

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.4. Southern Ocean Harpacticoida (Crustacea, Copepoda)

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1. Introduction

With approximately 4300 known species distributed over 622 genera and 65 families (Wells 2007), the Harpacticoida (Crustacea, Copepoda) comprise one major free-living copepod order (Lang 1948, Huys & Boxshall 1991). By far the most harpacticoids are benthic organisms that can be found in marine or freshwater habitats. They occur from the supralittoral down to the deepest so far sampled abyssal localities and are even found in terrestrial mosses and in tropical bromelian axilla, if sufficient moisture is provided (Lang 1948, Huys & Boxshall 1991).

Together with many other benthic organismic groups (e.g. Gastrotricha, Halacarida, Kinorhyncha, Loricifera, Nematoda), Harpacticoida are united to the size group called "meiofauna" or "meiobenthos", consisting of animals showing certain typical characteristics, like e.g. small body size (up to ~1.0 mm), lack of planktonic life stages, and a more or less strict bondage to substrata (Mare 1942, Higgins & Thiel 1988, Giere 2009). One would assume that such properties might affect the ability of marine meiofauna for dispersal in the world's oceans, and indeed Dahms (1992) considered members of the meiobenthos as probably more suitable for biogeographic analyses than most macrobenthic taxa due to their restricted dispersal abilities (see also Dahms & Qian 2004). However, many meiobenthic species actually show a wide or even worldwide distribution, which has been coined the "meiobenthic paradox" by Giere (2009). Nonetheless, actual distribution patterns of most meiobenthic taxa are far from understood. Regarding the Southern Ocean sensu lato and particularly the Antarctic Region, the number of meiobenthic investigations remains rather low as yet, and several studies focus on ecological aspects (e.g. Bradford 1978, Bouvy & Soyer 1989, Herman & Dahms 1992, Vanhove et al. 1995, 1998, Fabiano & Danovaro 1999, Gradinger 1999, Günther et al. 1999, Veit-Köhler 2005, Veit-Köhler et al. 2011) rather than on biogeographic inventories. These started much earlier and concentrated on distinct meiobenthic major taxa, such as the Copepoda Harpacticoida (e.g. Giesbrecht 1902, Brady 1910, T. Scott 1912, Lang 1934, Bovée & Soyer 1975, George 1999). Since the beginning of Antarctic meiobenthic research many papers were dedicated to the description of new Antarctic species that contribute to our knowledge of Antarctic harpacticoid assemblages.





Photos 1–2 Harpacticoidea Photo 1. *Emertonia andeep* (Veit-Köhler, 2004), female specimen, left: dorsal view, right: lateral view; body Length: 0.32 mm; reported Locations: Northern Weddell Sea as well as South East Atlantic deep sea basins; depth range: 4538–5415 m. Image © G. Veit-Köhler. Photo 2. *Wellsopsyllus antarcticus* Kottmann & Veit-Köhler, 2013, male specimen, left: dorsal view, right: ventral view; body Length: 0.35 mm; reported Locations: Weddell Sea (East of Antarctic Peninsula and Northern Weddell Sea) and Indian Ocean (Crozet Island); reported depth range: 1107–4540 m. Image © J. Kottmann, T.C. Kihara & G. Veit-Köhler.

2. Sampling meiobenthic Copepoda in Antarctic waters and comparability of samples

The earliest Antarctic expeditions sampling among other taxa Harpacticoida took place at the end of the 19th and at the beginning of the 20th century, for instance the "Expédition Antarctique Belge 1897-1899" (Giesbrecht 1902), the "Swedish Antarctic Expedition 1901-1903" (Lang 1934), the "Deutsche Südpolarexpedition 1901–1903" (Brady 1910), and the Scottish National Antarctic Expedition 1902–1904" (T. Scott 1912). Sampling of sublittoral meiofauna was undertaken by dredging and tow-netting, whereas littoral meiofauna was collected by washing algae and sediment (e.g. Brady 1910, Lang 1936). Later on, also material obtained from Agassiz trawls, box corers, multicorers and SCUBA-diving was treated (e.g. Gee & Fleeger 1986, George 1998, 2005, Veit-Köhler & Willen 1999, Willen 1996). Because of such different gears and methods, and because gears like dredge, Agassiz-trawl and box corer do not provide undisturbed meiobenthic material, the obtained samples cannot be compared directly. Any quantitative aspect must be ignored, and missing a species in a sample might rather be interpreted by sampling artefacts than by the actual absence of the species in the area. Thus, faunistic comparisons of

localities are difficult and more quantitative samples are necessary for such an approach. However, the presence of species certainly provides information, and in the following the results of a revision of corresponding literature regarding Harpacticoida are presented.

