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► CHAPTER 5.13. POLYCHAETES.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.13. Polychaetes

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1. Introduction

The contribution of polychaetes to the total benthic faunal diversity is somewhat smaller in the Southern Ocean than elsewhere in temperate latitudes where polychaetes usually contribute about 42 to 50% of all species (Blake & Hilbig 1994, Hilbig 1994, Hilbig & Blake 2000, 2006). Nonetheless, polychaetes are found in all substrates from the intertidal to abyssal depths, displaying a wide variety of life forms. As polychaetes are found wherever samples are taken, distributional patterns of many taxa — sometimes down to species level — may reflect sampling effort.

The biogeographic regions in the Southern Ocean are in the process of re-definition as more material is being collected and analyzed with new methods such as molecular genetics (Schiaparelli & Hopcroft 2011 and articles cited therein). We are here recognising the regions Weddell Sea, Ross Sea, eastern Antarctic seas, and the western Antarctic Bellingshausen and Amundsen Seas.

There are 723 species (including 135 synonyms), listed in the Register of Antarctic Marine Species (RAMS) i.e., 588 validated species for polychaetes, RAMS includes all occurrences south of the Polar Front. Of the 588 validated species in RAMS, 403 currently have georeferenced occurrences in SCAR-MarBIN, amounting to nearly 70% (De Broyer & Danis 2011).

1.1. Sampling gaps (knowledge gaps) vs data gaps

Polychaete data entered into the SCAR-MarBIN database suggest that practically all records (90%) come from the Atlantic sector of the Southern Ocean (Weddell Sea, Antarctic Peninsula, Scotia Arc Islands and adjacent areas) (Table 1). However, there are numerous publications dealing with Ross Sea polychaetes in the literature, especially from Italian, New Zealand, and U.S. American studies (e.g., Benham 1927, Blake 1983, Cantone 1994a, b, 1995, Cantone & Di Pietro 1998, Cantone & Sanfilippo 1992, Cantone *et al.* 2000, Gambi *et al.* 1997, Hartman 1952, Knox & Cameron 1998, Lowry 1976, Orensanz 1990, Rota & Carchini 1999).

Comparably little or no data have been compiled outside the Weddell and Ross Seas and adjacent waters, e.g., in the Amundsen and Bellingshausen Seas in the west (with only one recent pertinent publication by Parapar *et al.* 2011) and almost the entire eastern Antarctic Seas. In part this may depend on the localities of research stations along the coastline of Antarctica, in part on the inaccessibility of these areas which are exposed to weather and sea state, and consequently in huge gaps in our sampling effort to date. A major reason, at least for upper shelf sites, may be related to the fact that compiled data are yet to be submitted to existing databases such as SCAR-MarBIN, suggesting that presented patterns are rather a result of data gaps than of sampling gaps.

1.2. Taxonomic limitations

The history of the identification of Antarctic benthos is often reflected in the species names which clearly were taken from already existing monographs of the European fauna (e.g., the works of Hartman 1964, 1966, 1967, 1978). While numerous new species have been described since the age of the great expeditions to the Southern Ocean, there are still many “cosmopolitans” which

Table 1 Information on geographic and bathymetric distribution of valid polychaete records and species in the SCAR-MarBIN database.

	Total	Weddell Sea	Ross Sea	Eastern Antarctica
Records total	5607	5031	186	390
Records with depth information	5347	4790	382	175
Shelf records	3851	3504	256	91
Slope records	740	683	28	29
Deep-sea records	756	603	98	55
Species total	403	373	117	26
Locally restricted species	272			
Circumpolar species	128			
Eurybathic species	86			
Shelf species	184			
Deep-sea species	26			
Circumpolar & eurybathic species	53			
Locally restricted shelf species	144			
Locally restricted deep-sea species	21			

will most likely turn out to be species complexes of locally restricted species. Especially the use of molecular genetics will help to discover such complexes. The terebellid *Thelepus cincinnatus* (Fabricius, 1780), for example, is such a potential species complex, with the type locality being Greenland and records present not only from European waters, but also the Southern Ocean and

scattered locations worldwide. Molecular studies on polychaetes have already served to discover species complexes and better resolve distribution patterns in the past (e.g., Wiklund *et al.* 2009; Barroso *et al.* 2010). However, molecular phylogeographic studies on Southern Ocean polychaetes, with exception of the one study by Schüller (2011) on deep-sea *Glycera* populations, are missing to date, giving way to a whole new field in Southern Ocean polychaete taxonomy and biogeography that has yet to be uncovered. Another aspect is the study of the biology of Southern Ocean polychaetes, and probably other taxa as well, to gain a better understanding of distributional patterns and species definitions. The design of experiments to test biological traits such as larval dispersal and trophic structure of benthic polychaetes in the Southern Ocean is another challenge of the future that might yield unexpected results. Last not least, well-trained traditional taxonomists are still very much needed to discover the diversity of life in the Southern Ocean.

