Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 6.5. SOUTHERN OCEAN SQUID.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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6.5. Southern Ocean Squid

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1. Introduction

Data on Antarctic cephalopods have accumulated since the expeditions of *HMS Challenger* and *HMS Alert* in the 19th century and the heroic era of Antarctic exploration in the early years of the 20th century. After the 1920s there was little activity in the field until the 1960s when several nations started to send research ships to the Southern Ocean for biological research. Antarctic teuthology has since grown and matured and has been the subject of a symposium and four reviews (Clarke & Okutani 1985, Rodhouse *et al.* 1994, Filippova 2002, Collins & Rodhouse 2006).

Much of our knowledge of squid biogeography in the Antarctic and worldwide derives from the work of the Russian scientist Kir Nesis who died in 2003. His world survey of cephalopods (Abridged key to the cephalopod molluscs of the world) was published in Russian in 1982 and later in English with new material (Nesis 1987). This secondary source of information has been used here where the original papers in Russian, many by Nesis himself, are difficult to access. Xavier *et al.* (1999) published maps of all known and available records of squid captured in the Southern Ocean and, with subsequent additions, these form the basis of the maps published here.

The most sampled areas in the Southern Ocean are in the region of the larger peri-Antarctic islands, the Antarctic Peninsula and the Prydz Bay area. The least sampled region lies in the Pacific sector, roughly between 180° and 90°W.

The Southern Ocean squids (order Teuthida) are restricted to the suborder Oegopsida. The suborder Myopsida is absent from the Antarctic and Sub-Antarctic regions but one species, *Doryteuthis gahi*, occurs over the southern Patagonian Shelf. Of the octopuses (order Octopoda) both suborders Cirrata and Incirrata are represented. The nautiluses (Subclass Nautiloidea), the cuttlefish (Order Sepiida), the sepiolids (order Sepiolida) and the vampire squid (Order Vampyromorpha) are all absent.

The following southern hemisphere species, which have been included in lists of Antarctic cephalopods elsewhere, are not included here as there is little evidence that they are found south of the Sub-Tropical Front: *Promachoteuthis* sp., *Pholidoteuthis massyae, Octopoteuthis rugosa, Taningia danae*, *Histioteuthis macrohista* and *H. miranda*. A single specimen of the cranchiid squid *Taonius pavo* (Rodhouse, 1990) has also not been included.

Photo 1 *Martialia hyadesi* Rochebrune & Mabille, 1889. Image: © CP. Rodhouse.

2. Biogeography and depth distribution

There are some nineteen species of squid known to inhabit Antarctic and sub-Antarctic waters. Their latitudinal range can be divided into six categories from high Antarctic endemics to cosmopolitan species whose range extends into Antarctic waters. This is a loose categorisation for several reasons: the surface signatures of the fronts are often not well defined, their position vary and they do not reflect the deep structure of the water masses of the Southern Ocean. Furthermore, the interfaces between water masses probably do not form impenetrable barriers to squid dispersal.

2.1. Antarctic endemics extending north to the Antarctic Polar Front (APF)

Moroteuthis knipovitchi Filippova, 1972 (Map 1): one of four members of the family Onychoteuthidae known in the Southern Ocean; maximum ML 450 mm; circumpolar; mesopelagic and near bottom. The species occurs north of the APF at South Georgia, Kerguelen, Crozet and Prince Edward Islands. Literature: Filippova & Yukhov (1979), Rodhouse (1988, 1989), Rodhouse *et al.* (1996), Piatkowski *et al*. (1998).

Alluroteuthis antarcticus Odhner, 1923 (Map 2): sole member of the family Neoteuthidae known in the Southern Ocean; maximum ML 270 mm; circumpolar; mesopelagic. Literature: Filippova & Yukhov (1982), Rodhouse (1988, 1989); Piatkowski *et al*. (1994), Jackson *et al.* (2002).

Mastigoteuthis psychrophila Nesis, 1977 (Map 3): single member of the family Mastigoteuthidae known in the Southern Ocean; maximum ML 180 mm; circumpolar; mesopelagic and bathypelagic. Literature: Rodhouse (1990), Lu & Williams (1994a), Piatkowski *et al.* (1994), Rodhouse *et al.* (1996).

Mesonychoteuthis hamiltoni Robson, 1925 (Map 4): one of two members of the family Cranchiidae known in the Southern Ocean; maximum ML 2500 mm; circumpolar; bathypelagic and near bottom; young specimens have been recorded north of the APF. Large adults have only been caught south of the APF. They are an occasional by-catch in the South Georgia long-line fishery for Patagonian toothfish (*Dissostichus eleginoides*) and the Ross Sea fishery for Antarctic toothfish (*Dissostichus mawsoni*). Literature: Filippova & Yukhov (1979), Rodhouse & Clarke (1985), Jackson *et al*. (2002), Filippova (2002), Collins et al. (2010), Roberts *et al.* (2011).

2.2. Antarctic endemics extending north to the Sub-Antarctic Front (SAF)

Kondakovia longimana Filippova, 1972 (Map 5): one of four members of the family Onychoteuthidae known in the Southern Ocean; maximum ML 1100 mm; circumpolar; epipelagic, mesopelagic, bathypelagic and near bottom. Literature: Rodhouse (1990), Lu & Williams (1994a, b), Vacchi *et al*. (1994), Lynnes & Rodhouse (2002).

Psychroteuthis glacialis Thiele, 1920 (Map 6): the only species of the family Psychroteuthidae described; maximum ML 440 mm; circumpolar; mesopelagic, bathypelagic, near bottom. Literature: Filippova (1972), Filippova & Yukhov (1979), Kubodera (1989), Rodhouse (1989), Piatkowski *et al*. (1990, 1994, 1998), Lu & Williams (1994a), Gröger *et al.* (2000), Anderson & Rodhouse (2002), Collins *et al*. (2004).

Slosarczykovia circumantarctica Lipinski, 2001 (Map 7): the only member of the family Brachioteuthidae found in Antarctic waters apart from *Brachioteuthis linkovskyi* Lipinski, 2001 which is occasionally found in the Sub-Antarctic; maximum ML 90 mm; circumpolar; epipelagic, mesopelagic and bathypelagic. Literature: Kubodera (1989), Rodhouse (1989, 1990), Rodhouse *et al*. (1996), Piatkowski *et al*. (1994), Anderson & Rodhouse (2002), Collins *et al*. (2004) (referred to as notalian-Antarctic *B. riisei* by Nesis (1987) and as *B.* sp. and *B.* ?*picta* by other authors prior to Lipinski (2001).

