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SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.14. Southern Ocean biogeographic patterns in Pycnogonida

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1. Introduction

Pycnogonids or sea spiders have seen resurgence in research interest in recent years due to their controversial phylogenetic relationships both among arthropod groups and within the class (Dunlop & Arango 2005, Arango & Wheeler 2007, Nakamura *et al.* 2007, Regier *et al.* 2010, among others). A pycnogonid world species checklist is found in PycnoBase ([www. http://www.marinespecies.org/pycnobase/](http://www.marinespecies.org/pycnobase/)) (Bamber & El Nagar 2013) although the taxonomic classification presented therein is yet to be phylogenetically tested.

Although pycnogonids have a worldwide distribution, the uniqueness of the Antarctic pycnogonid fauna has been well recognised in international programs such as the Census of Marine Life (CoML) and especially the Census of Antarctic Marine Life (CAML). Antarctic pycnogonids have been studied since the 19th century, with the main monographs being those from Hoek (1881), Hodgson (1907), Gordon (1938), Fry & Hedgpeth (1969), Pushkin (1993) and Child (1994a, b, 1995a, b, c). The most detailed information about the historical background of several families is contained in Child's publications, while the Pushkin monograph shows the geographical distribution of many species. Recently, Munilla & Soler-Membrives (2009) published an updated check-list of Antarctic and sub-Antarctic pycnogonids with a discussion of their general biogeographic pattern and Griffiths *et al.* (2011) were the first to analyze Southern Ocean (SO) pycnogonids in terms of biogeography and biodiversity patterns using geographic information systems (GIS) techniques. So far 40,000 specimens have been found in the Antarctic and sub-Antarctic waters, which belong to 31 genera and 262 different species (Munilla & Soler-Membrives 2009), making pycnogonids excellent representatives of highly diverse and abundant marine invertebrates inhabiting the Southern Ocean region compared to other parts of the world (Clarke & Johnston 2003).

This work aims to highlight few biodiversity patterns in Antarctic pycnogonids: 1) high diversity, 2) circumpolarity, 3) endemism, 4) bathymetric patterns and 5) zoogeographic divisions.



Photo 1 *Colossendeis* sp., south of Dundee Island (*Polarstern* ANT-XXIII/8, st. 727-1). Photograph: J. Gutt © AWI/Marum, University of Bremen, Germany.

2. Methods

All available data on the occurrence of pycnogonids in the Southern Ocean have been selected from the SOMBASE (Griffiths *et al.* 2003) (Map 1). At present, SOMBASE contains 7399 records of occurrences of pycnogonid taxa, accessible through SCAR-MarBIN (<http://www.scarmarbin.be/AntobisMapper.php?taxid=1302>). It comprises 332 species of pycnogonids from 1837 sample locations around continental Antarctica, the sub-Antarctic islands, South America, and New Zealand.

3. High diversity

The SO pycnogonid species represent almost 20% of the known species worldwide (262 from the 1344 described) while Antarctic species (192) are 14%. The latter is relatively high compared to other more speciose taxa such as polychaetes ($\approx 12\%$), amphipods ($\approx 8\text{--}14\%$), echinoderms (4.9%), sponges (6.2%), or fish and gastropods ($<2\%$) (Munilla 2001, Clarke & Johnston 2003, Griffiths *et al.* 2011).

One quarter of the world's *Nymphon* species (~ 250 spp.) occur in the Southern Ocean indicating this region may be a speciation hotspot, i.e. a source rather than a sink of biodiversity (Clarke & Johnston 2003, Griffiths *et al.* 2009). *Nymphonidae* is the most abundant family (71 species) with *Nymphon* being the most diverse genus (67 species) and *Nymphon australe* the most frequently recorded and abundant species (Child 1995a, Soler-Membrives *et*

al. 2009, Arango *et al.* 2011). *Nymphon australe* reveals both, circumpolar and eurybathic distributions (8–4136 m depth).

