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BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 6.6. SOUTHERN OCEAN PELAGIC COPEPODS.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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6.6. Southern Ocean Pelagic Copepods

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1. Introduction

Pelagic copepods are a key component of the zooplankton fauna in the Southern Ocean, being numerically the dominant group with huge biomasses in the productive seasons (Foxton 1956, Longhurst 1985). They are important elements in the Antarctic food chain, being preyed upon by krill and other carnivorous macroplankton, cephalopods, all kinds of juvenile fish, whales (caught up with krill) and diving seabirds. They occur from ice-edge to bathy-abyssal environments. The Antarctic sea ice sometimes houses hundreds of thousands copepods per square meter of ice (Hoshiai & Tanimura 1986, Swadling *et al.* 1997, 2000, Schnack-Schiel *et al.* 2001).

Diets vary from herbivore in the genera *Calanus, Calanoides, Eucalanus* and *Rhincalanus*, omnivore/carnivore in some Aetideidae, Oithonidae, Oncaeidae and Corycaeidae to strict carnivory feeding strategies in the genera *Paraeuchaeta, Euaugaptilus, Pseudochirella* and *Gaetanus*. The speciose and abundant Scolecithricidae are suggested to be the major detritivores in the Southern Ocean.

The distribution and diversity of Antarctic copepods have been well studied in the past two centuries. The *Challenger* expedition (1873–1876) was the first of many expeditions to the Southern Ocean and provided material for taxonomic studies. Brady (1883) described dominant and widespread species, based on the *Challenger* collections, Giesbrecht (1902), based on *Belgica* collections, Wolfenden (1905, 1906, 1911), based on the *Gauss* collections, and Farran (1929), based on the British *Terra Nova* collections. Two important monographs (Vervoort 1951, 1957) contain redescriptions of many previously known Southern Ocean species. Tanaka (1960, 1964) reported on the copepods collected by the Japanese Antarctic Expedition in 1957 and 1959. On the basis of collections made by the Soviet Antarctic expeditions, 1955–1958, Brodsky (1958, 1962, 1964, 1967) published several studies of the important herbivorous genus *Calanus*. Bradford (1971, 1981), and Bradford & Wells (1983) contributed important taxonomic knowledge regarding Southern Ocean copepods. Taxonomic works by Park (1978, 1980, 1982, 1983a, 1983b, 1988, 1993) are based on the U.S. *Eltanin* collections, and significantly increased our taxonomic understanding of most pelagic copepods. The *Eltanin* collections are included in an interactive database of Antarctic Invertebrates from the Smithsonian National Museum of Natural History: http://invertebrates.si.edu/antiz/taxon_view.cfm?taxon=7611 (Lemaitre *et al.* 2009). Many other important works followed (Björnberg 1968, 1973, Heron & Bowman 1971, Yamanaka 1976, Fontaine 1988, Razouls *et al.* 2000, Markhaseva 2001, Park & Ferrari 2009).

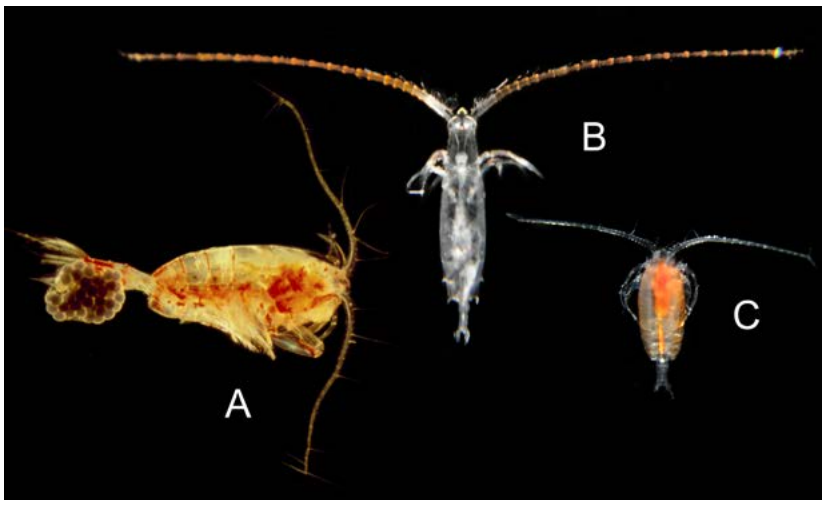


Photo 1 Morphologically typical pelagic Antarctic copepods: (a) *Paraeuchaeta* sp., female with egg batch; (b) *Rhincalanus* sp.; (c) unidentified calanoid. Images © (a), C. Razouls, Observatoire Océanologique, Banyuls; (b), (c), A. Van de Putte, RBINS.

Recently, new bathybenthic and abyssal species were described from just above the deep-sea floor, at 3000-4000 m (Markhaseva & Schulz 2006a, 2007, 2008a, b, 2009, Markhaseva 2010, Markhaseva *et al.* 2010, Markhaseva & Renz 2011, Renz *et al.* 2012).

The endemic inshore and ice-edge species are adapted to the coldest temperatures. The non-endemics, drifting with ocean currents, show various ways of distribution within- and outside the Southern Ocean: by surface currents, mid-ocean and deep currents. Considering the complex hydrodynamics of ocean currents in space and time, fluctuating upwelling patterns and vertical migration behaviour of many copepod species, the mechanisms controlling distribution patterns are numerous. Many species cross the Polar Front and/or the Sub-Antarctic Front and/or the Sub-Tropical Front. This pattern works in both directions. Species abundant in Antarctic waters may range to north-temperate/Sub-Arctic zones and some show bipolar distribution. Contrary, (sub)-tropical or north-temperate species may be found in the Antarctic Zones. It is often difficult to distinguish between the different distribution mechanisms. Also, the existing potential of human-related species introductions (hull-fouling species on ships) may interfere with natural biogeographic patterns (Lewis *et al.* 2003).

2. Methods

In this synthesis the Southern Ocean includes both the Antarctic Region, (south of the Polar Frontal Zone, including the ice-edge), and the Sub-Antarctic Region, (north of the Polar Frontal Zone, between the Sub-Antarctic Front and the Sub-Tropical Front).

Occurrence data are based on Razouls *et al.* (2000), Park & Ferrari (2009), Razouls *et al.*, (2005–2012) and Vanden Berghe (2007), including all species updates in the Southern Ocean. Copepod distribution and abundance data were also consulted at the OBIS website: "http://iobis.org/Maps/distribution" and included in the results for key species. For several Antarctic species the abundance details are known (McLeod *et al.* 2010). The data from the Southern Ocean Continuous Plankton Recorder Survey were assessed online (http://data.aad.gov.au/aadc/cpr), comprising surface samples from the region south of Australia.

In addition to the copepods in the order Calanoida, addressed in Park & Ferrari (2009), species belonging to the Orders Cyclopoida (Families Lubbockiidae, Oithonidae, Oncaeidae, Corycaeidae, Sapphirinidae), Harpacticoida (Family Ectinosomatidae), Misophrioida (Family Misophriidae) and Monstrilloida (Family Monstrillidae) are also included here.

Emphasis is given to both common and rare Southern Ocean endemics, mapping the distribution for the most common and abundant species. Species showing distribution ranges over more latitudes are also listed according to their main depth ranges. Key-species distribution patterns are figured using Maps from OBIS.

3. Copepod distribution in the Southern Ocean: from ice edge endemism to wide range distribution patterns

A total of 388 species, 15.5% of the global marine copepod fauna, have been reported in the Antarctic Ocean (continent and southern parts of the three oceans). 273 species are presently described occurring in the South Pacific, 224 species in the southern Indian Ocean and 221 species in the South Atlantic. Several are circumpolar species, encountered in the southern parts of all three oceans. One hundred and fourteen species live in contact with the continent or near the ice pack. In view of the imprecisely defined latitudinal limits for the Polar Frontal Zone, it is probable that 223 forms observed in the Sub-Antarctic Zone come from sub-tropical and temperate zones, carried by surface or deep-water currents. This relatively high immigration level for Copepoda is perhaps accidental, and may constitute pseudo-populations as described for coccolithophores by Winter *et al.* (1999) in the Weddell Sea.