3. Harpacticoid distribution in the Southern Ocean

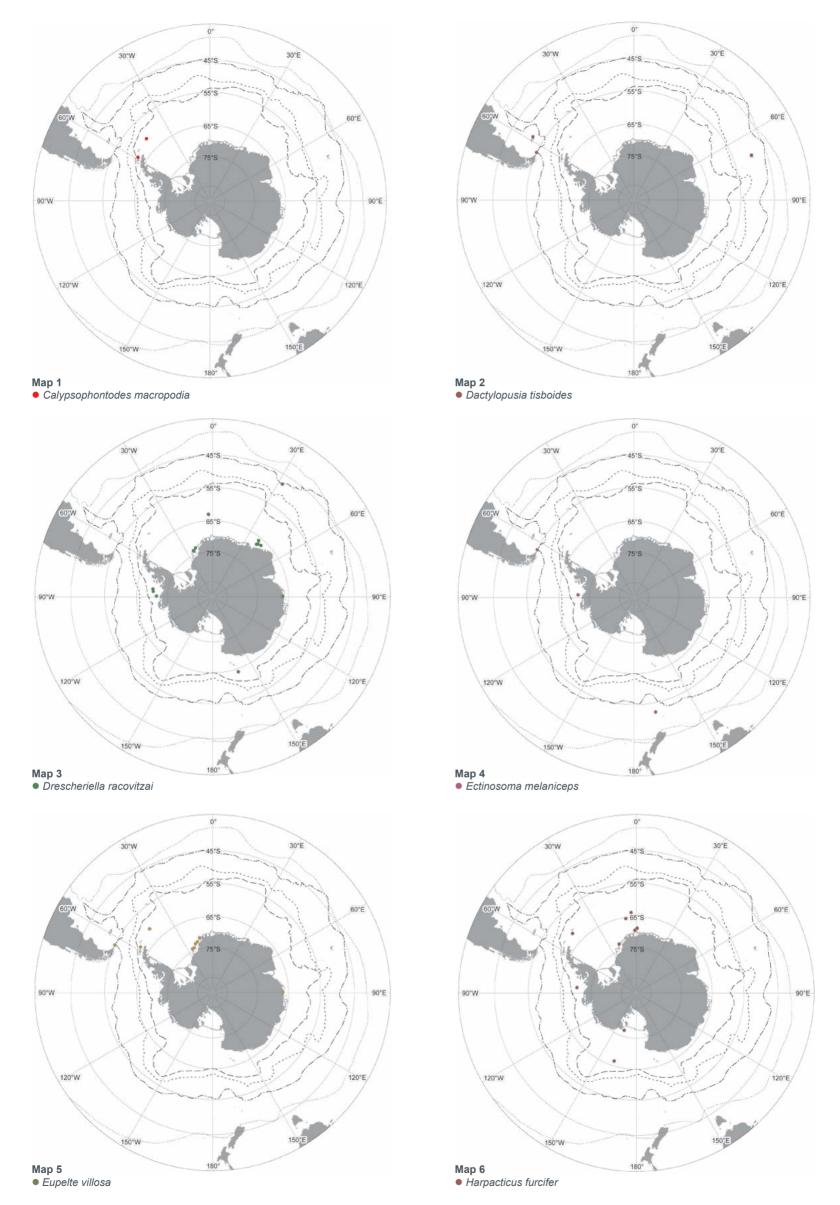
In the Southern Ocean sensu lato, i.e. in an area passing the APF and reaching the sub-Tropical Front (STF) (cf. De Broyer & Danis 2011), 261 harpacticoid species have been described up to date, belonging to 29 families. The records comprise species from shallow-water areas (e.g. the [sub-]littoral of Antarctic islands, the southern tip of South America, the Falkland, Kerguelen, Macquarie and Crozet Islands) and deep-sea areas (>200 m, e.g. in the Weddell and Ross Sea). Compared with records from other regions of the world, the number of harpacticoid species known from the Southern Ocean appears to be somewhat small. For instance, George (1999, 2005) listed 122 species for an area enclosing only the Magellan Straits, the Beagle Channel, and the eastern Patagonian continental slope. However, most of the species have not yet been described, keeping therefore a status as "working species" that are useless for any chorological or biogeographic investigation. Just 18 species have been determined or described (George 1999, 2005), so they could be included in the here presented chorological analysis. That means that the number of Harpacticoida reported so far from the Southern Ocean does in no case reflect the actual number of species inhabiting that realm; much more (known and unknown) Harpacticoida are to be expected.