The fact that high-latitude pycnogonid species are particularly large-bodied, which in some cases could be related to a polar gigantism, is not yet understood (see Woods *et al.* 2009). Possibly, the gigantism would be linked to low metabolism conditioned by the low temperature conditions, given that some cold and deep water species from non-Antarctic zones are also large. In general, the large body size (20–700 mm in leg span) of most Antarctic species makes them easier to detect during sampling cruises compared to most shallow tropical or temperate species (1–50 mm in leg span).

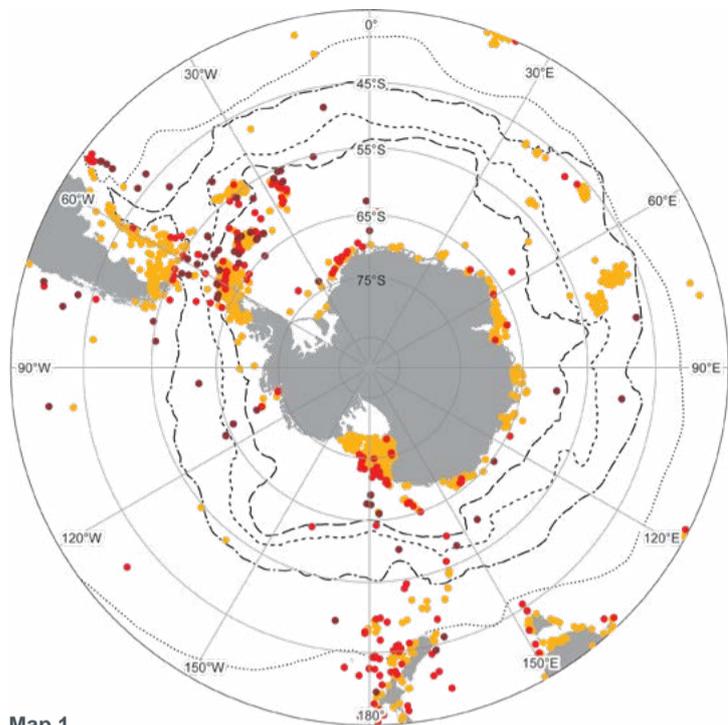
While all nine pycnogonid lineages are cosmopolitan, Antarctica can be definitely considered a centre of radiation for some lineages at genus and species levels. Estimates of divergence times and possible factors that might have contributed to colonisation and radiation in the SO waters are currently being investigated. After Gondwana break up and continental separation more than 100 Ma, the main factor likely responsible of the isolation of Antarctic species is the low water temperature (Clarke & Johnston 2003, Clarke *et al.* 2005). In present times, rapid global warming might promote colonisation by non-Antarctic species further increasing pycnogonid diversity in the SO, but relative Antarctic endemism would then decrease. The Scotia Arc, and particularly the South Shetland Islands, account for high values of species richness (Munilla & Soler-Membrives 2009, Griffiths *et al.* 2011). This apparent richness hotspot might be partially explained by the high level of sampling in the region and paucity of sampling elsewhere (Griffiths *et al.* 2011). Recent work off Adélie Land in East Antarctica has revealed comparable levels of diversity and abundance on the opposite side of the continent (Arango *et al.* unpublished).

It is likely that detailed taxonomic studies of material collected from deep-sea and lesser studied areas (e.g. Amundsen and Bellingshausen Seas) will result in the discovery of several new pycnogonid species. Additionally, genetic data will help to resolve cryptic or overlooked species and problematic species complexes, which will also contribute to a better understanding of the diversification processes in Antarctic pycnogonids.