2. Pelagic species

The great majority of all pelagic records is from the Eastern Antarctic sector (Map 1) where a thorough and regular plankton sampling has been undertaken by the Australian Antarctic Division. More than half of these records are of the lopadorhynchid *Pelagobia longicirrata* (394), whereas the genus *Tomopteris* is represented by only 113 records for 4 species. This finding is somewhat surprising because in other regions of the world ocean *Tomopteris* is very common and abundant (Knox & Cameron 1998). Given that most records are from only one institute, the Australian Antarctic Division, which has focused its research activities in Pacific waters, Atlantic regions like the Weddell Sea and Antarctic Peninsula are underrepresented. Moreover, in the general scientific scope of most planktonic investigations pelagic polychaetes are considered of little interest and thus possibly caught much more often than recorded.



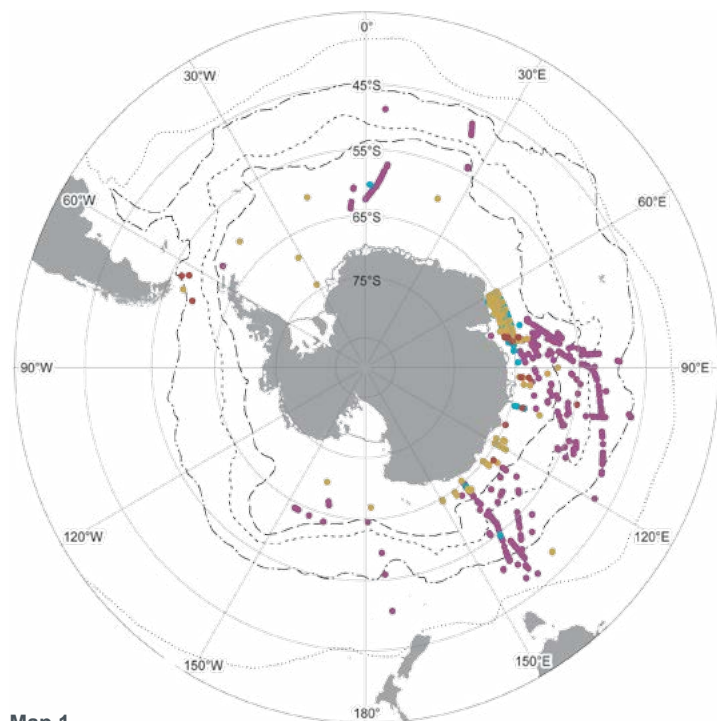
Photo 1 *Tomopteris* sp., Cosmonaut Sea (RV *Aurora Australis*, 2006 BROKE-West expedition). Image: A. Van de Putte © RBINS.

3. Benthic species

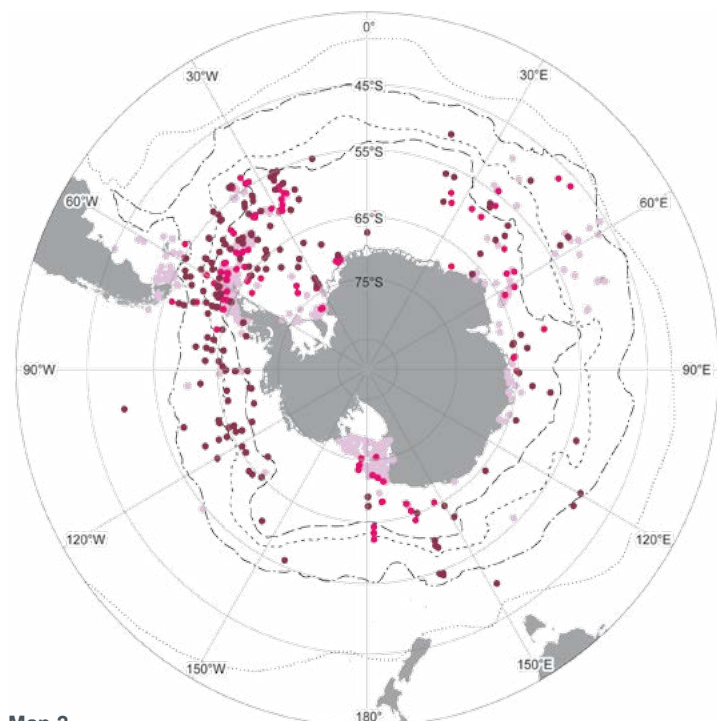
The total of 5607 benthic records represents 403 species belonging to 53 families (Map 2) (Tab. 1). Among about 30 known families that are not recorded from the Southern Ocean are interstitial forms, such as polygordiids and protodrilids, which are certainly present in coarse sediments but to date not investigated in macrobenthic studies.