The Antarctic Region (i.e. the Southern Ocean *sensu stricto*), covering an area from the Antarctic continent itself to the Antarctic Polar Front (APF), presents 96 harpacticoid species distributed over 21 families (Table 1).

Table 1 List of harpacticoid families (Crustacea, Copepoda) reported from the High and Sub-Antarctic, with the number of determined species in the respective area.

	High Antarctic	Sub-Antarctic	
Ameiridae	4	10	
Ancorabolidae	8	14	
Argestidae	0	8	
Canthocamptidae	2	6	
Cletodidae	0	8	
Cristacoxidae	0	1	
Dactylopusiidae	5	15	
Ectinosomatidae	8	5	
Harpacticidae	6	16	
ldyanthidae	4	1	
Laophontidae	9	19	
Leptastacidae	0	2	
Leptopontiidae	0	3	
Longipediidae	1	0	
Miraciidae	5	22	
Neobradyidae	1	0	
Normanellidae	0	2	
"Orthopsyllidae"	2	1	
Paramesochridae	4	7	
Parastenheliidae	2	4	
Peltidiidae	5	5	
Porcelliidae	1	1	
Pseudotachidiidae	9	4	
Superornatiremidae	0	1	
Tegastidae	2	2	
Tetragonicipitidae	0	3	
Thalestridae	6	8	
Tisbidae	11	14	
Zosimeidae	1	0	
Total	96	182	

Most of the reported species, like e.g. *Breviconia echinata* (Brady, 1910), *Seleno psyllus antarcticus* Moura & Pottek, 1998, and *Drescheriella glacialis* Dahms & Dieckmann, 1987 have not been found in any other region of the world. While this may partly be the case because of very specific ecological requirements that inhibit a wider distribution of certain species – *D. glacialis* for example is a sympagic species inhabiting the brine channels within the Antarctic sea ice (Dahms & Dieckmann 1987, Günther *et al.* 1999) – the "absence" of other Antarctic species in sampling material of localities from other parts of the oceans may by all means be due to sampling artefacts rather than because of the actual absence of the species. Such assumption is supported by the quite disjunctive distribution patterns of marine Harpacticoida, which often may be better explained by insufficient sampling than by actual dispersal



Harpacticoidea Maps 1–6 Map 1. Calypsophontodes macropodia (Gee & Fleeger, 1986). Map 2. Dactylopusia tisboides (Claus, 1863). Map 3. Drescheriella racovitzai (Giesbrecht, 1902). Map 4. Ectinosoma melaniceps Boeck, 1865. Map 5. Eupelte villosa (Brady, 1910). Map 6. Harpacticus furcifer (Giesbrecht, 1902).



▶ Meiobenthos : Harpacticoida

patterns. For instance, both Idomene forficata Philippi, 1843 (Pseudotachidiidae) and Idyellopsis typica Lang, 1948 (Idyanthidae) were collected in the Antarctic Region but also in the northern Atlantic (Idyellopsis typica) or in the whole eastern Atlantic and the Mediterranean Sea (Idyellopsis typica) (Lang 1948), but they have not (yet?) been reported from any sub-Antarctic locality. Similar applies to the paramesochrids *Emertonia andeep* (Veit-Köhler 2004) (Photo 1) and E. diva (Veit-Köhler 2005), which were reported from the Antarctic Region and the SE Atlantic (Gheerardyn & Veit-Köhler 2009) but not in sub-Antarctic areas. In contrast, Alteutha depressa (Baird 1837) (Peltidiidae), Ectinosoma melaniceps Boeck, 1864 (Ectinosomatidae) (Map 4), Orthopyllus linearis (Claus 1866) ("Orthopsyllidae"), and Tigriopus californicus (Baker 1912) (Harpacticidae) show a worldwide distribution (Lang 1948) including both the Antarctic Region and the Sub-Antarctic. Widely to globally distributed species that were found in sub-Antarctic areas but not in the Antarctic Region are Laophonte cornuta Philippi, 1840 (Laophontidae) (Map 9), Parastenhelia spinosa (Fischer, 1860), and Zaus abbreviatus Sars, 1904 (Harpacticidae).