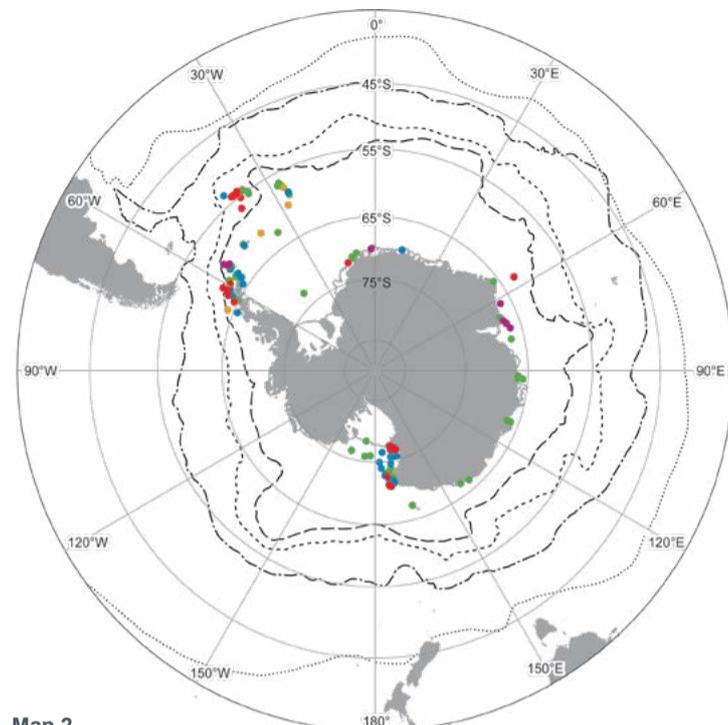
4. Circumpolarity

The distribution of most of the benthic Antarctic fauna is considered circumpolar (Hedgpeth 1971, Arntz & Gallardo 1994, Clarke & Crame 1997), almost certainly due to the powerful Antarctic Circumpolar Current (Clarke & Johnston 2003). Munilla & Soler-Membrives (2009) noted that 55 of the 192 Antarctic species recorded (29%) are circumpolar. The circum-Antarctic pattern in the sea spiders has increased during the last years, as there has been an increase in sampling effort. Thus, the endemism of the species from each zone has decreased (Munilla & Soler-Membrives 2009). Pycnogonids are assumed to have limited dispersal capacity given their life history does not involve a planktonic stage and the fertilised eggs (and sometimes larvae) are carried by the father (Arnaud & Bamber 1987). Consequently, the existence of widespread species remains partly unexplained. The strong currents and the large effective population size could partly explain the circumpolar distribution of some species with strong isolation by distance, even without planktonic life stages. The transport of specimens by bottom currents, by debris or other living organisms should not be neglected. Genetic analyses of the intraspecific variability in some species may be the basis for the separation from single circumpolar species into a group of species each endemic of a specific zone. Arango *et al.* (2011) found *Nymphon australe* to be a single circumpolar species, with prominent geographic genetic differences suggesting limited or no ongoing gene flow between regions. The apparent limited ongoing gene flow and the displayed metapopulation structure, suggest an incipient process of allopatric speciation. On the other hand, a study of *Colossendeis megalonyx* from the Antarctic Peninsula and the sub-Antarctic islands found six cryptic lineages, four of them apparently geographically restricted (Krabbe *et al.* 2010). However, the authors also found indications of recent gene flow or at least recent colonisation between locations separated by more than 1000 km. In fact, novel data from a more extensive sampling suggest that some of these cryptic lineages are actually circumpolarly distributed, a distribution pattern not detected before by Krabbe *et al.* (2010) due to the limited sampling (F. Leese pers. comm.).