2.3. Antarctic endemics extending north to the Sub-Tropical Front (STF)

Galiteuthis glacialis Chun, 1906 (Map 8): one of two members of the family Cranchiidae known in the Southern Ocean; maximum ML 330 mm; circumpolar; may occur north of the APF when Antarctic intermediate water moves north; bathypelagic and mesopelagic to lower epipelagic; Antarctic squid most commonly caught in research nets. Literature: Dell (1959), Filippova (1972), Lu & Mangold (1978), Kubodera & Okutani (1986), Rodhouse & Clarke (1986), Rodhouse (1989), Lu & Williams (1994a), Piatkowski & Hagen (1994), Rodhouse *et al*. (1996), Nesis *et al*. (1998), Piatkowski *et al*. (1994, 1998), Anderson & Rodhouse (2002), Jackson *et al.* (2002), Van de Putte *et al.* (2010).

Parateuthis tunicata Thiele, 1921 (Map 9): family *incertae sedis*: only larvae (<8 mm ML) known from deep water (>2000 m). Literature: Nesis (1987).

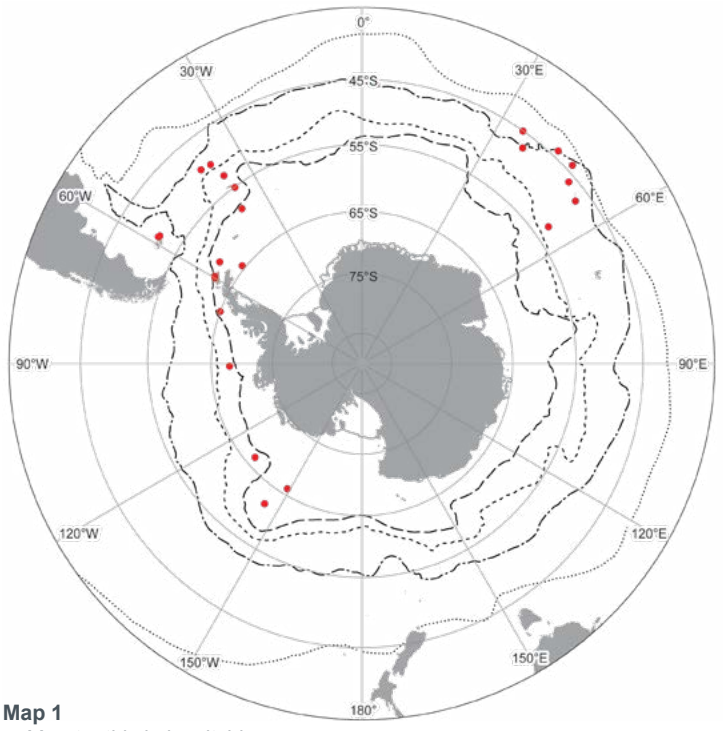
Batoteuthis skolops Young and Roper, 1968 (Map 10): the only known species of the family Batoteuthidae; circumpolar; maximum ML 95 mm; mesopelagic and bathypelagic. Literature: Filippova & Yukhov (1979), Rodhouse *et al.* (1992, 1996), Anderson & Rodhouse (2002), Jackson *et al*. (2002), Collins *et al*. (2004).

Histioteuthis eltaninae N. Voss, 1969 (Map 11): one of two members of the family Histioteuthidae known in the Southern Ocean; maximum ML 105 mm; circumpolar (more abundant north of the APF); mesopelagic and bathypelagic. Literature: Lu & Mangold (1978), Alexeyev (1994), Piatkowski *et al*. (1994), Rodhouse *et al.* (1996), Voss *et al.* (1998), Jackson *et al.* (2002).

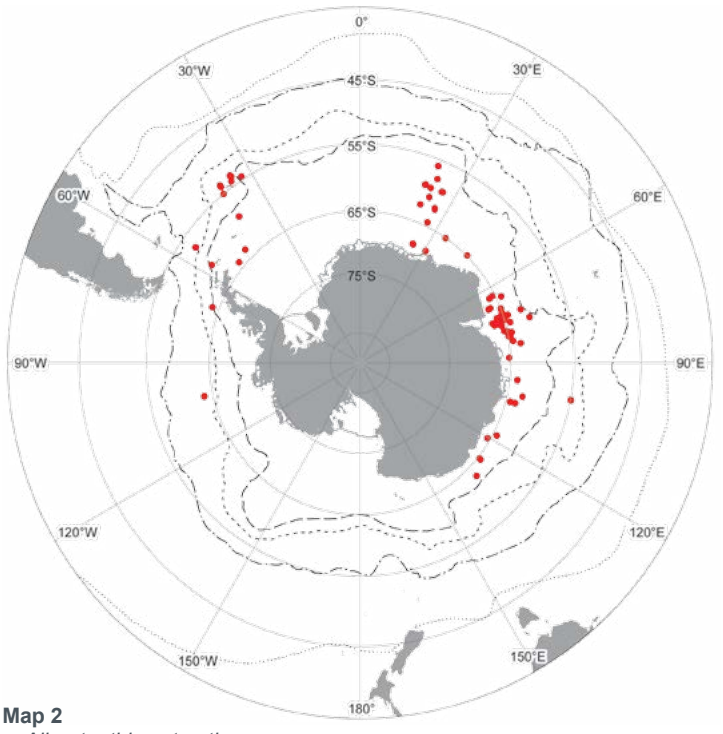
2.4. Sub-Antarctic (APF – STF)

Moroteuthis ingens Smith, 1881 (Map 12): one of four members of the family Onychoteuthidae known in the Southern Ocean; circumpolar; maximum ML 940 mm; near seabed from shelf to bathyal. Literature: Massy (1916), Filippova (1972), Filippova & Yukhov (1979), Alexeyev (1994).