With 182 species distributed over 26 families the Sub-Antarctic Region, lying between APF and STF, presents approximately twice as much species than the Antarctic Region (Table 1, Fig. 1). Even if keeping in mind possible sampling artefacts, such strong difference in species number and composition is remarkable. The differences are already detectable at family level: in the Antarctic Region, eight families are not represented (Argestidae, Cletodidae, Cristacoxidae, Leptastacidae, Leptopontiidae, Normanellidae, Superornatiremidae, Tetragonicipitidae), while in the sub-Antarctic area three families are missing (Longipediidae, Neobradyidae, Zosimeidae). Also with respect to the species diversity inside the families both regions show differences; while in the Antarctic Tisbidae presents highest species number, followed by Laophontidae and Pseudotachidiidae, in the sub-Antarctic Region the Miraciidae is the species-richest taxon, followed by Laophontidae and Harpacticidae (Table 1, Fig. 1).

At species level it can be noted that most species seem to restrict to their respective regions. Only 13 species (5.0%) were reported from both the Antarctic and the Sub-Antarctic Regions (Table 2). Moreover, as mentioned above, 11 species (4.2%) have been reported from outside the Southern Ocean sensu lato (Table 2). Thus, an inventory of the Antarctic Region basing on the available literature since the beginning of the 20th century results in 75 exclusive species (28.7%) and for the Sub-Antarctic Region in 162 exclusive species (62.1%). Future detailed meiobenthic sampling may elucidate whether parts of these species might be considered as endemic ones, or if the amount of species inhabiting both the Antarctic and the Sub-Antarctic Regions or showing an even wider distribution may increase.

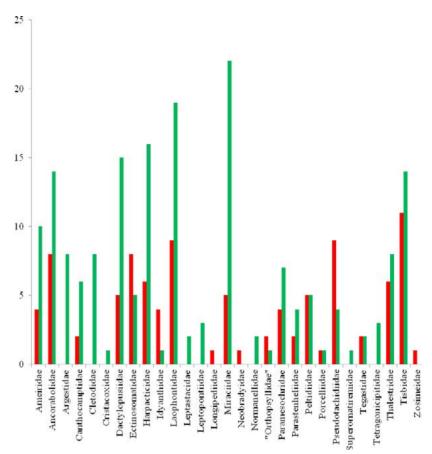


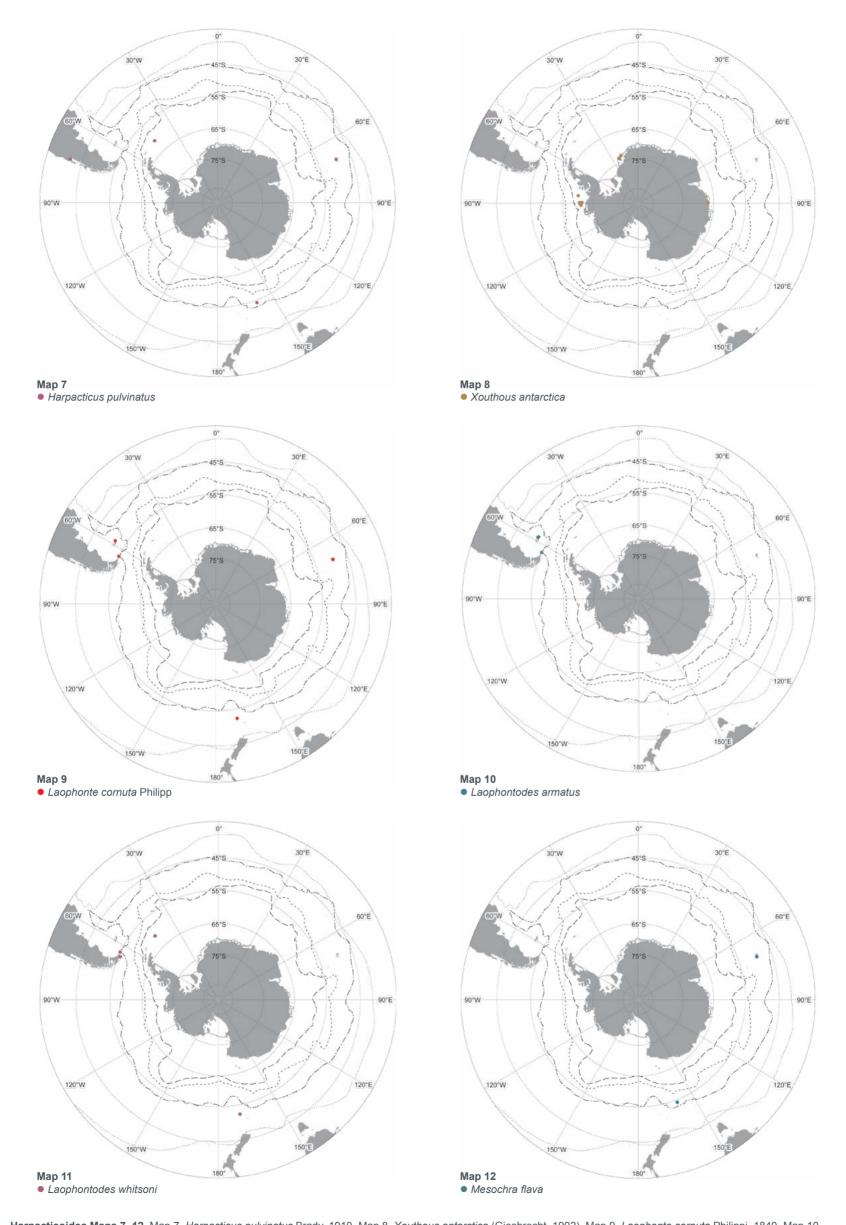
Figure 1 Number of harpacticoid species (Crustacea, Copepoda) reported per family in the Antarctic (red columns) and the Sub-Antarctic Regions (green columns).