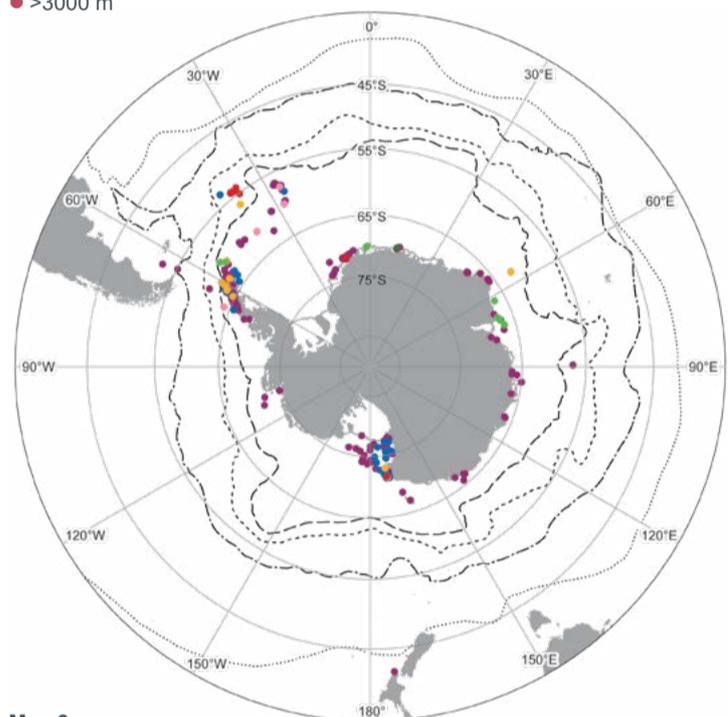
The differences in the distribution of intra-specific variation in SO pycnogonid taxa might relate to differences in timing, rates of speciation and physical drivers among them (Griffiths *et al.* 2011). The apparent lack of a free-swimming planktonic stage of pycnogonids together with their exceptional high diversity throughout the Antarctic waters make this group key taxon to study diversification and speciation processes in the Antarctic benthic fauna. Current research is aimed at investigating the genetic connectivity and phylogeographic patterns of different pycnogonid species to better understand the interrelationships of Antarctic regions as well as between Antarctic and sub-Antarctic zones. How this common trend of circumpolar distribution will change with the increase of sampling effort together with a better taxonomic resolution and molecular data is still uncertain (Griffiths *et al.* 2011).



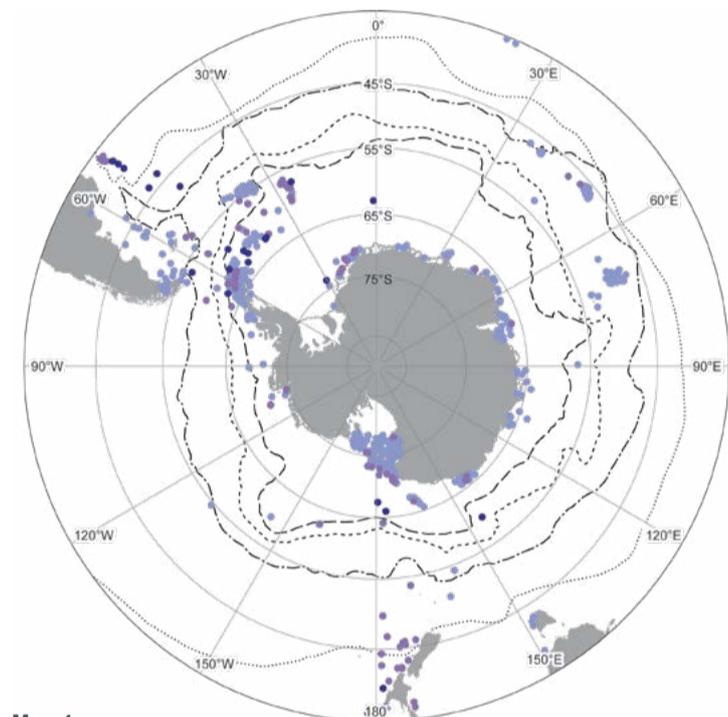
Map 1
Pycnogonida: all records
● 0 - 1000 m
● 1000 - 3000 m
● >3000 m



Map 2
Endemic genera
● *Austroraptus*
● *Decolopoda*
● *Dodecolopoda*
● *Pentapycnon*
● *Sexanymphon*



Map 3
Polymerous species
● *Decolopoda australis*
● *Decolopoda qasimi*
● *Dodecolopoda mawsoni*
● *Pentanymphon antarcticum*
● *Pentapycnon bouvieri*
● *Pentapycnon charcoti*
● *Sexanymphon mirabilis*