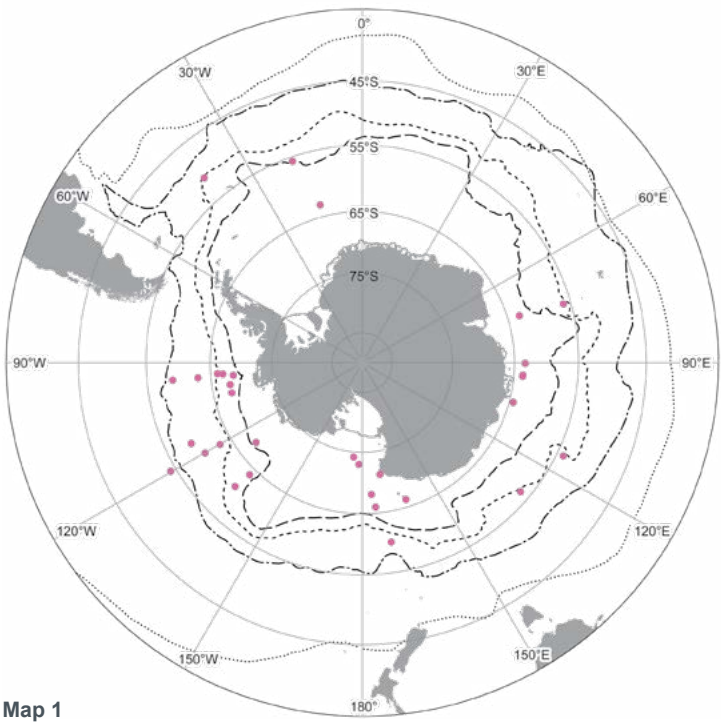
Drifting in intermediate and deepwater currents many Antarctic species range further north, some as far as the Arctic basin. Likewise, Arctic species may be found far south, penetrating the Antarctic waters, like *Epicalymma schmitti* Heron, 1977; *Epicalymma umbonata* Heron, 1977; *Oncaea lacinia* Heron, English & Damkaer, 1984 and *Mimocalanus distinctocephalus* Brodsky, 1950.

3.1. Endemic Antarctic species south of the Polar Frontal Zone

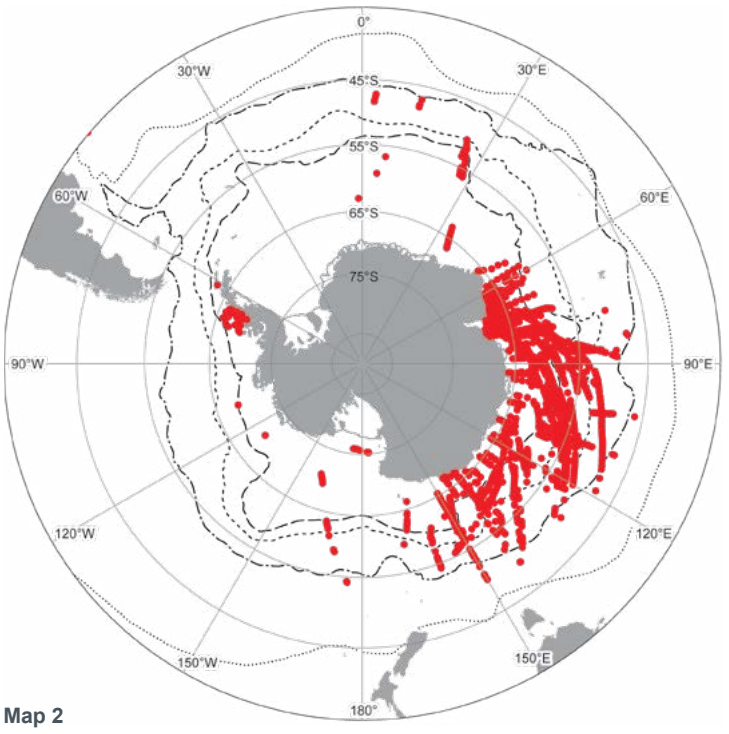
There are 53 endemic species occurring south of the Polar Frontal Zone, of which 49 are very rare and three common: *Drepanopus bispinosus* Bayly, 1982; *Euaugaptilus antarcticus* (Wolfenden, 1911), and *Paraeuchaeta similis* (Wolfenden, 1908).

Fourteen species are endemic in the Pacific Antarctic: *Chiridiella megadactyla* Bradford, 1971; *Euaugaptilus hadrocephalus* Park, 1993; *Frigocalanus rauscherti* Schulz, 1996; *Monstrilla conjunctiva* Giesbrecht, 1902; *Mospicalanus schielae* Schulz, 1996; *Oncaea bowmani* Heron, 1977; *Oncaea petila* Heron, 1977; *Paraeuchaeta erebi* Farran, 1929; *Paraeuchaeta tycodesma* (Park, 1978); *Paralabidocera grandispina* Waghorn, 1979; *Pseudoamallothrix incisa* (Farran, 1929); *Xantharus renatehaassae* Schulz, 1998; *Xanthocalanus antarcticus* Wolfenden, 1908; *Xanthocalanus harpagatus* Bradford & Wells, 1983. All of these are rare to very rare species, habitats varying from ice-edge to Antarctic deep water and sea floor.

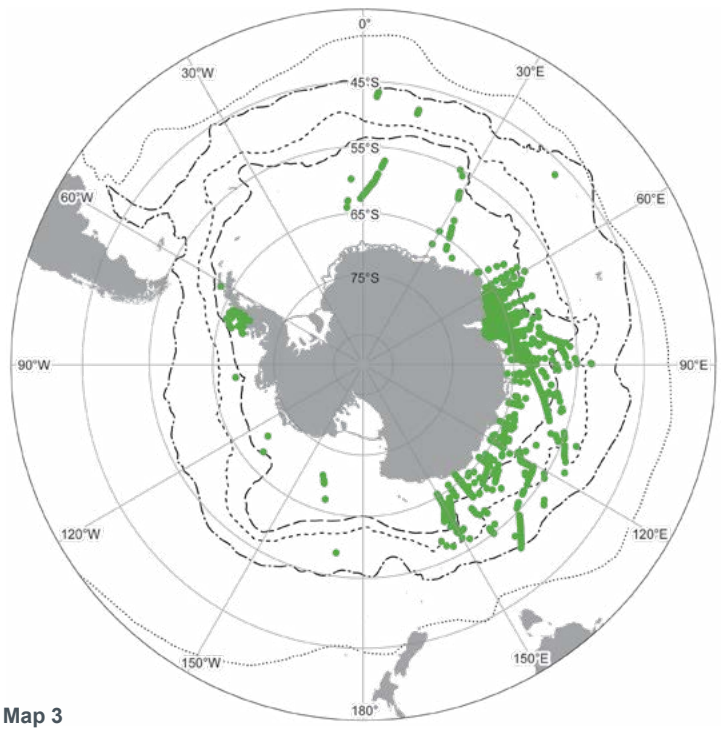
Twenty-four species are endemic in the Atlantic Antarctic, all very rare and most are recently described from bathypelagic and abyssal environments: *Brachycalanus antarcticus* Schulz, 2005; *Bradyetes curvicornis* Markhaseva & Schulz, 2006; *Bradyetes weddellanus* Markhaseva & Schulz, 2006; *Brodskius abyssalis* Markhaseva & Schulz, 2007; *Caudacalanus mirus* Markhaseva & Schulz, 2008; *Cenognatha antarctica* (Hulsemann, 1985); *Comantenna gesinae* Schulz, 2002; *Damkaeria bicornuta* Schulz, 2004; *Diaiscolecithrix andeep* Markhaseva, Schulz & Renz, 2010; *Kunihulsea antarctica* Schulz, 2004; *Lamiantennula longifurca* Markhaseva & Schulz, 2006; *Misophriella schminkei* Martinez Arbizu & Jaume, 1999; *Misophriopsis australis* Martinez Arbizu & Jaume, 1999; *Omorius curvispinus* Markhaseva & Schulz, 2007; *Parabradyidius angelikae* Schulz & Markhaseva, 2000; *Paraxantharus brittae* Schulz, 2006; *Paraxantharus victorbergeri* Markhaseva, 2010; *Plesioscolecithrix juhlae* Markhaseva & Dahms, 2004; *Pseudeuchaeta*