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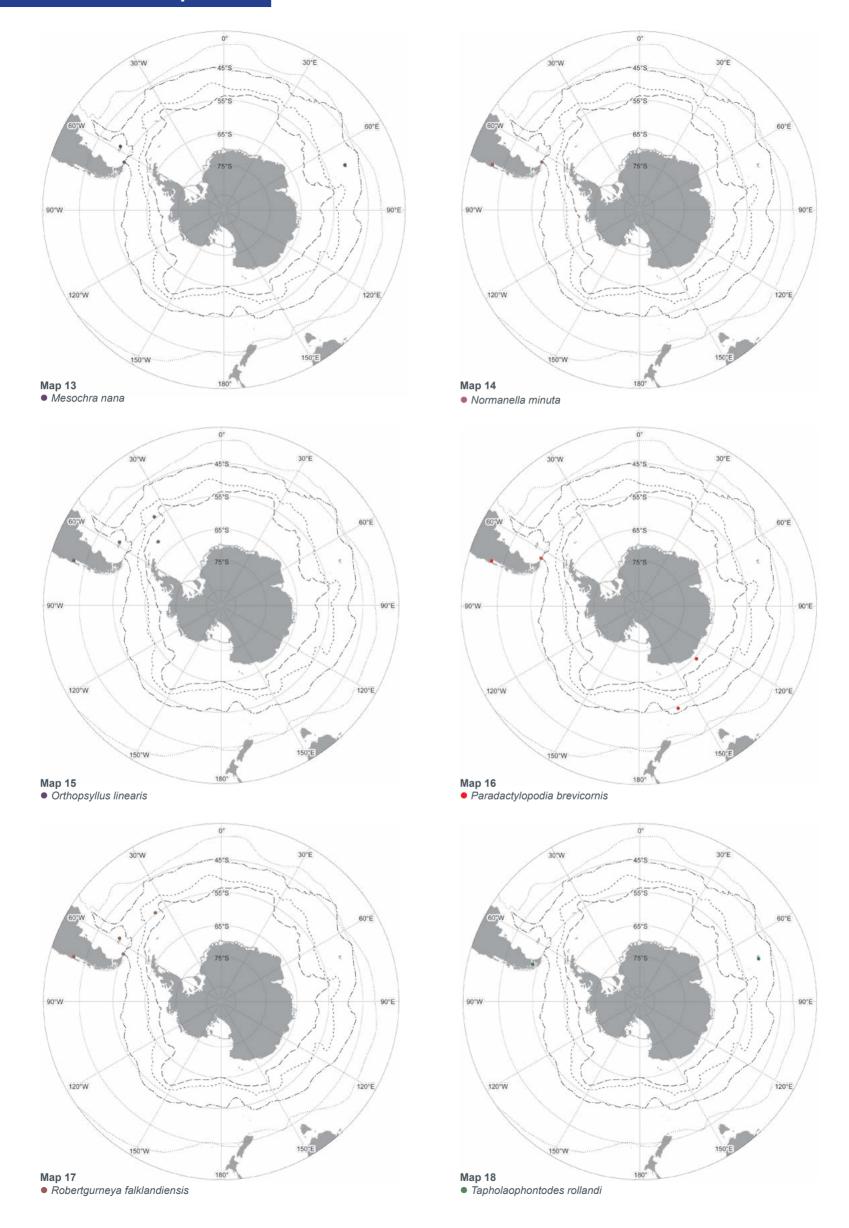
Table 2 List of harpacticoid species (Crustacea, Copepoda) showing an Antarctic, sub-Antarctic or even wider distribution.