Map 4
Nymphon spp.
● 0 - 1000 m
● 1000 - 3000 m
● 3000 - 6000 m

Pycnogonida Maps 1–4 Map 1. Pycnogonida, endemic and non-endemic species. Map 2. Endemicity at genus level within the Southern Ocean. The SO species of endemic genera (*Austroraptus*, *Decolopoda*, *Dodecolopoda*, *Pentapycnon*, *Sexanymphon*) are selected to demonstrate endemicity patterns within the Antarctic. Map 3. Polymerous species in the Southern Ocean. Seven of the ten polymerous species (*Decolopoda australis*, *D. qasimi*, *Dodecolopoda mawsoni*, *Pentanymphon antarcticum*, *Pentapycnon bouvieri*, *P. charcoti*, *Sexanymphon mirabilis*) distributed in the SO, shown here as an example of SO and Antarctic endemism at the species level. Map 4. Bathymetry of the genus *Nymphon*. Shelf break is used to divide into continental shelf and slope occurrences.

5. Endemism

Antarctic endemism is common in many invertebrate marine taxa and the Pycnogonida are a clear example. More than half of the species recorded in the Antarctic region are endemic (that is 107 from 192 species). Moreover, 63 species are common between Antarctic and sub-Antarctic waters and 62 species from the 141 cited in the sub-Antarctic regions are endemic. Sixty-four percent of the SO recorded species (169 of 262) (Munilla & Soler-Membrives 2009) are endemic to the SO waters and 40% endemic to Antarctic region (107 of 262). This high proportion of endemic species corroborates suggestions by Stock (1957), Hedgpeth (1969), Munilla (2001) and Munilla & Soler-Membrives (2009), that the Antarctic is a center of speciation, geographic dispersal and evolutionary radiation for pycnogonids. The examples of *Nymphon* and *Colossendeis* hint at high speciation rates which may be attributed to migration and subsequent isolation, as suggested by Stock (1957) for the genus *Austrodecus*.

Ten genera are reported exclusively from SO waters, and three of them — *Sexanymphon*, *Dodecolopoda*, and *Austroraptus* — are endemic to the Antarctic region (Munilla 2003) (Map 2). The species in these polymerous

genera or extra-legged ones, *Sexanymphon* and *Dodecolopoda* (and SO *Decolopoda* and *Pentanymphon*) seem to be sister taxa of similarly looking eight-legged Antarctic species (Arango & Wheeler 2007, Krabbe *et al.* 2010), but the phylogenetic affinities of *Austroraptus* are as yet unknown.

Five ten-legged and two twelve-legged species are found in SO waters, while only two polymerous forms are found elsewhere. Six of the seven SO species are endemic to the Antarctic (see Map 3). The only exception is *Pentanymphon antarcticum*, first considered an Antarctic endemic (Munilla & Soler-Membrives 2009), later a Southern Ocean endemic. However, the circumpolar distribution of this species (Map 3) might be challenged, as it is possible there are some undescribed or possibly cryptic species revealed by current DNA analysis (Arango *et al.* unpublished). The nature of these polymerous forms is still unknown, but the event is unique among the Arthropoda (Arnaud & Bamber 1987). The relationship between Antarctic endemism of these species and the phenomenon of polymery is yet to be understood (Hedgpeth 1969).