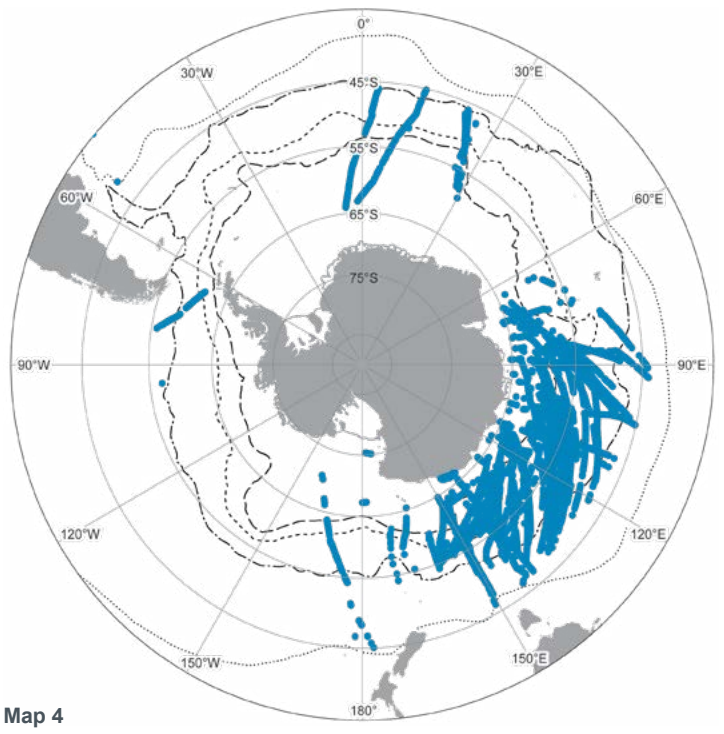
Map 1
● *Euaugaptilus antarcticus*



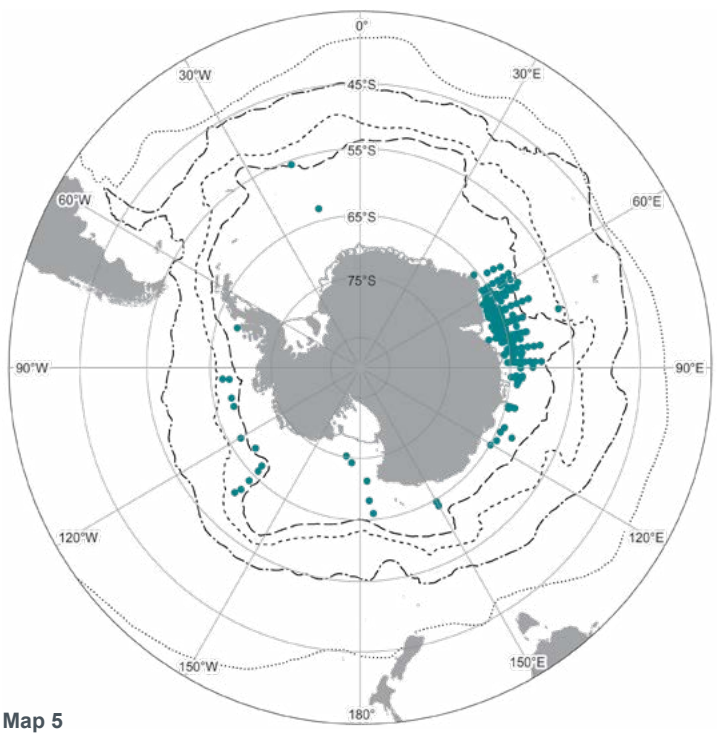
Map 2
● *Calanoides acutus*



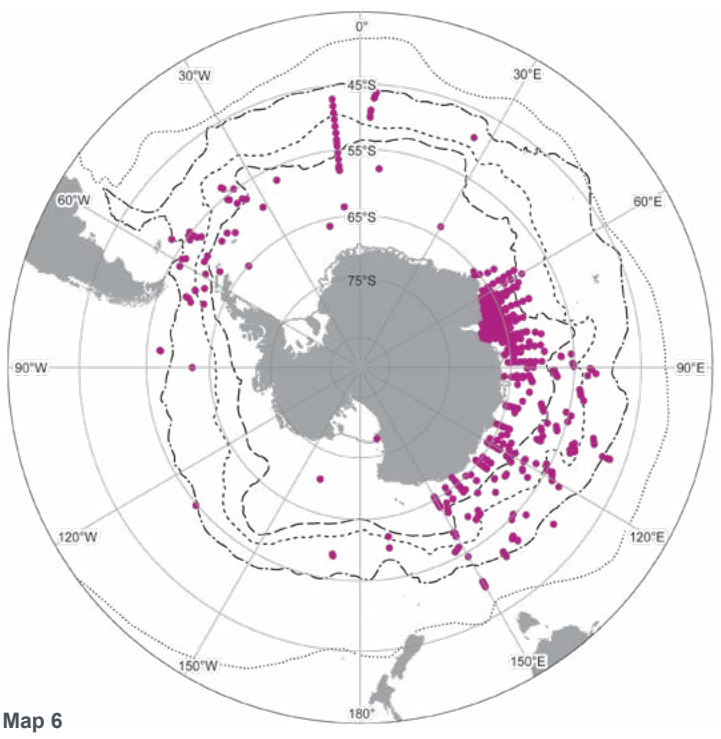
Map 3
● *Calanus propinquus*



Map 4
● *Calanus simillimus*



Map 5
● *Haloptilus ocellatus*



Map 6
● *Paraeuchaeta antarctica*

Pelagic copepods Maps 1–6 Map 1. Distribution of *Euaugaptilus antarcticus* (Wolfenden, 1911). Map 2. Distribution of *Calanoides acutus* (Giesbrecht, 1902). Map 3. Distribution of *Calanus propinquus* Brady, 1883. Map 4. Distribution of *Calanus simillimus* Giesbrecht, 1902. Map 5. Distribution of *Haloptilus ocellatus* Wolfenden, 1905. Map 6. Distribution of *Paraeuchaeta antarctica* (Giesbrecht, 1902).

acuticornis Markhaseva & Schulz, 2006; *Pseudotharybis polaris* Markhaseva & Schulz, 2008; *Ryocalanus antarcticus* Renz, Markhaseva & Schulz, 2012; *Rythabis asymmetrica* Markhaseva & Schulz, 2007; *Scolecitrichopsis elenae* Schulz, 2005; *Sensiava longiseta* Markheseva & Schulz, 2006.

Six species are endemic in the Indian Antarctic: *Batheuchaeta antarctica* Markhaseva, 1986; *Batheuchaeta pubescens* Markhaseva, 1986; *Drepanopus bispinosus* Bayly, 1982, common in brackish waters of Antarctic lakes (Razouls *et al.*, 2000); *Paralabidocera separabilis* Brodsky & Zvereva, 1976; *Pseudochirella formosa* Markhaseva, 1989; *Xanthocalanus tenuiserratus* Wolfenden, 1911. These are very rare abyssopelagic forms, except the inshore, ice-edge dwellers *D. bispinosus* and *P. separabilis*.

Seven species have a circumpolar distribution: *Aetideopsis antarctica* (Wolfenden, 1908); *Euaugaptilus antarcticus* (Wolfenden, 1911) (Map 1); *Paraeuchaeta austrina* (Giesbrecht, 1902); *Paraeuchaeta similis* (Wolfenden, 1908); *Paralabidocera antarctica* (I.C. Thompson, 1898); *Stephos longipes* Giesbrecht, 1902; *Xanthocalanus gracilis* Wolfenden, 1911. These species live along the ice-edge, some sampled to very deep on the sea floor. Low copepod diversity is characteristic for the sea ice habitat, because of special adaptations to the low temperatures and high salt concentrations. Dominant species show high abundance (Swadling 2000). *Stephos longipes* is the dominant sea-ice calanoid in the Weddell, Amundsen and Bellingshausen Seas. Nauplii live in extreme habitats formed by highly saline brine channels and pockets in the frozen seawater, where their number reaches up to 200,000 individuals m^{-2} (Schnack-Schiel *et al.* 1995). Although it was also found off the South African coast (Namibia), we describe it to the dominating Antarctic endemics. Likewise, the dominant *Paralabidocera antarctica*, also found in the Sub-Antarctic Zone, is considered an endemic associate for the Antarctic sea-ice. Nauplii and copepodids remain within the sea-ice matrix (up to 900,000 ind. m^{-2}), older stages leave for the ice-water interface (Arndt & Swadling 2006).

Two species occur in two Antarctic subzones: *Stephos antarcticus* Wolfenden, 1908 lives under the ice in both the Indian and Pacific sector, whereas the hyperbenthic ice-associated *Tharybis magna* Bradford & Wells, 1983 occurs in both the Atlantic and Pacific sector near the Antarctic continent.

3.2. Endemic species of the Southern Ocean: occurring in both the Antarctic and Sub-Antarctic Zones

Thirteen species are typical endemics in the Southern Ocean, occurring from the Antarctic Continent ice-edge to the Sub-Tropical Zone (the broad zone of transition, between tropical/temperate and polar ocean dynamics): *Byrathis arnei* Schulz, 2006; *Calanoides acutus* (Giesbrecht, 1902) (Map 2). (This epi-mesopelagic species is considered a dominant herbivore of the Southern Ocean (Park & Ferrari, 2009), together with *Calanus propinquus* Brady, 1883 and *Calanus simillimus* Giesbrecht, 1902); *Drepanopus pectinatus* Brady, 1883; *Heterostylites nigrotinctus* (Brady, 1918); *Landrumius antarcticus* Park, 1983; *Metridia pseudoasymmetrica* Markhaseva, 2001; *Mixtocalanus vervoorti* (Park, 1980); *Onchocalanus paratrigoniceps* Park, 1983; *Onchocalanus wolfendeni* Vervoort, 1950; *Scaphocalanus antarcticus* Park, 1982; *Scaphocalanus parantarcticus* Park, 1982. Most are large species (prosome length 4–6 mm), making up more than 40% of total copepod biomass during the most productive periods. Some typically Southern Ocean species have been found north of its northern limits, a frontal region of limited width, known as the Sub-Tropical Front.