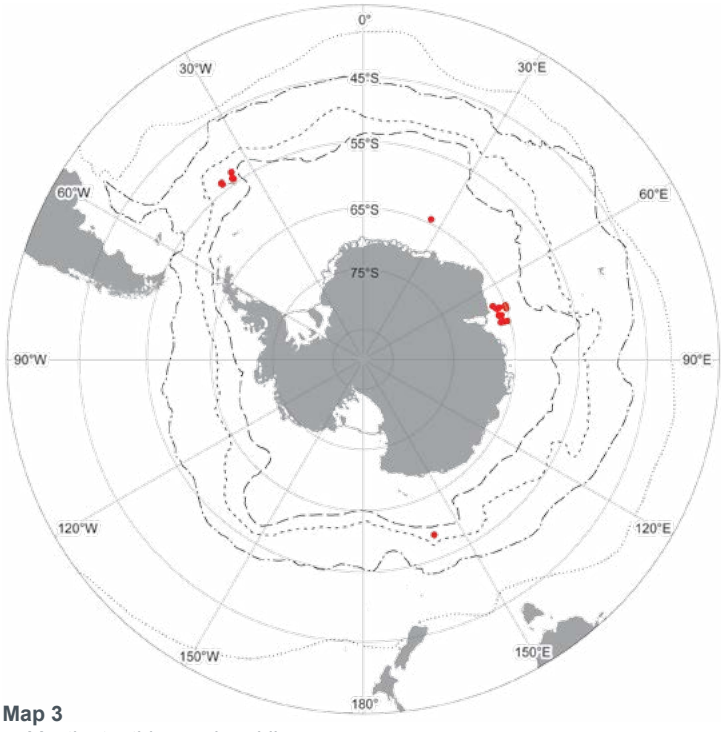
Gonatus antarcticus Lönnberg, 1898 (Map 13): single member of the family Gonatidae described from the Southern Ocean; maximum ML 350 mm; circumpolar (extends south of the APF in the Scotia Sea); mesopelagic, bathypelagic. Literature: Kubodera & Okutani (1986), Rodhouse (1990), Rodhouse *et al.* (1996), Nesis (1999), Anderson & Rodhouse (2002).