6. Bathymetric patterns

Some specific bathymetric ranges for Antarctic and sub-Antarctic species have been described by Munilla & Soler-Membrives (2009) and Griffiths *et al.* (2011), but basic information regarding bathymetric distribution patterns and diversity of species and community composition related to depth are scarce. Depth is generally the most important factor accounting for differences in benthic communities (Brandt *et al.* 2007, Carney 2005). Soler-Membrives *et al.* (2009) analyzed the Eastern Weddell Sea pycnogonid communities regarding their bathymetric distributions finding that the shelf fauna differs in species composition from that of the slope. Although Clarke & Johnston (2003) defined the shelf break at 1000 m, depth at which pycnogonid communities changed in the Eastern Weddell Sea seem to be 900 m. While many species are confined to shelf depths, forming a 'shallow community', only some extend across the shelf break into the slope. The deep community (species occurring deeper than 900 m) is mainly characterised by the presence of members of the genus *Nymphon* (see Map 4). Soler-Membrives *et al.* (2009) found that the Weddell Sea pycnogonid communities changed with depth with a clear drop from 78 species and 14 genera from the shelf to nine species and three genera from the slope. It is clear that sampling is biased toward shallower areas (Griffiths 2010), but the pattern of diversity decreasing with depth seems to occur even when the sampling effort is taken into account (Griffiths *et al.* 2011). The differences found between the continental shelf and deep waters regarding the number of species found and the community composition support the hypothesis that these taxa have evolved and radiated on the shelf. Nevertheless, some taxa could have submerged into the deep sea — probably forced by advancing ice shelves during glacial periods — where they co-occur in apparently less rich communities (Soler-Membrives *et al.* 2009). Contrary to the SO shelf, which is zoogeographically well isolated by the temperature gradient through the Polar Front, the SO deep-sea fauna can freely migrate (Brandt *et al.* 2007, Munilla & Soler-Membrives 2009). Data from the deep Eastern Weddell Sea show that species of pycnogonids do not differ generally from those from adjacent deep-sea basins (Soler-Membrives *et al.* 2009). More recently, a survey of pycnogonid assemblages off Adélie Land in East Antarctica found no clear segregation between shallow and deep communities with samples collected from 120 to 2000 m in depth (Arango *et al.* unpublished). The different routes for pycnogonid colonisation from Antarctic marine shallow water ecosystems to the deep-sea and vice versa are yet to be understood.

Synthetic data about bathymetric distribution of SO pycnogonid species are found in Munilla (2001). Species found exclusively between 0 and 100 m (7%) and below 1000 m (14%) are very scarce. About 2/3 of the species have been found only on the continental shelf and upper slope, and the number of species decrease dramatically down to 1000 m. However, eurybathy in SO waters is common, as among half of the SO recorded species have a bathymetric distribution range superior to 500 m and 26–37% of the species superior to 1000 m (Munilla 2001, Griffiths *et al.* 2011). This fact could be explained by the stability of the environmental conditions in the water column, mainly temperature and salinity. The great extension of the continental glacial ice plates on the Antarctic shelves, forcing the fauna to survive at great depths, is another possible explanation for widely spread eurybathy among benthic taxa.

Bathymetric speciation in the SO is a key factor to consider (Schüller 2011), as it may reveal significant information to help understanding the possible origin and dispersal routes of Antarctic pycnogonids and the interaction between Antarctic and sub-Antarctic fauna. Genetic connectivity between shelf and slope populations of pycnogonids is yet to be tested in SO waters.

7. Zoogeographic divisions

Previous works have examined SO taxa distribution patterns using biogeographic sub-regions defined by maritime areas such as seas and archipelagos (Barnes & De Grave 2000) or those proposed by Hedgpeth (1969) (Clarke & Johnston 2003, Munilla & Soler-Membrives 2009, Griffiths *et al.* 2011).

Pycnogonid biogeographic patterns show that each sub-Antarctic area (such as the New Zealand plateau, South America and sub-Antarctic Islands) is isolated and separated from each other (see Fig. 1). The low level of similarity between the distinct groupings from sub-Antarctic islands and other Antarctic geographic regions implies that the Polar Front and the geographical isolation of these islands might have led to speciation. Of the sub-Antarctic zones, the Magellanic area is the closest to the Antarctic region in terms of species similarity (Griffiths *et al.* 2011). Independent isolation has occurred in New Zealand, as shown by different taxa (Griffiths *et al.* 2009), due to its early separation from the Gondwana and the proximity to the Indo-West Pacific diversity hotspot (Griffiths *et al.* 2011).

Fig. 1 shows the similarity among Antarctic and sub-Antarctic zones. The results of the recent biogeographic studies (Munilla 2001, Munilla & Soler-Membrives 2009, Griffiths *et al.* 2009, Griffiths *et al.* 2011) strongly suggest a relatively homogeneous Antarctic shelf fauna for the pycnogonids, differing from the deep sea (see Map 4).