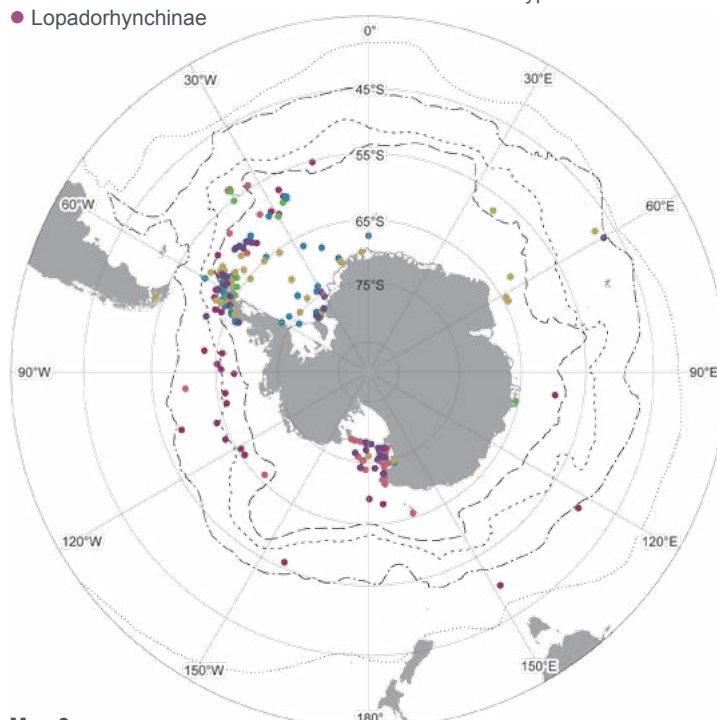
Photo 2 Unidentified Sabellidae, King George Island. Image © Dirk Schories, Universität Rostock.



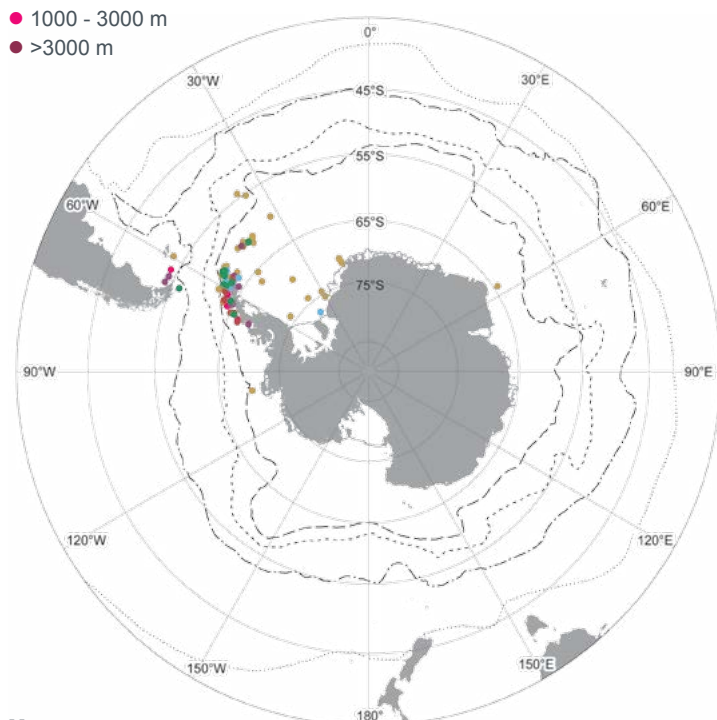
Map 1
Records of pelagic Polychaeta
● Tomopteridae
● Alciopidae
● Lopadorhynchinae
● Typhloscolecidae