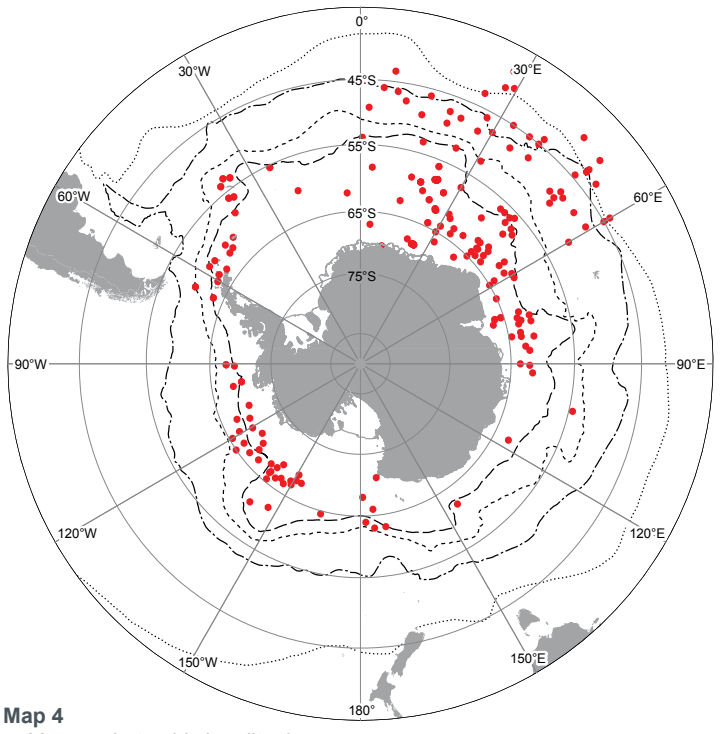
Map 1
● *Moroteuthis knipovitchi*



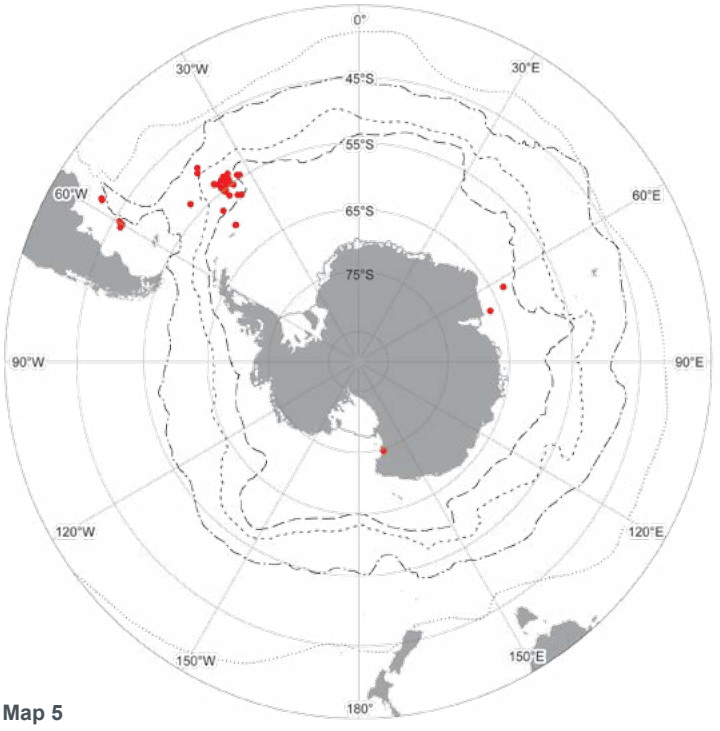
Map 2
● *Alluroteuthis antarcticus*



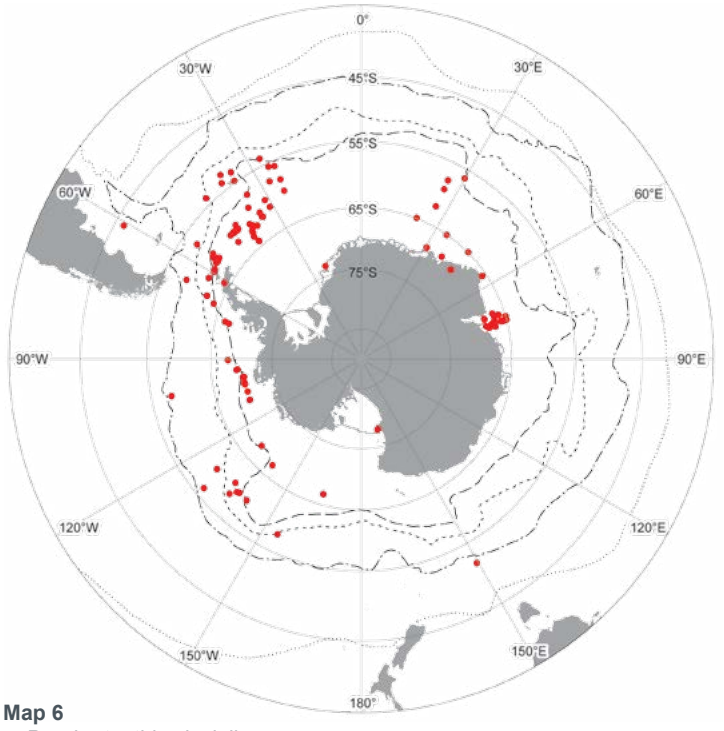
Map 3
● *Mastigoteuthis psychrophila*



Map 4
● *Mesonychoteuthis hamiltoni*

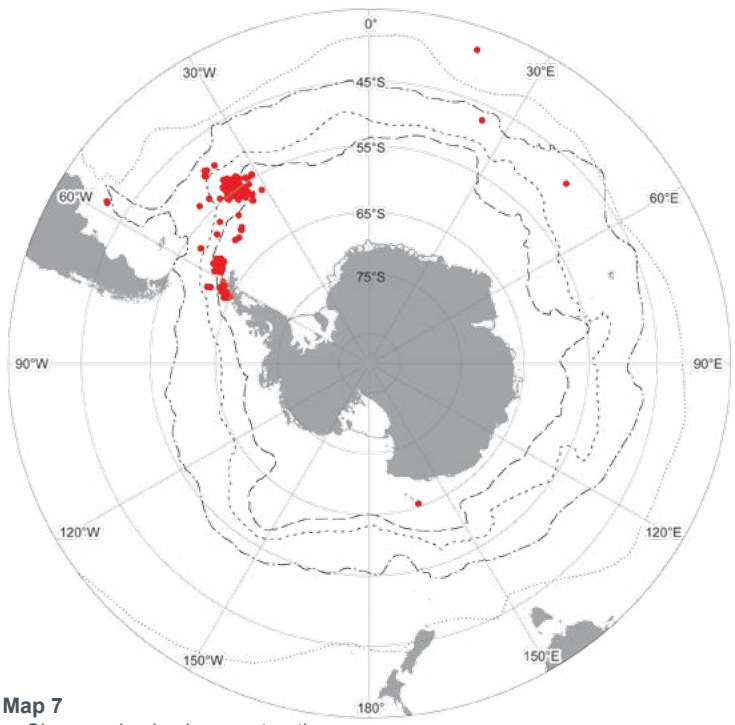


Map 5
● *Kondakovia longimana*

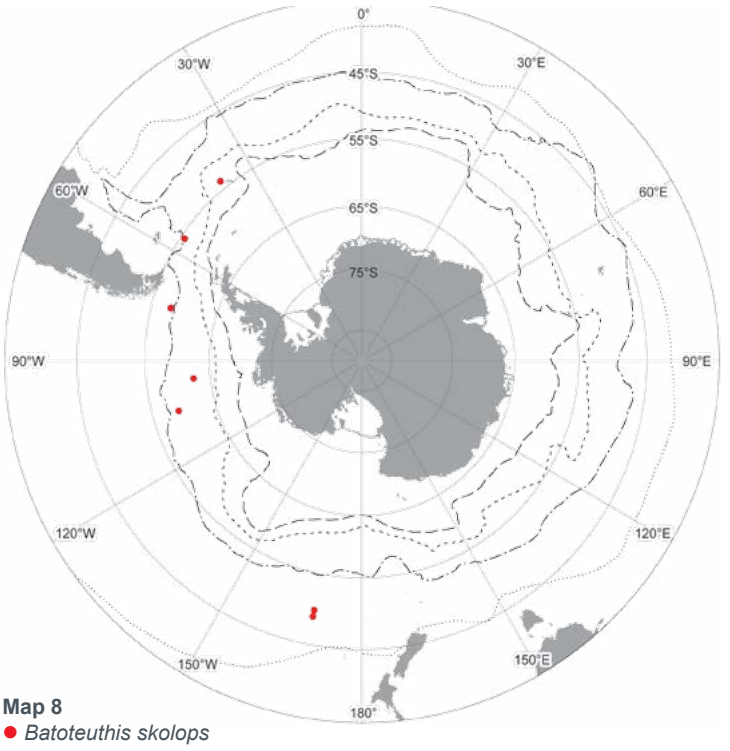


Map 6
● *Psychroteuthis glacialis*

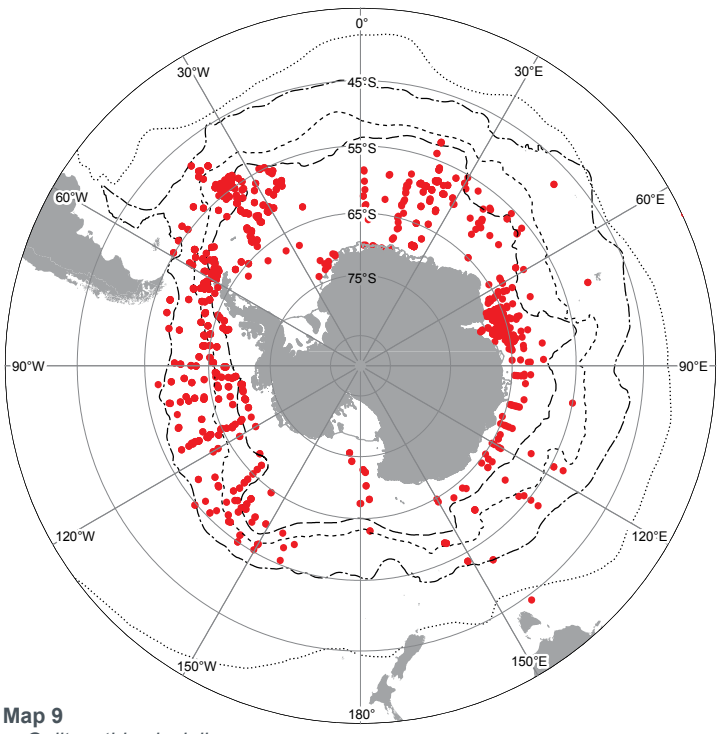
Cephalopoda Decapodiformes Maps 1–6 Map 1. *Moroteuthis knipovitchi*. Map 2. *Alluroteuthis antarcticus*. Map 3. *Mastigoteuthis psychrophila*. Map 4. *Mesonychoteuthis hamiltoni.* Map 5. *Kondakovia longimana*. Map 6. *Psychroteuthis glacialis*. On all maps fronts shown from south to north are: Antarctic Polar Front, Sub-Antarctic Front and Sub-Tropical Front