3.3. Species surpassing the Sub-Tropical Front

3.3.1. Present in the Antarctic Zone, Sub-Antarctic Zone and north of the Sub-Tropical Front

Species ranging from the Antarctic Zone to south temperate latitudes

Epipelagic: *Oithona frigida* Giesbrecht, 1902.
Epi-mesopelagic: *Aetideopsis tumorosa* Bradford, 1969; *Calanus propinquus* Brady, 1883 (Map 3) (see comment *Calanoides acutus*); *Calanus simillimus* Giesbrecht, 1902 (Map 4); *Candacia maxima* Vervoort, 1957; *Clausocalanus brevipes* Frost & Fleminger, 1968; *Drepanopus forcipatus* Giesbrecht, 1888 (neritic, littoral, restricted to Atlantic and Pacific coastal and shelf areas along southern South America, including the Falkland Islands, and around South Georgia Island (Hulsemann 1985a); *Haloptilus ocellatus* Wolfenden, 1905 (Map 5), [according to Vervoort (1951: 144), its dorsal black eye spot, its exceptional size (8.2-8.5 mm) and its pointed forehead make the species recognizable at a glance; in situ, the black spot is the only visible part]; *Oncaea curvata* Giesbrecht, 1902; *Pleuromamma antarctica* Steuer, 1931; *Pseudochirella mawsoni* Vervoort, 1957; *Subeucalanus longiceps* (Matthews, 1925); *Triconia antarctica* (Heron, 1977); *Triconia inflexa* (Heron, 1977).
Epi-meso-bathypelagic: *Aetideus australis* (Vervoort, 1957); *Metridia gerlachei* Giesbrecht, 1902; *Paraeuchaeta antarctica* (Giesbrecht, 1902) (Map 6); *Rhincalanus gigas* Brady, 1883; *Scaphocalanus vervoorti* Park, 1982 (confusions possible with *S. subbrevicornis*).
Meso-bathypelagic: *Amallothrix dentipes* (Vervoort, 1951); *Bathycalanus eltaninae* Björnberg, 1968; *Bathycalanus inflatus* Björnberg, 1968; *Bradycalanus pseudotypicus* Björnberg, 1968; *Cornucalanus robustus* Vervoort, 1957; *Euaugaptilus aliquantus* Park, 1993; *Euaugaptilus perasetosus* Park, 1993; *Euchirella rostromagna* Wolfenden, 1911; *Heterorhabdus pustulifer* Farran, 1929; *Paraeuchaeta dactylifera* (Park, 1978); *Paraeuchaeta eltaninae* (Park, 1978); *Paraeuchaeta exigua* (Wolfenden, 1911); *Paraeuchaeta rasa* Farran, 1929; *Paraeuchaeta parvula* (Park, 1978); *Paraeuchaeta regalis* (Grice & Hulsemann, 1968); *Paraheterorhabdus (Paraheterorhabdus) farrani* (Brady, 1918); *Pseudoamallothrix hadrosoma* (Park, 1980); *Pseudochirella hirsuta* Wolfenden, 1905 (Map 7); *Scaphocalanus farrani* Park, 1982.
Bathy-abyssopelagic: *Byrathis divae* Markhaseva & Renz, 2011 (hyperbenthic, abyssal); *Metridia ferrarii* Markhaseva, 2001.

Species ranging from the Antarctic Zone to (sub) tropical latitudes

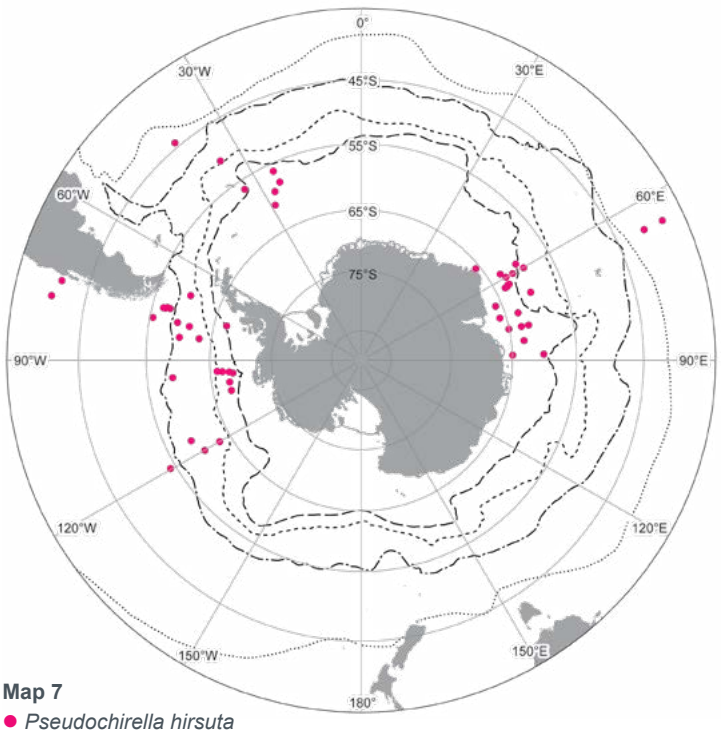
Epipelagic: *Centropages brachiatus* (Dana, 1849).
Epi-meso-bathypelagic: *Clausocalanus laticeps* Farran, 1929 **(**Map 8**)** (There is a possibility of confusion with *C. ingens* Frost & Fleminger, 1968. Park & Ferrari (2009) describe the species as endemic to Antarctic waters and among the copepods most often associated by planktonologists with the Southern Ocean); *Ctenocalanus citer* Heron & Bowman, 1971; *Lucicutia clausi* (Giesbrecht, 1889); *Paraeuchaeta biloba* Farran, 1929.
Meso-bathypelagic: *Euaugaptilus maxillaris* Sars, 1920; *Heterorhabdus austrinus* Giesbrecht, 1902; *Mixtocalanus alter* (Farran, 1929); *Oncaea rotunda* Heron, 1977; *Paraeuchaeta aequatorialis* Tanaka, 1958; *Pseudoamallothrix cenotelis* (Park, 1980); *Scaphocalanus elongatus* A. Scott, 1909; *Spinocalanus terranovae* Damkaer, 1975.
Bathypelagic: *Amallothrix parafalcifer* (Park, 1980); *Cephalophanes frigidus* Wolfenden, 1911; *Cornucalanus robustus* Vervoort, 1957 (a characteristic Antarctic deep water copepod. The species probably has a much wider distribution in the deep water of the Atlantic Ocean); *Valdiviella oligarthra* Steuer, 1904.

Species ranging from the Antarctic Zone to north temperate latitudes

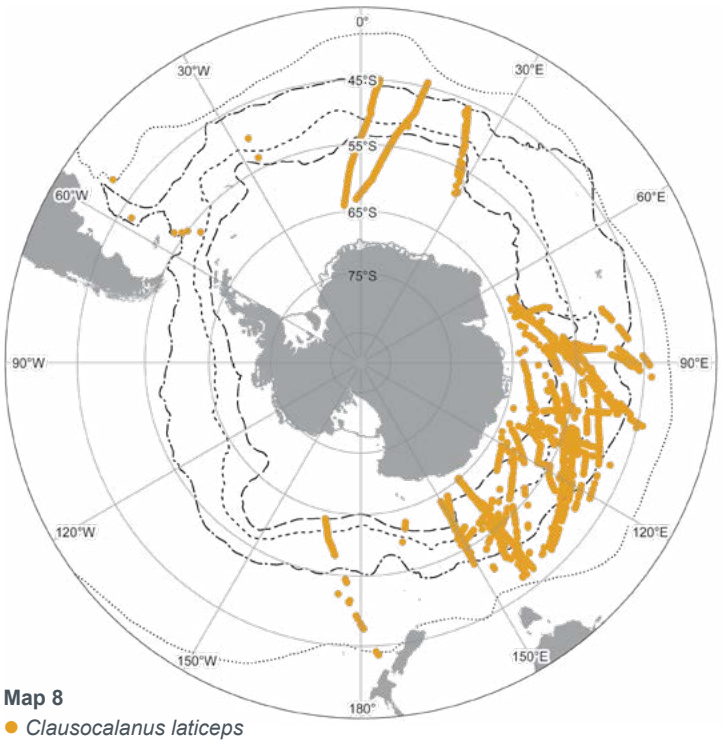
Epipelagic: *Labidocera acutifrons* (Dana, 1849).
Epi-mesopelagic: *Scolecithricella dentata* (Giesbrecht, 1892).
Mesopelagic: *Neocalanus tonsus* (Brady, 1883).
Meso-bathypelagic: *Gaetanus antarcticus* Wolfenden, 1905; *Haloptilus fons* Farran, 1908; *Paraeuchaeta abbreviata* (Park, 1978).
Bathypelagic: *Homeognathia flemingi* (Heron & Damkaer, 1978); *Oncaea macilenta* Heron, 1977; *Oncaea prolata* Heron, 1977; *Pseudoamallothrix obtusifrons* (Sars, 1905); *Paraeuchaeta scotti* (Farran, 1908).

