

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN



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SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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6.3. Southern Ocean Gelatinous Zooplankton

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1. Introduction

The final years of the 19th century and the first few decades of the 20th century were perhaps the golden age for studies of Southern Ocean gelatinous zooplankton (Moser 1909, Browne 1910, Vanhöffen 1912, etc.) with only sporadic reports thereafter (Kramp 1948, 1949, 1957) until samples taken by the USNS Eltanin were analysed and reported after the mid-1980s (Larson 1986, Alvariño et al. 1990, Navas-Pereira & Vannucci 1990). The vast majority of the occurrence data for gelatinous Antarctic zooplankton comes from the USNS Eltanin cruises and, as such, is concentrated mainly in waters south of the 35th parallel, between 20°W and 130°W. Other data harvested from the Ocean Biogeographic Information System (OBIS) included a small taxonomic subset of easily recognizable species recorded in the Discovery data from the Southampton Oceanography Centre (erroneous depth records not included) and Rectangular Midwater Trawl (RMT) data from the Australian Antarctic Data Centre, as well as a more taxonomically comprehensive dataset compiled from the literature, centering on high quality vertical distribution data produced by Francesc Pagès and others (Lindsay 2012), that are nevertheless unfortunately quite limited in their geographic range. Most Antarctic planktonic species are considered circumpolar in their distribution, so although the maps in the present Atlas seem to show limited geographical distributions this is most likely an artefact of the sampling rather than a reflection of the true distributions. Furthermore, the southern hemisphere in general is vastly understudied and, as a result, although many of the occurrence patterns in the present Atlas seem to infer that distributions are confined to the Antarctic or sub-Antarctic, this may not actually be the case.

2. Biogeography and depth distribution

2.1. Generalities

Including undescribed species, approximately 12 species of ctenophores, 18 species of scyphomedusae, >30 species of siphonophores and >71 species of hydromedusae are known to inhabit the Antarctic and sub-Antarctic waters of the Southern Ocean. Their latitudinal ranges can be divided into several categories - from coastal Antarctic endemics primarily concentrated close to the ice or confined to the continental shelf, to cosmopolitan species, the range of which extends into Antarctic waters. In contrast to more mobile animals such as squids or fishes, gelatinous zooplankton, being planktonic, are more liable to be transported out of their "home" ranges and either into or out of Antarctic waters through horizontal advection. This is particularly true of the holoplanktonic groups such as siphonophores, trachymedusae, narcomedusae, ctenophores and the coronate scyphomedusae Periphylla periphylla (Péron & Lesueur, 1810) and Atolla spp., and less true for those meroplanktonic species for which the origin of their medusa stage is from benthic polyps. The distributions of the planktonic stages are closely tied to the water masses that they inhabit and the depths of these water masses can change with latitude or indeed longitude. Unfortunately, much of the published data consists of records from nets that traversed multiple water masses but only depth of capture data was available for graphically presenting this data in map form

The taxonomy of gelatinous zooplankton is still relatively undeveloped compared to many other groups of organisms, especially those with shells or other hard body parts. Indeed, one of the commoner polar siphonophores, Muggiaea bargmannae Totton, 1954, was only described in 1954 and is therefore missing from the data from the early Discovery or Gauss expeditions, even though it certainly occurred — probably being misidentified as Dimophyes arctica (Chun, 1897) with which it shares many morphological features. Information on the various developmental stages of species is either nonexistent or scattered through the literature in a variety of languages. Usually only the easily-recognizable polygastric stage of siphonophore species is reported and, therefore, where the life history stage is not explicitly stated in the original reference, these records are plotted on the same map as the polygastric stages, albeit with a different symbol. Failure to recognize younger stages can lead to apparent distributions that are quite different to the real distributions of a species. An example of this can be seen in the physonect siphonophore Pyrostephos vanhoeffeni Moser, 1925, where its younger stages have apparently been misidentified as Bargmannia elongata Totton, 1954, giving an erroneous, apparent distribution for B. elongata including many points south of the Antarctic Polar Front but with very few records of P. vanhoeffeni in this area, where the younger stages of P. vanhoeffeni

actually apparently predominate. An up-to-date taxonomic treatment of Southern Ocean gelatinous zooplankton is sorely needed to enable further biogeographic work to proceed with the correct species assignations.

2.2. Neritic Antarctic endemics

This group contains neritic animals presumably bound to the shallow coast due to the habitat of their benthic polyp stage. It includes species such as the ulmarid scyphomedusae *Desmonema glaciale* Larson, 1986 (Fig 1, Map 1) and *Diplulmaris antarctica* Maas, 1908. The anthomedusa *Leuckartiara brownei* Larson & Harbison, 1990 would also seem to be in this group although the adult medusa stage has a lower epipelagic/upper mesopelagic distribution. Some holopelagic organisms, such as the beroid ctenophore *Beroe compacta* Moser, 1909 also appear to be confined to coastal waters close to the continent (Lindsay pers. obs.).