Map 2
Records of benthic Polychaeta
● 0 - 1000 m
● 1000 - 3000 m
● >3000 m



Map 3
● *Aglaophamus trissophyllus*
● *Augeneria tentaculata*
● *Glycera kerguelensis*
● *Lumbrineris kerguelensis*
● *Ophelina breviata*
● *Paronuphis benthaliana*



Map 4
● *Asychis amphiglyptus*
● *Exogone obtusa*
● *Genetyllis polyphylla*
● *Neanthes kerguelensis*
● *Neosabellides elongatus*
● *Notalia picta*

Polychaeta Maps 1–4 Map 1. Records of pelagic polychaete families: Alciopidae, Lopadorhynchinae, Tomopteridae and Typhloscolecidae around the Southern Ocean. Map 2. Records of benthic polychaetes around the Southern Ocean. Map 3. Examples of benthic Antarctic polychaete species with circumpolar distribution: *Aglaophamus trissophyllus* (Grubbe, 1877), *Augeneria tentaculata* (Monro, 1930), *Glycera kerguelensis* (McIntosh, 1885), *Lumbrineris kerguelensis* (Grubbe, 1878), *Ophelina breviata* (Pettibone, 1954). Map 4. Examples of benthic Antarctic polychaete species with restricted distribution: *Asychis amphiglyptus* (Ehlers, 1897), *Exogone obtusa* (Hartmann-Schröder & Rosenfeldt, 1988), *Genetyllis polyphylla* (Ehlers, 1897), *Neanthes kerguelensis* (McIntosh, 1885), *Neosabellides elongatus* (Ehlers, 1912), *Notalia picta* (Kinberg, 1866).

3.1. General geographic and bathymetric patterns of benthic species

Among the 403 recorded benthic species in the SCAR-MarBIN database, 373 species are recorded in the Weddell Sea/Antarctic Peninsula/Scotia Arc area (20°E–100°W longitude, 5031 specimen records), 117 in the Ross Sea (100°E–140°W longitude, 390 specimen records) and only 26 in the Eastern Antarctic region (20°E–140°W longitude, 186 specimen records), displaying that in contrast to the planktonic realm, the benthic realm is best studied in the Weddell Sea/Peninsula/Scotia Arc. The total number of records for which depth information is available is 5347, of these 3851 are shelf (0–999 m) records, 740 slope (1000–3000 m) records, and 756 abyssal (>3000 m) records. In all depth ranges, the Weddell Sea/Peninsula/Scotia Arc is the area with the highest number of records, again reflecting the extensive sampling effort in this particular basin.

The species richness per depth range closely follows the number of records (and thus sampling effort) per depth. Brandt *et al.* (2009) published a survey on bathymetric patterns of Southern Ocean isopods, mollusks and polychaetes. Based on 657 polychaete species records they found an

apparent decline in species richness of almost 50% from upper shelf (<200 m) to the slope, and an additional much lesser decline from bathyal to abyssal depths (Fig. 1). A shift in the community structure of polychaetes from shelf to deep-sea species in the Southern Ocean is believed to occur in the lower bathyal zone around 2500–3000 m, in contrast to temperate waters where the upper slope constitutes the shift zone (Brandt *et al.* 1997, Hilbig 2004).

There is no obvious relation between wide bathymetric and wide geographic distribution of species. In the SCAR-MarBIN database 128 species are recorded from the Weddell Sea/Peninsula/Scotia Arc and at least one further sector defined herein (Ross Sea, Eastern Antarctica), and thus can be considered circumpolar. A total of 272 species are only recorded from one of the three sectors, and thus considered of locally restricted distribution herein (Tab. 1). Regarding bathymetric distribution patterns, a total of 86 species are eurybathic, which means they are reported from the shelf and the deep sea. However, only 53 of them (61.6%) can also be considered circumpolar species. In contrast to that, species with bathymetrically restricted distribution tend to also show restrictions in their geographical range. For example, 184 species recorded in the database are restricted to the shelf. Of these, 144 species (78%) display a locally restricted geographic distribution. Similarly,