Species ranging from the Antarctic Zone to sub-Arctic latitudes

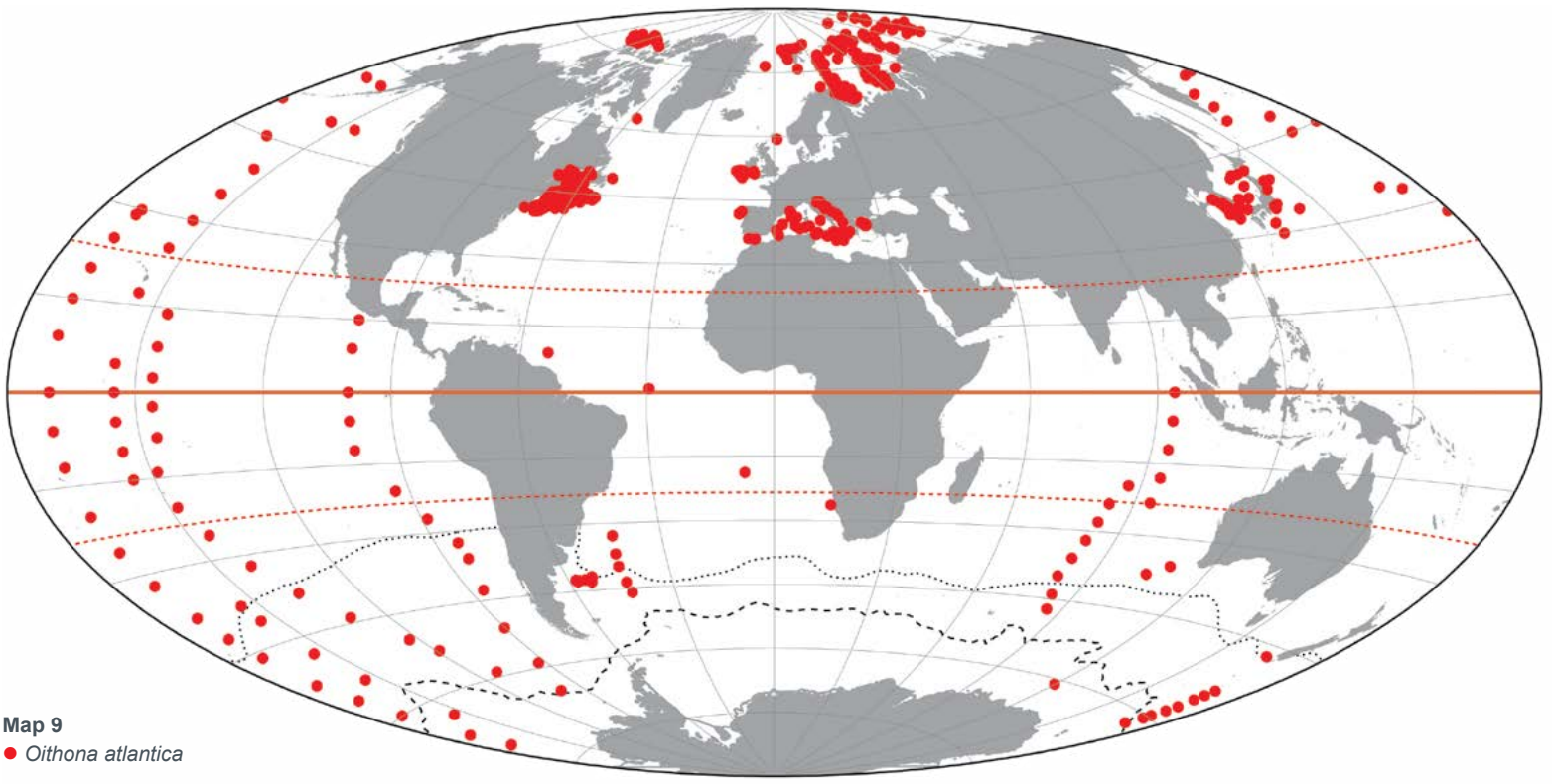
Epipelagic: *Farranula gracilis* (Dana, 1849); *Oithona plumifera* Baird, 1843; *Paracalanus parvus* (Claus, 1863).
Epi-mesopelagic: *Pleuromamma gracilis* (Claus, 1863).
Epi-meso-bathypelagic: *Aetideus armatus* (Boeck, 1872); *Aetideus bradyi* A. Scott, 1909; *Corycaeus (Agetus) flaccus* Giesbrecht, 1891; *Euchirella rostrata* (Claus, 1866); *Haloptilus longicornis* Brodsky, 1950; *Haloptilus oxycephalus* (Giesbrecht, 1889); *Heterorhabdus papilliger* Claus, 1863; *Heterorhabdus spinifrons* (Claus, 1863); *Lubbockia aculeata* Giesbrecht, 1891; *Lucicutia curta* Farran, 1905; *Lucicutia magna* Wolfenden, 1903; *Lucicutia ovalis* (Giesbrecht, 1889); *Nannocalanus minor* (Claus, 1863); *Oncaea illgi* Heron, 1977; *Oncaea venusta* Philippi, 1843; *Pleuromamma xiphias* (Giesbrecht, 1889); *Pseudochirella notacantha* (Sars, 1905); *Scaphocalanus echinatus* (Farran, 1905); *Triconia conifera* (Giesbrecht, 1891); *Undeuchaeta major* Giesbrecht, 1888.
Meso-bathypelagic: *Amallothrix robusta* (T. Scott, 1894); *Amallothrix valida* (Farran, 1908); *Archescolecithrix auropecten* (Giesbrecht, 1892); *Bathycalanus richardi* Sars, 1905; *Centraugaptilus rattrayi* (T. Scott, 1894); *Cornucalanus chelifer* (Thompson, 1903); *Euaugaptilus bullifer* (Giesbrecht, 1889); *Euaugaptilus laticeps* (Sars, 1905); *Euaugaptilus nodifrons* (Sars, 1905); *Euaugaptilus oblongus* (Sars, 1905); *Heterostylites longicornis* (Giesbrecht, 1889); *Heterostylites major* (F. Dahl, 1894); *Lucicutia macrocera* Sars, 1920; *Megacalanus longicornis* (Sars, 1905) [= *M. princeps Woldenden,* 1904], *Mormonilla phasma* Giesbrecht, 1891; *Nullosetigera bidentata* (Brady, 1883); *Onchocalanus trigoniceps* Sars, 1905; *Onchocalanus cristatus* (Wolfenden, 1904); *Paraeuchaeta kurilensis* Heptner, 1971; *Paraeuchaeta pseudotonsa* (Fontaine, 1967) (The discrimination between this species *P. tonsa* and *Euchaeta scaphula* (see *P. tuberculata*) is very difficult, hence the difficulties to determine with certainty its geographical distribution); *Pseudoamallothrix emarginata* (Farran, 1905); *Pseudochirella obtusa* (Sars, 1905); *Scaphocalanus major* (T. Scott, 1894); *Scaphocalanus subbrevicornis* (Wolfenden, 1911); *Scottocalanus securifrons* (T. Scott, 1894); *Undeuchaeta incisa* Esterly, 1911; *Undinella simplex* (Wolfenden, 1906).
Meso-abyssopelagic: *Bathycalanus bradyi* (Wolfenden, 1905); *Chiridius polaris* Wolfenden, 1911; *Euaugaptilus magnus* (Wolfenden, 1904]); *Metridia curticauda* Giesbrecht, 1889; *Metridia brevicauda* Giesbrecht, 1889; *Mimocalanus cultrifer* Farran, 1908.
Bathypelagic: *Bathycalanus princeps* (Brady, 1883); *Conaea rapax* Giesbrecht, 1891; *Gaetanus pungens* (Giesbrecht, 1895); *Lophothrix humilifrons* Sars, 1905; *Metridia ornata* Brodsky, 1950; *Onchocalanus magnus* (Wolfenden, 1906); *Paraeuchaeta sarsi* (Farran, 1908); *Valdiviella insignis* Farran, 1908 .
Bathy-abyssopelagic: *Augaptilus cornutus* Wolfenden, 1911; *Lucicutia wolfendeni* Sewell, 1932; *Paraeuchaeta tumidula* (Sars, 1905); *Pseudeuchaeta brevicauda* Sars, 1905; *Pseudochirella pustulifera* (Sars, 1905); *Valdiviella brevicornis* Sars, 1905.
Abyssopelagic: *Batheuchaeta lamellata* Brodsky, 1950.