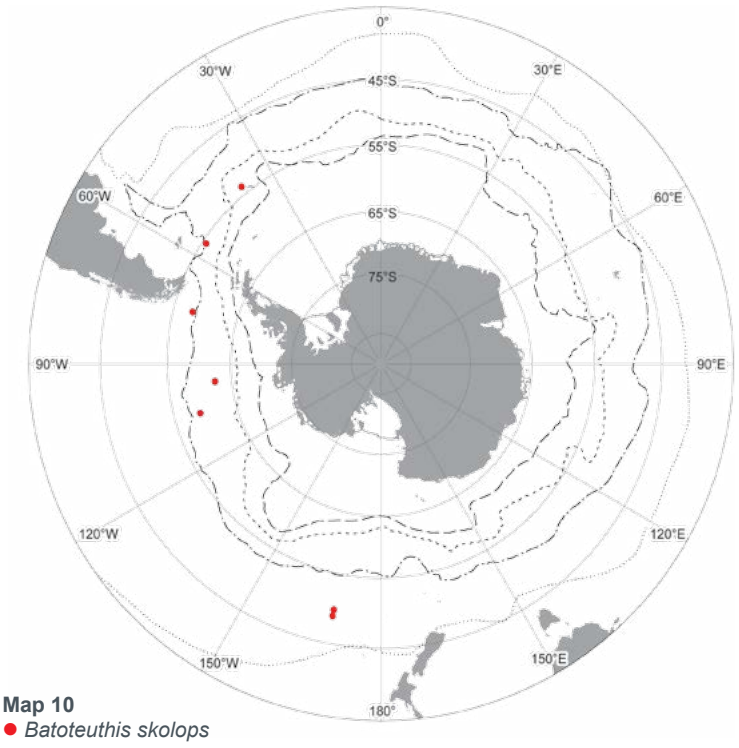
Map 7
● *Slosarczykovia circumantarctica*



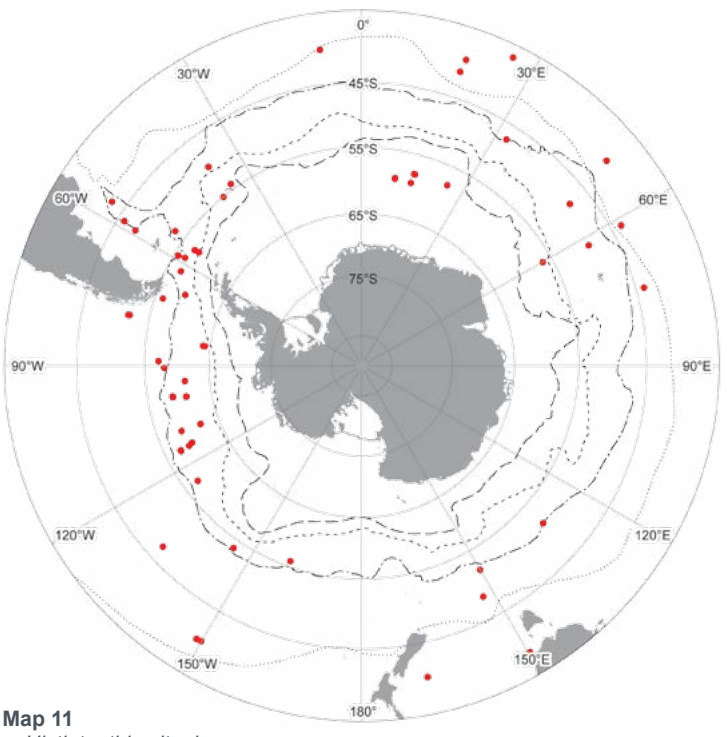
Map 8
● *Batoteuthis skolops*



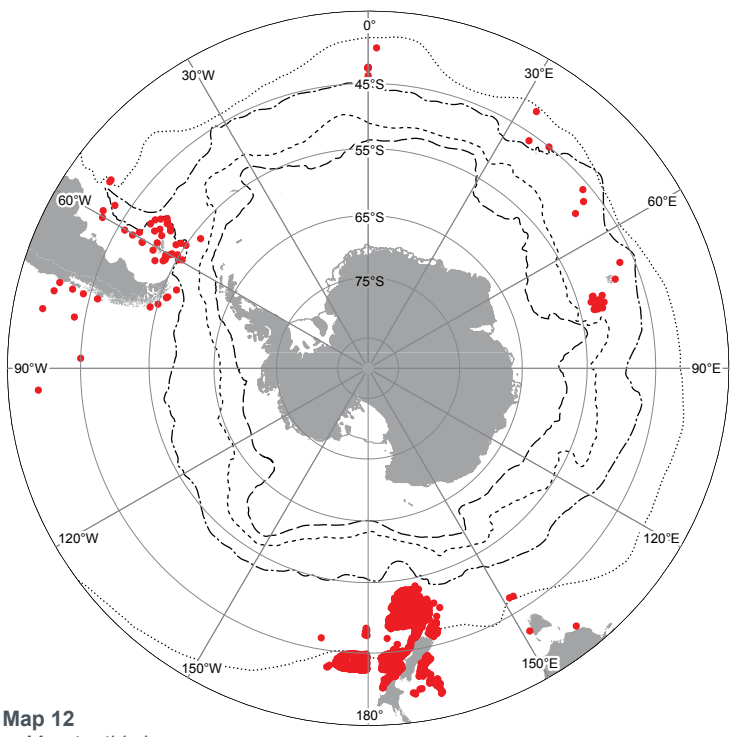
Map 9
● *Galiteusthis glacialis*



Map 10
● *Batoteuthis skolops*



Map 11
● *Histioteuthis eltaninae*



Map 12
● *Moroteuthis ingens*

Cephalopoda Decapodiformes Maps 7–12 Map 7. *Slosarczykovia circumantarctica*. Map 8. *Batoteuthis skolops*. Map 9. *Galiteuthis glacialis*. Map 10. *Parateuthis tunicata*. Map 11. *Histioteuthis eltaninae*. Map 12. *Moroteuthis ingens*.