Species	Antarctic Region	Sub-Antarctic	Outside Southern Ocean
Alteutha depressa (Baird, 1837)	+	+	+
Amphiascus gracilis Lang, 1936	+	+	
Diarthrodes imbricatus (Brady, 1910)	+	+	
Ectinosoma melaniceps Boeck, 1864	+	+	+
Emertonia andeep (Veit-Köhler, 2004)	+		+
Emertonia diva (Veit-Köhler, 2005)	+		+
Eupelte villosa (Brady, 1910)	+	+	
Harpacticus falklandi T. Scott, 1914	+	+	
Harpacticus furcatus Lang, 1936	+	+	
Harpacticus pulvinatus Brady, 1910	+	+	
Idomene forficata Philippi, 1843	+		+
Idyellopsis typica Lang, 1948	+		+
Laophonte cornuta Philippi, 1840		+	+
Laophontodes whitsoni T. Scott, 1912	+	+	
Microsetella norvegica (Boeck, 1864)	+	+	
Orthopsyllus linearis (Claus, 1866)	+	+	+
Parastenhelia gracilis Brady, 1910	+	+	
Parastenhelia spinosa (Fischer, 1860)		+	+
Rhynchothalestris tenuicornis (Brady, 1910)	+	+	
Robertgurneya falklandiensis (Lang, 1936)	+	+	
Scutellidium australe (T. Scott, 1912)	+	+	
Tigriopus californicus (Baker, 1912)	+	+	+
Tisbe tenuimana (Giesbrecht, 1902)	+	+	
Zaus abbreviatus Sars, 1904		+	+

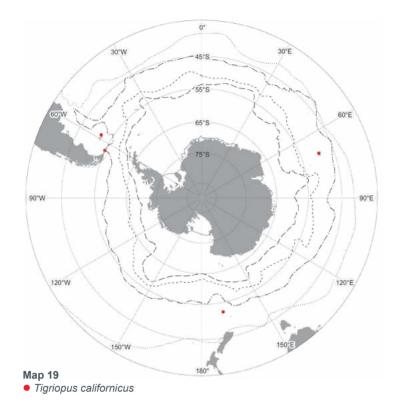


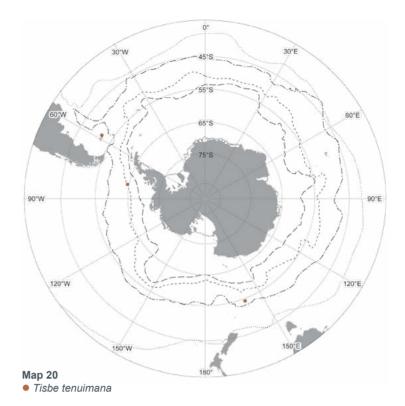
Harpacticoidea Maps 7–12 Map 7. Harpacticus pulvinatus Brady, 1910. Map 8. Xouthous antarctica (Giesbrecht, 1902). Map 9. Laophonte cornuta Philippi, 1840. Map 10. Laophontodes armatus Lang, 1936. Map 11. Laophontodes whitsoni T. Scott, 1912. Map 12. Mesochra flava Lang, 1933.





Harpacticoidea Maps 13–18 Map 13. Mesochra nana Brady, 1910. Map 14. Normanella minuta (Boeck, 1873). Map 15. Orthopsyllus linearis (Claus, 1866). Map 16. Paradactylopodia brevicornis (Claus, 1866). Map 17. Robertgurneya falklandiensis (Lang, 1936). Map 18. Tapholaophontodes rollandi Soyer, 1975.





Harpacticoidea Maps 19-20 Map 19. Tigriopus californicus (Baker, 1912). Map 20. Tisbe tenuimana (Giesbrecht, 1902).

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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

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)

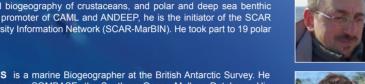
CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against 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





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.



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.



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.



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.



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 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.



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.



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.



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.



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



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



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



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.

