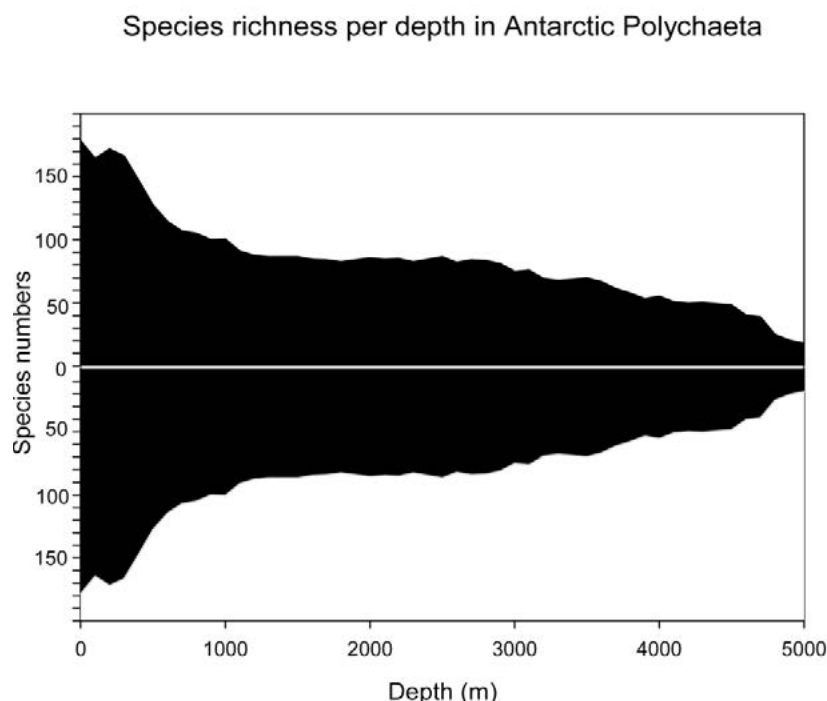


Figure 1 Antarctic polychaete species richness per depth (after Brandt *et al.* 2009).

restricted. As mentioned before, all statements about distributions have to be viewed with caution as they might rather reflect the scarcity especially of deep-sea samples that were foremost concentrated to the Weddell Sea. In general, only a pitiful 2–3% of all benthic records originate from samples below 3000 m, surprisingly even less originate from the slope.

3.2. Circumpolar species

Map 3 shows a typical distribution for what are considered circumpolar, and in these cases also eurybathic species. Shown are the records for the Glyceridae *Glycera kerguelensis* (137 records, 112–4928 m depth), the Lumbrineridae *Augeneria tentaculata* (46 records, 91–4077 m) and *Lumbrineris kerguelensis* (72 records, 38–3144 m), the Nephtyidae *Aglaophamus trissophyllus* (103 records, 10–4698 m), the Onuphidae *Paronuphis benthaliana* (41 records, 403–4930 m) and the Opheliidae *Ophelina breviata* (70 records, 10–4817 m). These species are all recorded for the Weddell Sea/Peninsula and the Ross Sea regions, in the cases of *A. trissophyllus* and *P. benthaliana* also records from the Eastern Antarctic sector are known. The high number of records suggests that all these species can be regarded as common and are thus identified consistently by involved working groups worldwide. In contrast to rare species, a lack in records of these species for a region might actually indicate their true absence there.

An interesting aspect of the distribution among these six widely distributed species is their difference in life habit. Although little is known about polychaete ecology in the Southern Ocean, some assumptions based on body form and knowledge of temperate-water relatives of the species can be made. *Paronuphis tentaculata*, as most Onuphidae, is a tube dwelling polychaete with limited mobility. Similar limitations in mobility account for *O. breviata*, which is a burrowing species, and possibly also for *G. kerguelensis*. Some species of the genus *Glycera* are known to live in semi-permanent tubes in the sediment and lurk for their prey (e.g. Böggemann 2005), a behaviour that might also be imaginable for *G. kerguelensis* as glycerids have a very similar body morphology. The remaining three species belong to families known for comparably higher mobility and thus higher distribution potential than the former three. Hence, it seems that circumpolar distribution of species is not necessarily hindered by their ecology per se, and possibly underlies a long evolutionary history of species. As very little is known about reproduction and larval development of Southern Ocean polychaetes, the potential for dispersal through larvae cannot be assessed but presumably plays an important role. Generally, the role of larval dispersal on different temporal and spatial scales is not well understood (Levin 2006).

Moreover, it has to be kept in mind that new methods of taxonomy, such as genetics, for several years have resulted in a new point of view on widely distributed species in general, including “cosmopolitan” polychaetes. Of the above mentioned widespread species, *G. kerguelensis* has already been shown by Schüller (2011) to consist of more than one species. Several populations found in different depth within only a small region of the Weddell Sea and even sympatric specimens at one sampling site were separated by genetic distances in their COI-sequence (barcoding gene sequence) at levels proposed to represent separated species. Given that specimens in the study by Schüller (2011) were undistinguishable morphologically, the common issue of cryptic species in the Southern Ocean (e.g. Held & Wägele 2005) might be a source of erroneously reported wide distribution in polychaetes as well.