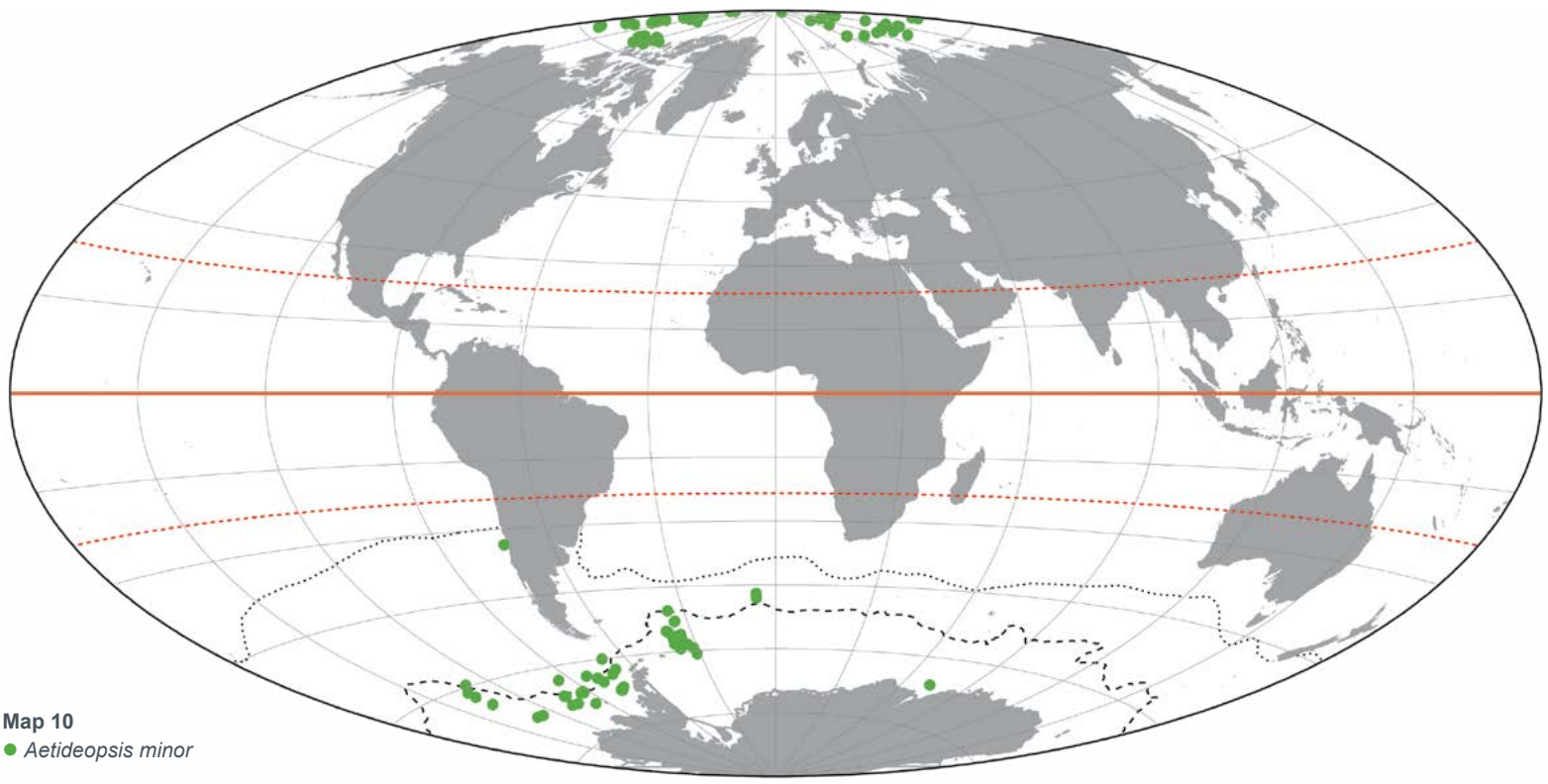
Map 7
● *Pseudochirella hirsuta*



Map 8
● *Clausocalanus laticeps*



Map 9
● *Oithona atlantica*



Map 10
● *Aetideopsis minor*

Pelagic copepods Maps 7–10 Map 7. Distribution of *Pseudochirella hirsuta* (Wolfenden, 1905). Map 8. Distribution of *Clausocalanus laticeps* Farran, 1929. Map 9. Distribution of *Oithona atlantica* Farran, 1908. Map 10. Distribution of *Aetideopsis minor* (Wolfenden, 1911).

Species ranging from the Antarctic Zone to the Arctic Ocean

Most of the species listed here have a wide depth range, which allows transport by different current regimes.
Epipelagic: *Oithona atlantica* Farran, 1908 (Map 9); *Oithona similis* Claus, 1866 (cosmopolitan).
Epi-mesopelagic: *Bradyidius armatus* Giesbrecht, 1897 (also hyperbenthic); *Metridia lucens* Boeck, 1864 (For Kosobokova & al. (2011, Table 3) this species is an expatriate species from Atlantic to the Arctic Ocean Basins, because the reproduction is not assumed in polar waters); *Microcalanus pusillus* Sars, 1903.
Epi-meso-bathypelagic: *Aetideopsis minor* (Wolfenden, 1911) (Map 10); *Gaetanus tenuispinus* (Sars, 1900) (characteristic in intermediate depths); *Haloptilus acutifrons* (Giesbrecht, 1892); *Microcalanus pygmaeus* (Sars, 1900); *Microsetella norvegica* (Boeck, 1864) (cosmopolitan); *Oncaea englishi* Heron, 1977; *Pseudoamallothrix ovata* (Farran, 1905); *Racovitzanus antarcticus* Giesbrecht, 1902; *Rhincalanus nasutus* Giesbrecht, 1888 (cosmopolitan); *Scolecithricella minor* (Brady, 1883). For Park (1980, p.35) the latter species is the most common of the genus in Antarctic waters; it seems to be the only species that inhabits mainly the epipelagic parts of the antarctic seas.
Epi-meso-bathy-abyssopelagic: *Spinocalanus magnus* Wolfenden, 1904.
Epi-meso-bathy-abysso-hadopelagic: *Scaphocalanus magnus* (T. Scott, 1894).
Mesopelagic: *Chiridius gracilis* Farran, 1908.
Meso-bathypelagic: *Aetideopsis multiserrata* (Wolfenden, 1904); *Augaptilus glacialis* Sars, 1900; *Neomormonilla minor* (Giesbrecht, 1891) (in the Arctic seas it could be confused with *N. polaris*); *Paraeuchaeta barbata* (Brady, 1883); *Pleuromamma robusta* (F. Dahl, 1893); *Pseudhaloptilus eurygnathus* (Sars, 1920); *Spinocalanus abyssalis* Giesbrecht, 1888; *Temorites brevis* Sars, 1900.
Meso-abyssopelagic: *Aetideopsis rostrata* Sars, 1903.
Meso-bathy-abysso-hadopelagic: *Gaetanus brevispinus* (Sars, 1900). *Talacalanus greeni* (Farran, 1905).
Bathy-abyssopelagic: *Paraheterorhabdus (Antirhabdus) compactus* (Sars, 1900).

3.3.2. Present in the Antarctic Zone, north of the Sub-Tropical Front and absent in the Sub-Antarctic Zone

Species in the Antarctic Zone, absent in the Sub-Antarctic Zone, ranging to south temperate latitudes

Bathypelagic: *Bradycalanus gigas* Sewell, 1947; *Scaphocalanus impar* (Wolfenden, 1911).
Bathy-abyssopelagic: *Prolutamator minor* Markhaseva & Schulz, 2008.
Abyssal (above the sea bed): *Caudacalanus vicinus* Markhaseva & Schulz, 2008.

Species in the Antarctic Zone, absent in the Sub-Antarctic Zone, ranging to (sub) tropical latitudes

Epi-mesopelagic: *Corycaeus (Urocorycaeus) furcifer* Claus, 1863.
Meso-bathypelagic: *Euaugaptilus austrinus* Park, 1993 (First occurrence in Indonesian waters by Matsuura *et al.* (2010)); *Farrania frigida* (Wolfenden, 1911); *Landrumius gigas* (A. Scott, 1909); *Pontoptilus ovalis* Sars, 1907; *Teneriforma meteorae* Schulz, 1989.
Meso-abyssopelagic: *Teneriforma naso* (Farran, 1936).
Bathypelagic: *Bradycalanus typicus* A. Scott, 1909; *Cornucalanus simplex* Wolfenden, 1905; *Euaugaptilus placitus* (A. Scott, 1909); *Oncaea setosa* Heron, 1977; *Valdiviella minor* Wolfenden, 1911.
Abyssal: *Benthomisophria cornuta* Hulsemann & Grice, 1964.

Species in the Antarctic Zone, absent in the Sub-Antarctic Zone, ranging to north temperate latitudes