Nevertheless, a slight separation between a Pacific branch (formed by the Ross Sea and Bellingshausen Sea) and a north-eastern branch (which includes the Antarctic Peninsula, the Weddell Sea and the East Antarctica) can be noted (Munilla & Soler-Membrives 2009). This supports the hypothesis that species distribution is highly influenced by the direction of the ACC. Results of the similarity analyses among regions show 60% similarity between Scotia Arc and the Antarctic regions (Fig. 1). The Scotia Arc is a highly diverse zone compared to its surrounding waters, as 75% of the Antarctic species are

reported from the area including a high number of endemic species (Munilla & Soler-Membrives 2009, Griffiths *et al.* 2011) (see Maps 2, 3 and 4). The Scotia Arc is the only major barrier to the ACC, and might act as a 'filter' retaining specimens drifting in the current. Regarding the benthic insular refuge hypothesis (the islands serve as a refuge and posterior exportation points of the current fauna by ACC), this zone is proposed as sub-centre of speciation (Munilla & Soler-Membrives 2009).

The possible stages in the origin and dispersal of the Antarctic pycnogonids proposed by Munilla & Soler-Membrives (2009) are:

1. An in situ origin (Munilla 2001), from the Cretaceous Gondwana fauna (141–65 Ma). This possibility is supported by the two most ancient families of sea spiders (Colossendeidae and Austrodecidae, Arango & Wheeler 2007 with morphological and molecular data, Bamber 2007, a holistic approach), having 48% and 42% respectively of their species in southern waters.
2. The Scotia Arc has acted as 'shelter' and centre of radiation of species since the Cretaceous.
3. From the Scotia Arc waters, the fauna could be exported towards the eastern (Weddell-East) and southern (Bellingshausen-Ross) zones via the AAC (see linkage in Fig. 1).
4. The background currents could be responsible for transporting the shelf and upper slope fauna, affected mainly by the ACC, to greater depths. This could be the case of dispersal between Magellan fauna and the Antarctic Peninsula or Weddell Sea through the Scotia Arc.

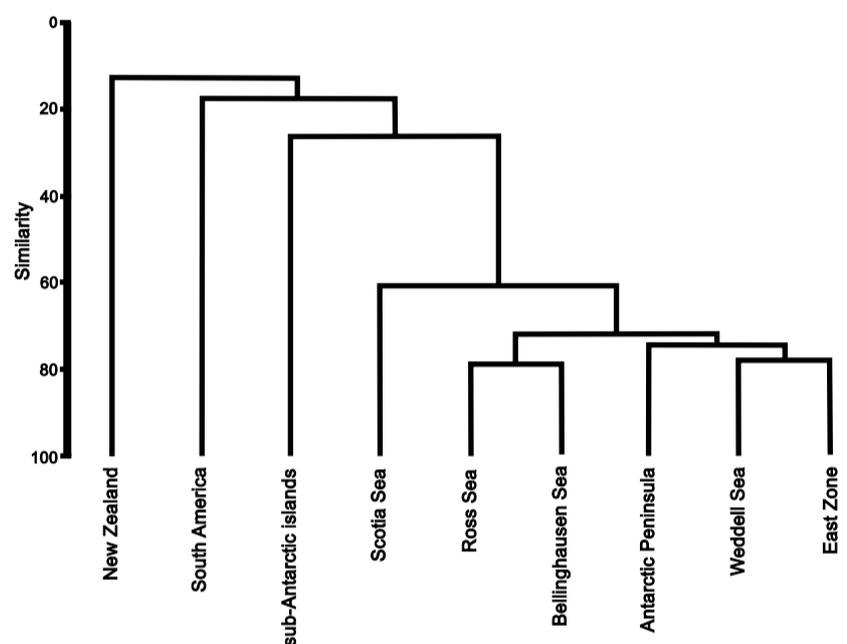


Figure 1 Dendrogram visualising the similarity among Antarctic and sub-Antarctic zones (Bray-Curtis Index, complete linkage), based on presence-absence data, from Munilla & Soler-Membrives (2009). Circum-Antarctic species are included.

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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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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.