3.3. Locally restricted species

As stated above, roughly 70% of all species recorded are currently only recorded from one of the areas distinguished herein. Of these species, the overwhelming majority is reported to occur exclusively in the Weddell Sea/Peninsula (246 species, 91% of all species with restricted distribution), while

very few species have been reported to occur in the Ross Sea only (10 species, nearly 4%) and eastern Antarctica, respectively (14 species, about 5%). As the proportion of records exclusively from the Weddell Sea, Ross Sea or the eastern Antarctic, respectively, is similar, distributional patterns deducted from the database may reflect undersampling and/or gaps in the data base to a greater extent than true distributional ranges.

In Map 4 the distribution patterns of six different, locally restricted species are shown. All six species, recorded only from the Weddell Sea region, were chosen because they are represented by comparably high numbers of records, giving rise to the assumption that the data reflect true distributional patterns.

Despite their similar geographic distribution, the shown species display different bathymetric patterns. The species with the highest number of records is *Neosabellides elongatus* (88 records, 62–5474 m depth), a tube-dwelling and thus hemi-sessile Ampharetidae, that is known from the shelf down to the abyss. Ampharetidae are surface deposit feeders (Fauchald & Jumars 1979), most typically found in soft bottom sediments, and possibly more adapted to different environments, including a wide range of depths, than e.g., predator polychaetes that rely on certain prey and high prey density.

In contrast, the species *Neanthes kerguelensis* (Nereididae, 26 records, 8–220 m) and *Genetyllis polyphylla* (Phyllodocidae, 22 records, 45–384 m) are only found on the Weddell Sea shelf, while in the case of *Notalia picta* (Phyllodocidae, 44 records, 50–1048 m) records cover the shelf and upper slope. All these species belong to families that are motile and believed to be potential predators, but also detritivores (Fauchald & Jumars 1979), possibly accounting for a high habitat specialisation either related to availability of prey organisms or the amount of detritus in the sediments.

The Syllidae *Exogone obtusa* is also reported only from the Weddell Sea shelf (57 records, 50–466 m), with its distributional range most likely reflecting sufficient quantities of diatoms for feeding (deep-sea Exogoninae may specialise on foraminiferans according to Fauchald & Jumars (1979)). A generalised relation between bathymetric distribution, mobility and feeding behavior is however far from possible. This is e.g., shown by a further species with restricted geographic and bathymetric distribution, *Asychis amphiglyptus* (38 records, 44–851 m), which is a tube-dwelling sub-surface deposit feeding Maldanidae that may request a certain organic content and grain size distribution of the sediment that is only present in small, well-defined areas of the Southern Ocean.

3.4. Endemism

One of the most prominent characteristics of the benthic organisms of the Southern Ocean, especially the shelf, is a high degree of endemism (Griffiths 2010, Clarke & Johnston 2003) which usually is related to the history of the Antarctic continent and its surrounding oceans. Knox and Cameron (1998) considered about 28% of the polychaete species from the Ross Sea to be endemic to the Southern Ocean. Hilbig (2004) reported nearly 40% of all polychaete species from the abyssal plains of the Weddell and Scotia Seas to be endemic. It should be kept in mind, however, that this percentage may have two biases: (1) newly described species are per se endemic until found again, possibly in a different region, and (2) the generally low sampling activity in the oceans of the southern hemisphere may prevent new records of “endemic” Southern Ocean species from neighboring oceans. Nonetheless, the abyssal polychaete fauna seems to exhibit a lesser degree of endemism than the shelf and slope fauna. For the former, the ACC apparently is not as high a barrier as originally thought. Distributional patterns of shelf species occurring in areas adjacent to the Southern Ocean but separated by the ACC are still not well understood, while the explanation for the occurrence of endemic shelf species (evolutionary history of Antarctica) is still valid.

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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



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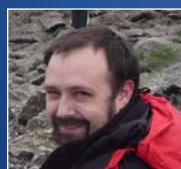
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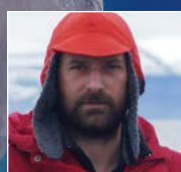
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Yan ROPERT COUDERT spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (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.