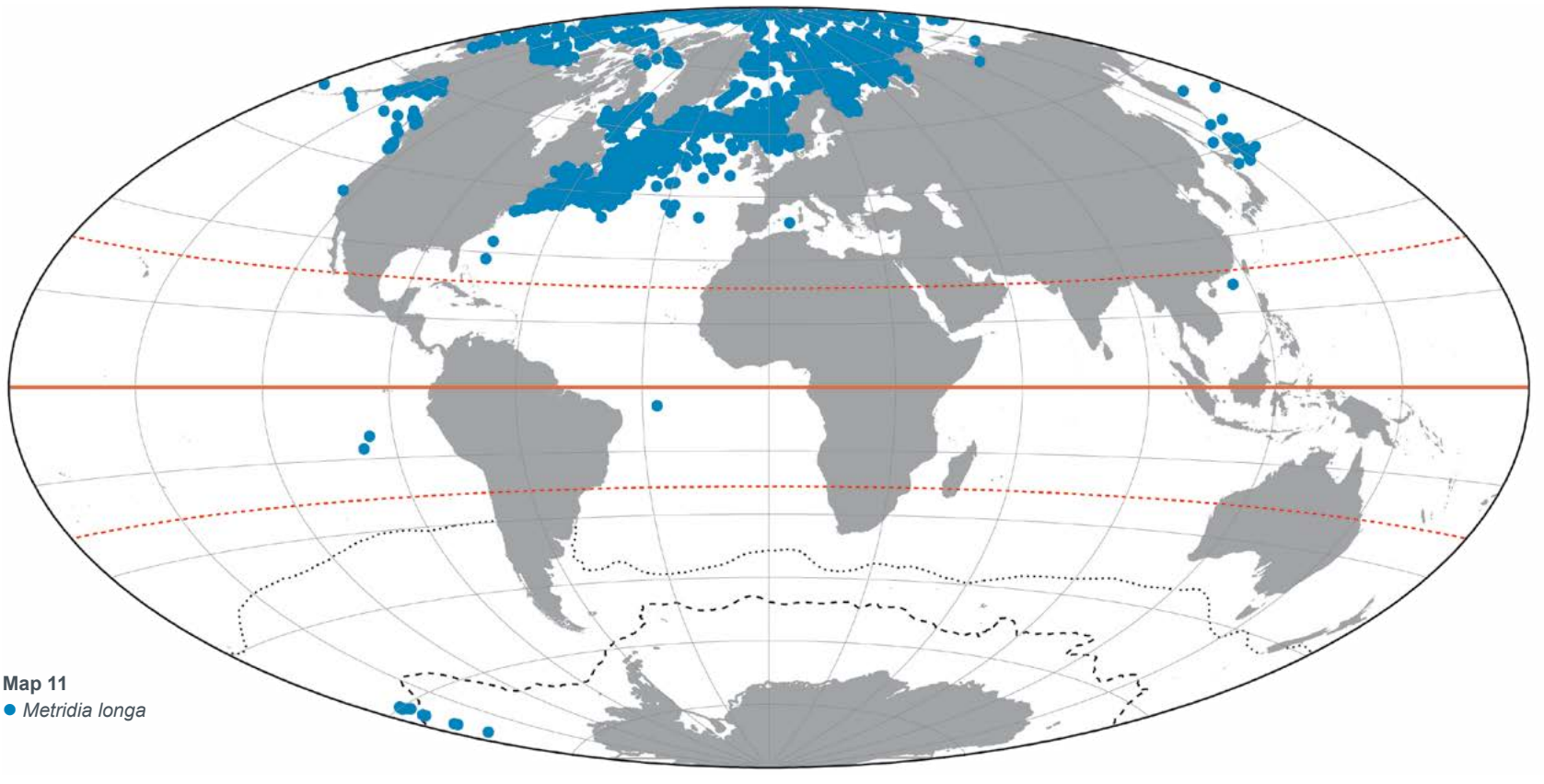
Epipelagic: *Sapphirina nigromaculata* Claus, 1863.
Epi-mesopelagic: *Sapphirina metallina* Dana, 1849; *Scolecithrix danae* (Lubbock, 1856).
Bathypelagic: *Mimocalanus nudus* Farran, 1908; *Oncaea convexa* Heron, 1977; *Oncaea walleni* Heron, 1977.

Species in the Antarctic Zone, absent in the Sub-Antarctic Zone, ranging to sub-Arctic latitudes

Meso-bathypelagic: *Candacia falcifera* Farran, 1929; *Pseudaugaptilus longiremis* Sars, 1907.
Bathypelagic: *Conaea hispida* Heron, 1977; *Conaea succurva* Heron, 1977; *Lubbockia wilsonae* Heron & Damkaer, 1969; *Oncaea brocha* Heron, 1977; *Oncaea damkaeri* Heron, 1977; *Oncaea olsoni* Heron, 1977; *Onchocalanus hirtipes* Sars, 1905 (This species is closely related to *O. wolfendeni*); *Ratania atlantica* Farran, 1926; *Rhamphochela carinata* (Heron & Damkaer, 1978); *Rhamphochela forcipula* (Heron & Damkaer, 1978).
Bathy-abyssopelagic: *Arietellus simple*x Sars, 1905 ; *Chiridiella subaequalis* Grice & Hulsemann, 1965; *Gaetanus paracurvicornis* Brodsky, 1950; *Haloptilus longicirrus* Brodsky, 1950; *Pseudochirella dubia* (Sars, 1905).
Abyssopelagic: *Batheuchaeta peculiaris* Markhaseva, 1983 (Originally described from localities adjacent to the Arctic Ocean).

Species in the Antarctic Zone, absent in the Sub-Antarctic Zone, ranging to the Arctic Ocean

Epi-meso-bathypelagic: *Metridia longa* (Lubbock, 1854) (Map 11); *Pseudochirella spectabilis* (Sars, 1900).
Meso-bathypelagic: *Pseudhaloptilus pacificus* (Johnson, 1936); *Spinocalanus antarcticus* Wolfenden, 1906.
Meso-abyssopelagic: *Mimocalanus distinctocephalus* Brodsky, 1950 (Voronina & Kolosova (1999) report this Arctic species for the first time in Antarctica); *Spinocalanus longicornis* Sars, 1900.
Bathypelagic: *Epicalymma umbonata* Heron, 1977; *Oncaea compacta* Heron, 1977; *Oncaea lacinia* Heron, English & Damkaer, 1984; *Oncaea parila* Heron, 1977; *Oncaea pumilis* Heron, 1977.
Bathy-abyssopelagic: *Epicalymma schmitti* Heron, 1977; *Metridia princeps* Giesbrecht, 1889 (near-cosmopolitan); *Pseudochirella batillipa* Park, 1978; *Spinocalanus horridus* Wolfenden, 1911.



Map 11
● *Metridia longa*

Pelagic copepods Map 11 Distribution of *Metridia longa* (Lubbock, 1854).

3.3.3. Present in the sub-Antarctic Zone and north of the Sub-Tropical Front, absent in the Antarctic Zone

Species ranging from the Sub-Antarctic Zone to south temperate latitudes

Epipelagic: *Acartia (Acartiura) ensifera* Brady, 1899; *Calocalanus longispinus* Shmeleva, 1978; *Monstrilla patagonica* Suarez-Morales, Ramirez & Derisio, 2008; *Monstrillopsis chilensis* Suarez-Morales, Bello-Smith & Palma, 2006; *Monstrillopsis igniterra* Suarez-Morales, Ramirez & Derisio, 2008; *Temora kerguelensis* Wolfenden, 1911 (Described from 2 males. Not observed in numerous samples off Kerguelen); *Calanoides patagoniensis* Brady, 1883 (a good indicator for the penetration of Sub-Antarctic waters into the NW Indian Ocean, if adult forms were captured there).
Epi-mesopelagic: *Aetideus pseudarmatus* Bradford, 1971; *Candacia cheirura* Cleve, 1904 (West Wind Drift species (Vervoort 1957)).
Epi-meso-bathypelagic: *Calanoides macrocarinatus* Brodsky, 1967;
Bathypelagic: *Euaugaptilus brevirostratus* Park, 1993; *Euchirella latirostris* Farran, 1929; *Lucicutia bradyana* Cleve, 1904.

Species ranging from the Sub-Antarctic Zone to (sub-)tropical latitudes

Epipelagic: *Centropages furcatus* (Dana, 1849); *Oithona fallax* Farran, 1913; *Oithona simplex* Farran, 1913.
Epi-mesopelagic: *Calocalanus elegans* Shmeleva, 1965; *Calocalanus elongatus* Shmeleva, 1968; *Calocalanus gresei* Shmeleva, 1973; *Calocalanus longisetosus* Shmeleva, 1965; *Calocalanus ovalis* Shmeleva, 1965; *Calocalanus pavoninus* Farran, 1936; *Calocalanus plumatus* Shmeleva, 1965; *Clausocalanus ingens* Frost & Fleminger, 1968; *Paracalanus indicus* Wolfenden, 1905; *Scolecithricella vittata* (Giesbrecht, 1892).
Meso-bathypelagic: *Calanoides carinatus* (Krøyer, 1848); *Calanus australis* Brodsky, 1959 (southern population of *C. finmarchicus* (Gunnerus, 1770)); *Chiridius molestus* Tanaka, 1957; *Euaugaptilus gibbus* (Wolfenden, 1904); *Euchirella similis* (Wolfenden, 1911); *Lucicutia maxima* Steuer, 1904 (Because of synonymies certain geographic distributions are to be confirmed); *Paraeuchaeta comosa* Tanaka, 1958; *Paraeuchaeta malayensis* Sewell, 1929; *Pseudochirella spinosa* (Wolfenden, 1905); *Scolecithricella profunda* (Giesbrecht, 1892).

Species ranging from the Sub-Antarctic Zone to north temperate latitudes

Epi-mesopelagic: *Acartia (Acanthacartia) tonsa* Dana, 1849; *Calocalanus contractus* Farran, 1926; *Calocalanus plumulosus* (Claus, 1863); *Clausocalanus pergens* Farran, 1926; *Oncaea mediterranea* (Claus, 1863); *Pleuromamma piseki* Farran, 1929; *Paracalanus aculeatus* Giesbrecht, 1888; *Scaphocalanus curtus* (Farran, 1926); *Temora turbinata* (Dana, 1849).
Meso-bathypelagic: *Aetideus arcuatus* (Vervoort, 1949); *Amallothrix pseudopropinqua* (Park, 1980) (this species seems to be similar to *Scolecithricella propinqua* (Sars, 1920); *Euaugaptilus angustus* (Sars, 1905); *Paraeuchaeta calva* Tanaka, 1958; *Paraeuchaeta confusa* Tanaka, 1958 (doubt on identification).