Martialia hyadesi Rochebrune & Mabille, 1887 (Map 14): one of two members of the family Ommastrephidae from the Southern Ocean; maximum ML 500 mm; circumpolar; epipelagic, mesopelagic and near the bottom from continental shelves to near-bathyal depths. Literature: O'Sullivan *et al.* (1983), Rodhouse & Yeatman (1990), Rodhouse (1991), Piatkowski *et al.* (1991), Uozomi *et al.* (1991), Alexeyev (1994), Rodhouse *et al.* (1996), Gonzalez *et al.* (1997).

2.5. Southern hemisphere extending south to the APF

Moroteuthis robsoni Adam, 1962 (Map 15): one of four members of the family Onychoteuthidae known in the Southern Ocean; maximum ML to 750 mm; circumpolar (extends South of APF in Scotia Sea - South Georgia); pelagic and near bottom. Literature: Nesis (1987).

Histioteuthis atlantica Hoyle, 1885 (Map 16): one of two members of the family Histioteuthidae known in the Southern Ocean; maximum ML 258 mm; circumpolar; mesopelagic, bathypelagic, abyssopelagic. Literature: Kubodera (1989), Alexeyev (1994), Voss *et al.* (1998), Jackson *et al.* (2002).

Todarodes filippovae Adam, 1975 (Map 17): one of two members of the family Ommastrephidae from the Southern Ocean; maximum ML >500 mm; circumpolar; epipelagic, mesopelagic, near seabed on continental slope. Literature: Kawakami (1976), Dunning & Brandt (1985), Dunning (1988, 1993), Roeleveld (1989), Piatkowski *et al.* (1991), Roeleveld *et al*. (1992), Alexeyev (1994), Yokawa (1994), Rodhouse (1998).

2.6. Cosmopolitan extending south of the APF

Bathyteuthis abyssicola Hoyle, 1885 (Map 18): single member of the family Bathyteuthidae known to extend into the Southern Ocean; maximum ML 70 mm; circumpolar; mesopelagic, epipelagic, juveniles lower epipelagic. Literature: Hoyle (1912), Odhner (1923), Roper (1969), Lu & Mangold (1978), Lu & Williams (1994a), Piatkowski *et al.* (1994, 1998). Rodhouse *et al.* (1996).

Chiroteuthis veranyi Ferussac, 1825 (Map 19): single member of the family Chiroteuthidae known to extend into the Southern Ocean; maximum ML 107 mm; circumpolar; bathyal, bathypelagic and mesopelagic. Literature: Alexeyev (1994), Rodhouse & Lu (1998).

3. Squid data from higher predator gut contents

Squid remain difficult to catch with scientific sampling gear and biogeographic knowledge of most species is patchy so conclusions about distribution are tentative. Gaps in data from nets are to some extent filled by information from studies on gut contents of higher predators. The beaks of squid are indigestible so they accumulate in predator stomachs and can be identified and used to estimate the biomass they represent (Clarke 1962). This approach has been particularly valuable in the Antarctic where an estimate has been made of total cephalopod biomass consumed by predators, especially sperm whales (Clarke 1980, 1983). Subsequent research has provided detailed information about the prey of all the major Antarctic cephalopod predators, including fish (Collins & Rodhouse 2006). The research field remains active and a project within the Census of Antarctic Marine Life Programme has resulted in the publication of an identification guide to the beaks of Southern Ocean cephalopods (Xavier & Cherel 2009). Although in this CAML Atlas predator data have been used to infer distribution of squid species in the text the distribution maps are solely based on specimens caught with scientific sampling gear or commercial fishing gear.

4. Inferring distribution

All the species listed here are probably circumpolar. Nevertheless, for most species there are large gaps in known distribution — there are areas that have not been sampled by nets and where predator data are scarce or absent. Productivity is low in large regions in the Antarctic Polar Current system where iron, a micronutrient, is at low concentrations despite fertile levels of macronutrients (de Baar *et al.* 1995). Cephalopods are voracious predators and have high metabolic rates so they need to forage in areas of high food supply and they are known to concentrate in the vicinity of islands, seamounts and mesoscale oceanographic features where productivity is elevated by nutrients off the land and the surrounding shelf or upwelled from the depths (Wadley 1983, Rogers 1994, Rodhouse *et al*. 1996). Analysis of remotely sensed sea surface temperature and ocean colour imagery should provide a reliable indication of the distribution of squid in the Southern Ocean.

Latitudinal distributions of all the squid species included here seem to be limited by the frontal systems of the Southern Ocean to the extent that it has been possible to classify them in terms of the frontal limits of their distribution. Nevertheless the conclusions drawn here are tentative. Sampling has been very unevenly spread and some species such as *Galitethis glacialis* have been observed to cross apparent frontal boundaries with incursions of large volumes of water (Nesis 1987). Other deep living species may extend northwards beyond and beneath the frontal boundaries given here. The so-called colossal squid *Mesonychoteuthis hamiltoni*, a deep living species, has been found in the gut contents of sperm whales as far north as southern Africa and Australia (Clarke 1980, Filippova 2002). It is possible that the whales had taken them further south but it is equally conceivable that the squid extends northwards in Antarctic deep water. Given the extremely limited sampling with gear suitable for catching large squid at great depth the question remains open.

5. Fisheries

There are commercial fisheries for squid on the Patagonian Shelf and slope bordering the Falkland Current, in the Humboldt Current and around New Zealand. Over the last 20 years there have been occasional exploratory fishing expeditions to the South Atlantic sector of the Southern Ocean to explore stocks of the ommastrephid squid *Martialia hyadesi* which is taken as a by-catch in the *Illex argentinus* fishery in the South Atlantic (Gonzalez & Rodhouse 1997, Dickson *et al.* 2004). To date no commercial fishery has developed in the Southern Ocean but catch data, combined with data from predators have been used to set precautionary measures in the event that a fishery might develop in the future (Rodhouse 1997).

