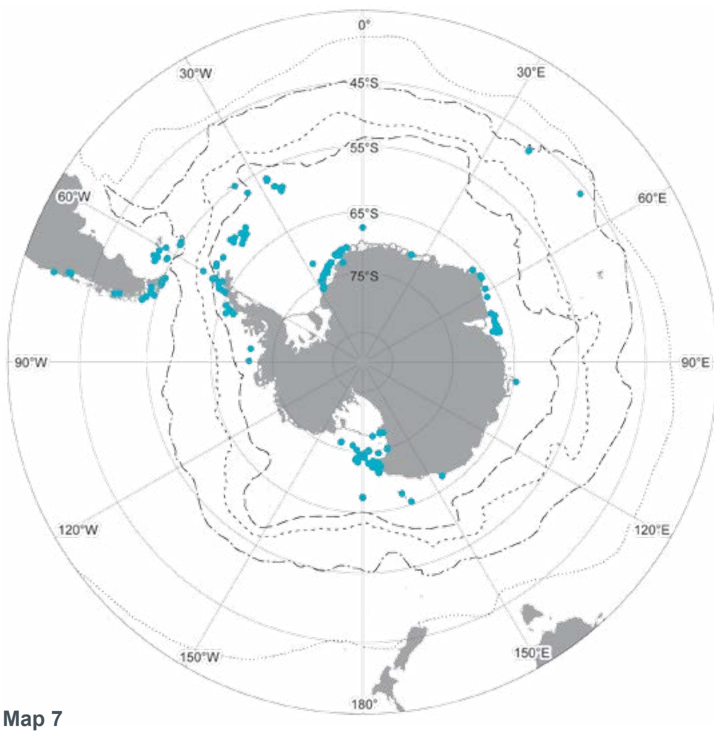
Among the major challenges in Antarctic marine biogeography is the integration of the latest molecular phylogeographic and taxonomic results with the existing species records based on collections spanning the last two centuries. While the large scale patterns of the Southern Ocean region are not likely to change, the within SO regional scale might change with the discovery of more cryptic specie groups. The next step would be to investigate the distribution patterns of these species groups and link them with physical, geological and biological parameters. These parameters will also enable habitat mapping on large to small scales followed by predictive modelling of bivalve species distributions in un-sampled regions.



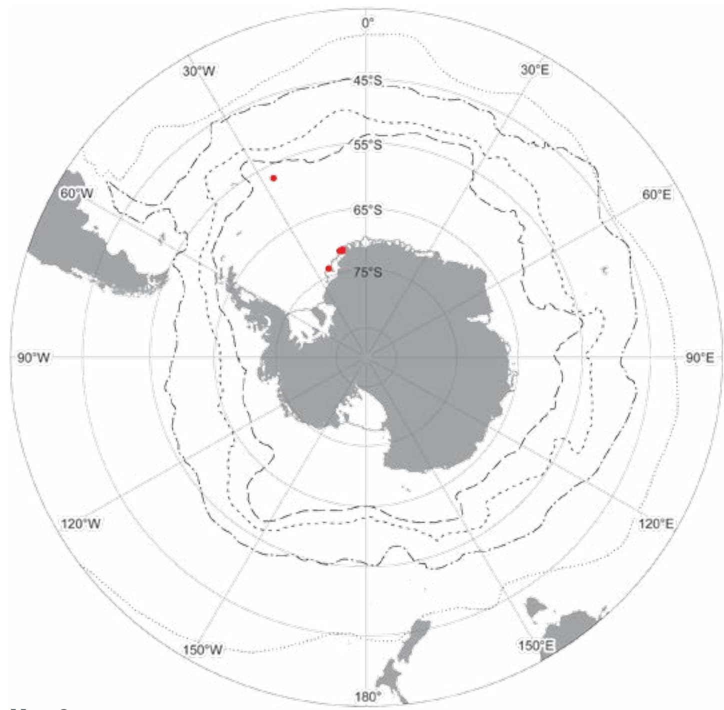
Map 5
● *Gaimardia trapesina*



Map 6
● *Yoldia eightsii*



Map 7
● *Limopsis marionensis*



Map 8
● *Cuspidaria multicostata*

Bivalvia Maps 5–8 Representative species for distribution ranges. Map 5. *Gaimardia trapesina*: sub-Antarctic distribution. Map 6. *Yoldia eightsii*: circum-Antarctic distribution also reaching the Magellan Region. Map 7. *Limopsis marionensis*: idem. Map 8. *Cuspidaria multicostata*: species with a restricted range.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team

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

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

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

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

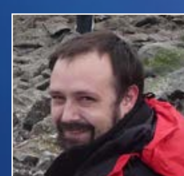
Susie GRANT is a marine biogeographer at the British Antarctic Survey. Her work is focused on the design and implementation of marine protected areas, particularly through the use of biogeographic information in systematic conservation planning.

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

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

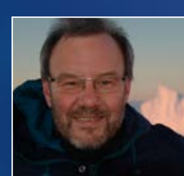
Philippe KOUBBI is professor at the University Pierre et Marie Curie (Paris, France) and a specialist in Antarctic fish ecology and biogeography. He is the Principal Investigator of projects supported by IPEV, the French Polar Institute. As a French representative to the CCAMLR Scientific Committee,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

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



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

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



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

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

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

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