Species ranging from the Sub-Antarctic Zone to sub-Arctic latitudes

Coastal, hyperbenthic: *Oculosetella gracilis* (Dana, 1852).
Epipelagic: *Centropages bradyi* Wheeler, 1901.
Epi-mesopelagic: *Atrophia minuta* (Wolfenden, 1905); *Calocalanus styliremis* Giesbrecht, 1888; *Candacia simplex* (Giesbrecht, 1889); *Euchaeta acuta* Giesbrecht, 1892; *Euchirella maxima* Wolfenden, 1905; *Macrosetella gracilis* (Dana, 1848) (observed in ballast waters); *Mecynocera clausi* Thompson, 1888; *Microsetella rosea* (Dana, 1848); *Phaenna spinifera* Claus, 1863; *Pleuromamma borealis* (F. Dahl, 1893); *Subeucalanus mucronatus* (Giesbrecht, 1888); *Undeuchaeta plumosa* (Lubbock, 1856).
Epi-bathypelagic: *Calocalanus pavo* (Dana, 1849); *Ctenocalanus vanus* Giesbrecht, 1888; *Eucalanus hyalinus* (Claus, 1866); *Gaetanus minor* Farran, 1905; *Mesocalanus tenuicornis* (Dana, 1849); *Neocalanus gracilis* (Dana, 1849); *Pleuromamma abdominalis* (Lubbock, 1856).
Epi-meso-bathy-abysso-hadopelagic: *Chirundina streetsii* Giesbrecht, 1895.
Meso-bathypelagic: *Aegisthus mucronatus* Giesbrecht, 1891; *Aetideus arcuatus* (Vervoort, 1949); *Corycaeus (Onychocorycaeus) pacificus* F. Dahl, 1894; *Gaetanus kruppi* Giesbrecht, 1903; *Gaetanus latifrons* Sars, 1905; *Gaetanus pileatus* Farran, 1903; *Heterorhabdus abyssalis* (Giesbrecht, 1889); *Heterorhabdus clausi* (Giesbrecht, 1889); *Metridia venusta* Giesbrecht, 1889; *Pleuromamma quadrungulata* (F. Dahl, 1893); *Paraeuchaeta hanseni* (With, 1915); *Scaphocalanus affinis* (Sars, 1905); *Scaphocalanus medius* (Sars, 1907); *Scottocalanus thori* With, 1915 (some distributions for the latter species are doubtful, because of confusions with *S. persecans* and *S. helenae* by various authors); *Spinocalanus brevicaudatus* Brodsky, 1950; *Triconia similis* (Sars, 1918).
Bathy-abyssopelagic: *Disseta palumbii* Giesbrecht, 1889; *Gaussia princeps* (T. Scott, 1894); *Lophotrix frontalis* Giesbrecht, 1895; *Metridia macrura* Sars, 1905.

Species ranging from the Sub-Antarctic Zone to the Arctic Ocean

There is only one species showing a distribution range from the Sub-Antarctic Zone to Arctic Ocean, however with doubt: *Eucalanus hyalinus* (Claus, 1866) (epi-bathypelagic depth range). For Goetze & Bradford-Grieve (2005, p.81) the identification given by the majority of workers cannot reliably be assigned to *E. hyalinus* s.s or *E. spinifer*.

4. Discussion

A general pattern can be distinguished in the wider distribution of the Southern Ocean pelagic copepods. Epi-to mesopelagic species mainly range from the Southern Ocean to south temperate, sub-tropical and tropical latitudes, while species with a deep migration pattern, covering a vertical amplitude of several thousands of meters (epi-to abyssopelagic) drift with different deep currents and are encountered from Antarctic to boreal seas (89 species) and Arctic Ocean (44 species). Some are (near) cosmopolitan. Sub-Antarctic species, absent in the Antarctic Zone, do not range to the Arctic. Their most northern distribution observed is in sub-Arctic regions for mainly deepwater forms.

The following species are considered as bipolar: *Aetideopsis minor*; *Batheuchaeta peculiaris*; *Epicalymma schmitti*; *Epicalymma umbonata*; *Oncaea compacta*; *Oncaea lacinia*; *Oncaea parila*; *Pseudochirella batillipa*; *Pseudochirella spectabilis*; *Racovitzanus antarcticus*; *Spinocalanus antarcticus*. The bipolar calanoid species listed by Park & Ferrari (2009) include also *Aetideopsis rostrata*; *Chiridius polaris*; *Metridia ornata*. These species were later recorded from several temperate and sub-tropical regions (Razouls *et al.* 2005–2012) suggesting a wider biogeographic pattern. Park & Ferrari (2009) described the ways of bipolarity for nine bipolar, rare species.

1) Originally described from the Southern Ocean, later reported in the Arctic basin and adjacent boreal seas (*Aetideopsis minor, Chiridius polaris, Pseudochirella batillipa* and *Spinocalanus antarcticus)*

2) Originally described from the Arctic Ocean or adjacent boreal seas and later reported from the Southern Ocean (*Batheuchaeta peculiaris* and *Metridia ornata)*

3) Originally different species, later found to be identical, have become bipolar after having been synonymised (*Aetideopsis rostrata* and *Pseudochirella spectabilis*).

Bipolar species can drift with deep currents to other regions than the Southern and Northern oceans and be encountered in areas with strong upwelling, for example N. Arabian Sea, Sargasso Sea, Japan, off California. It is often not known in which water mass the encountered species resided (vertical sampling other than MOCNESS net system). Also the succession of generations, vertical movements, (diel and ontogenetic migrations) should be taken into account. Then there is the existence of pseudo-populations far from the “normal” reproduction area of the species. Because of these aspects copepod biogeography is still progressive including bipolarity assignments. After the explosive increase of Polar Research Programmes (>200 projects, 60 nations) during the International Polar Year (IPY) from 2007 to 2009, new data are becoming available with respect to the bipolarity (or not) of marine copepods.

Large-size copepods are often associated with polar seas. The majority of Southern Ocean copepod species are of large size (4-6 mm prosome length). It is generally viewed that cold waters, including eutrophic upwelling systems, contain large species, while warm water communities, living under oligotrophic conditions contain smaller copepods. Considerable size variations were even observed within one, globally distributed species *Paraeuchaeta barbata* (Park & Ferrari, 2009). The size range of copepods increases with decreasing temperature and with depth. However, Hopcroft *et al.* (2001) pointed out that small copepods and early developmental stages dominate in tropical as well as in temperate oceans. Atkinson & Sinclair (2000) reported similar results for the Southern Ocean. Small copepods (*Microcalanus pygmaeus*, *Ctenocalanus* spp., *Oncaea* spp. and *Oithona* spp.) formed about 75% of total copepod abundance in the top 1000 m across all major zones from the Sub-Antarctic Front to the Weddell-Scotia Confluence. However, in terms of biomass, the large species make up more than 40% during the most productive periods (see also 3.2).

Some species have an uncertain distribution pattern due to taxonomic confusion. At a global level there are about one hundred uncertain forms and sixty-one have not been reported since 1911. Antarctic species not having been encountered since their description are a.o.: *Metridia trispinosa* Brady, 1918; *Xanthocalanus tenuiserratus* Wolfenden, 1911; *Temora kerguelensis* Wolfenden, 1911.

The numbers of endemism in the three sectors of the Antarctic Ocean are also a result of the sampling effort, and the available taxonomic effort (sample analysis, species descriptions) for each sector. Most of the 24 Atlantic endemics are from the last 10 years, most of the 6 Indian endemics are from the 1980s, and most of the 14 Pacific endemics were described between 1970/90s and early 20th century. Further effort on deep-sea sampling in the Antarctic will most probably increase the number of endemism in the selected sector(s).

Since the work of Park & Ferrari (2009) various Southern Ocean species considered endemic have been reported elsewhere. For example *Onchocalanus magnus* and *Scaphocalanus subbrevicornis* currently range to sub-arctic latitudes. It remains uncertain, however, whether wide-ranged species also have established stable populations north of the Sub-Tropical Front or whether there is gene flow. Barriers to gene flow, such as sub-tropical fronts, tropical waters (for cold water species) obviously leave passage for planktonic organisms, with the ability to establish successful populations outside the original distributional range. *Rhincalanus nasutus*, however, considered to be a cosmopolitan species, was found to be a cryptic species complex (Goetze 2003). There is a strong support through genetic data, that lineages, centered in different coastal boundary currents, do not exchange genes. Likewise, molecular phylogenetic results including Arctic and Antarctic

specimens of bipolar *Aetideopsis minor* and mesopelagic *Gaetanus tenuispinus* suggest different geographic forms, potentially cryptic species or sibling species (Laakman *et al.* 2012). On the other hand, these authors found great similarities in Arctic and Antarctic individuals of both bathypelagic *Gaetanus brevispinus* and *Paraeuchaeta barbata*, suggesting more gene flow at depth and/or less pronounced driving forces for speciation in these deep-sea species. Phylogeographic studies using molecular analyses may offer more insight in former or ongoing genetic exchange between disjunct populations, clarifying the possibly wider zoogeographic distribution of copepod species residing in the Southern Ocean.

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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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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.