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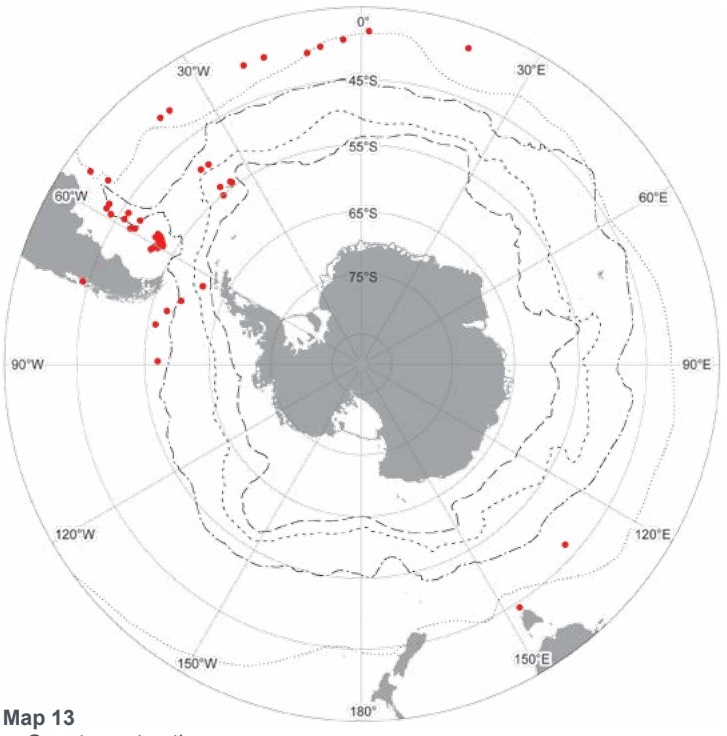
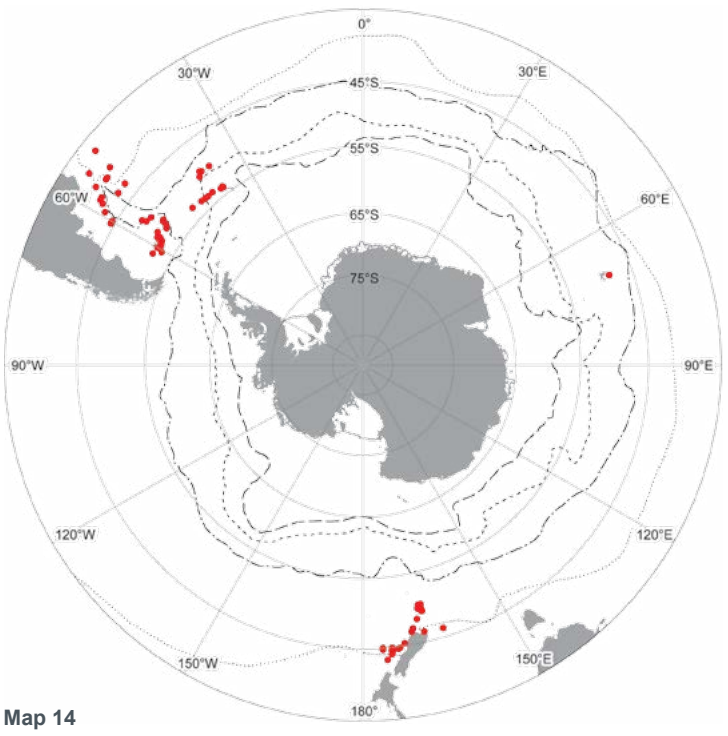
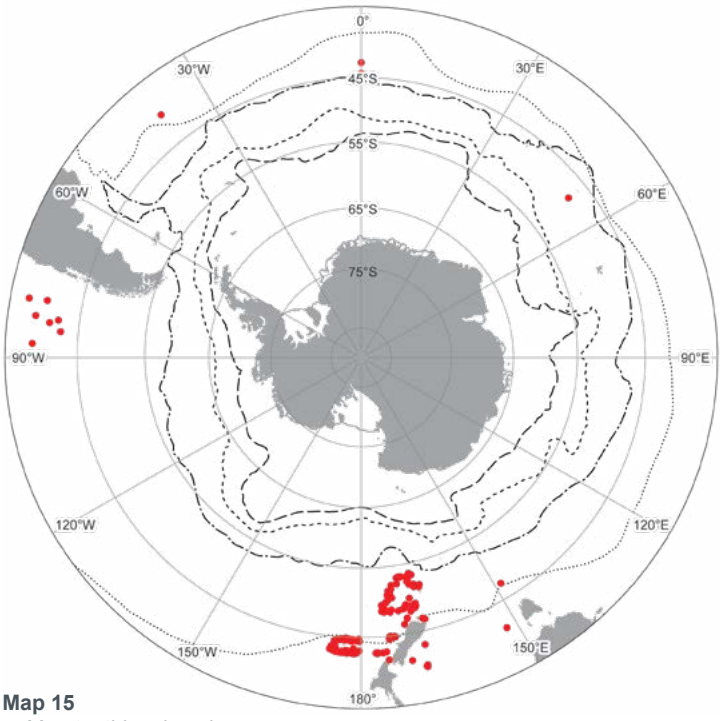


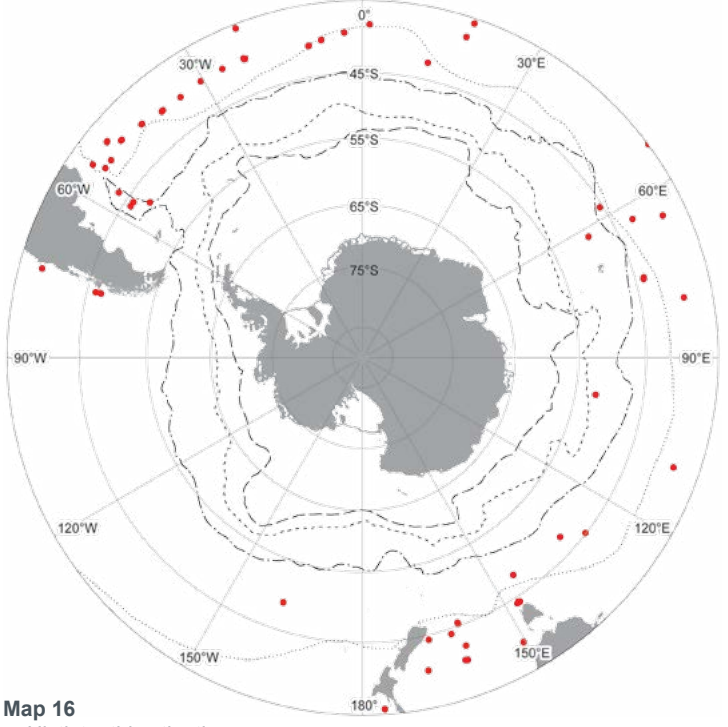
Map 13
● *Gonatus antarcticus*



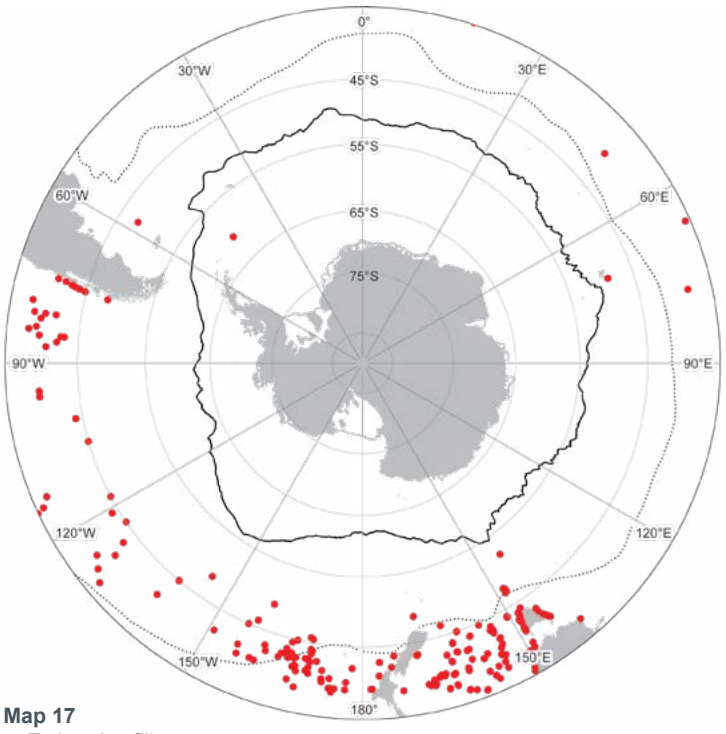
Map 14
● *Martialia hyadesi*



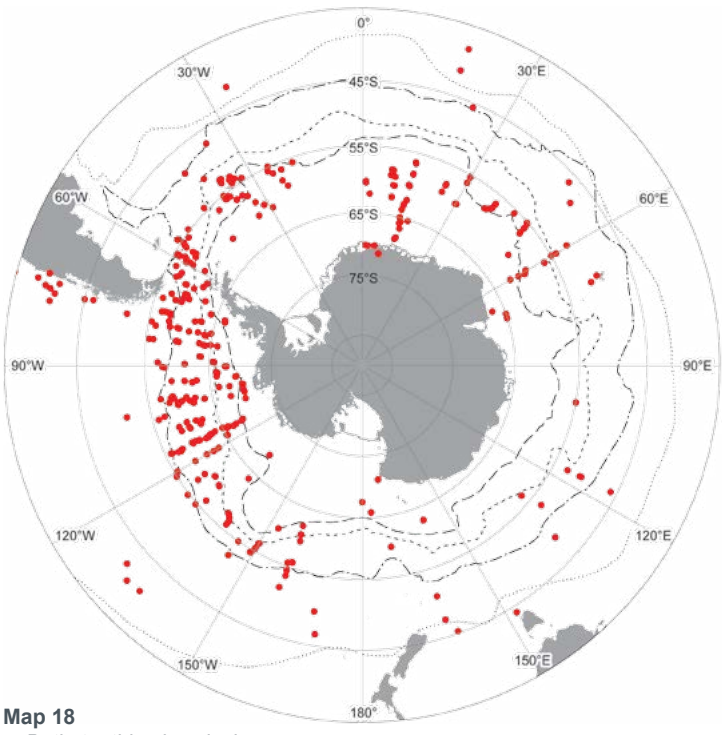
Map 15
● *Moroteuthis robsoni*



Map 16
● *Histioteuthis atlantica*

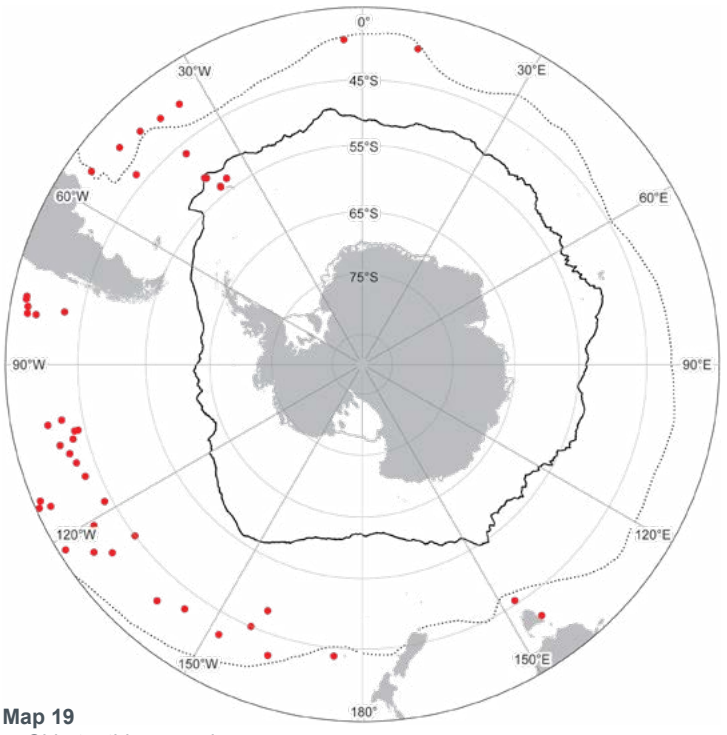


Map 17
● *Todarodes filippovae*



Map 18
● *Bathyteuthis abyssicola*

Cephalopoda Decapodiformes Maps 13–18 Map 13. *Gonatus antarcticus*. Map 14. *Martialia hyadesi*. Map 15. *Moroteuthis robsoni*. Map 16. *Histioteuthis atlantica*. Map 17. *Todarodes filippovae*. Map 18. *Bathyteuthis abyssicola*.



Map 19
● *Chiroteuthis veranyi*

Cephalopoda Decapodiformes Map 19 *Chiroteuthis veranyi.*

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

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

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