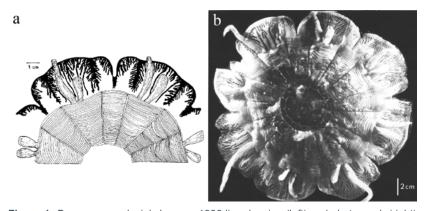
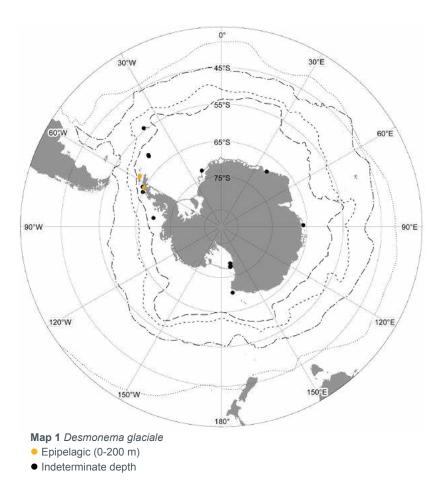


Figure 1 Desmonema glaciale Larson, 1986 line drawing (left) and photograph (right) extracted from the original description.



Gelatinous Plankton Map 1 Distribution of *Desmonema glaciale* based on available data.

2.3. Antarctic species concentrated primarily close to the coast

The species in this group have distributions centered around landmasses south of the Polar Front but can also be found near land in the Sub-Antarctic Zone. These include species with polyps probably living in deeper waters such as the anthomedusa *Zanclonia weldoni* Browne, 1910 (Fig. 2, Map 2), as well as those with polyps probably occurring in shallower waters such as the anthomedusa *Heterotentacula mirabilis* (Kramp, 1957), and the leptomedusa *Cosmetirella davisi* (Browne, 1902). The distributions of the medusae, mostly

off the continental shelf in the former species and over the shelf in the latter two species, probably mirror those of their benthic polyp stage. Younger stages of some species can be quite difficult to correctly identify, although records of *C. davisi* off south-west Africa and southern Patagonia seem to be valid. Some holopelagic organisms, such as the physonect siphonophore *Pyrostephos vanhoeffeni*, also seem to be associated with the coast/ice, not only around the Antarctic continent, and can be transported oceanwards of the coast as they mature (Fig. 3, Map 3).

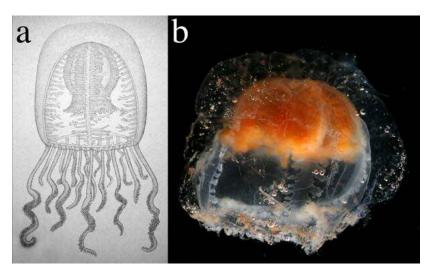
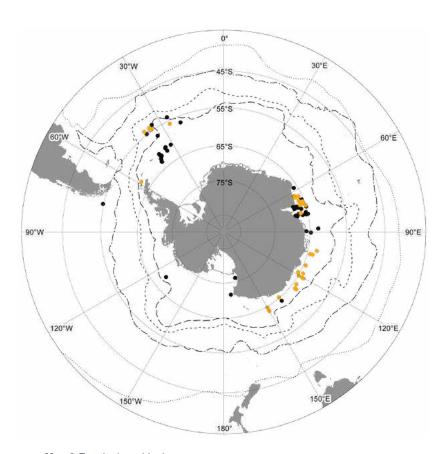


Figure 2 Original line drawing of *Zanclonia weldoni* (Browne, 1910) (a), and photograph of an RMT net-caught specimen by DJL (b).



Map 2 Zanclonia weldoniEpipelagic (0-200 m)

Indeterminate depth

Gelatinous Plankton Map 2 Distribution of *Zanclonia weldoni* based on available data, showing its coastal distribution over deeper water mostly within the Polar Front.

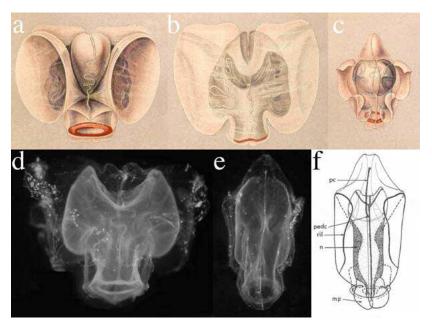
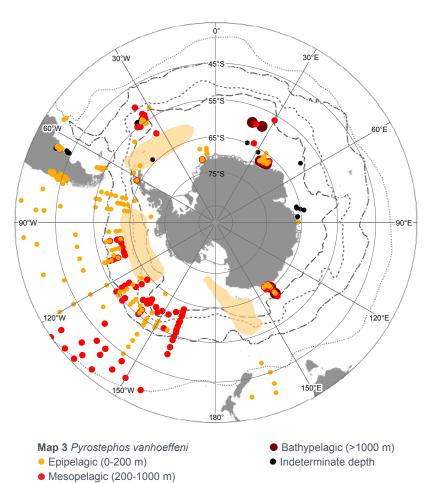


Figure 3 Original line drawing of *Pyrostephos vanhoeffeni* Moser, 1925 (mature nectophore in upper view (a) and lower view (b), immature nectophore (c), photograph of a mature (d) and immature (e) nectophore from an entire colony by EG, line drawing of a mature nectophore of *Bargmannia elongata* Totton, 1954 (f) from Pugh (1999).



Gelatinous Plankton Map 3 Distribution of *Pyrostephos vanhoeffeni* based on available data. At least a subset of the records of *Bargmannia elongata* by Alvariño (1990), such as those found within the Ross Sea, are assumed to actually be misidentified younger nectophores of *P. vanhoeffeni*. The paucity of records within the Polar Front suggests that this is where the majority of young colonies occur, maturing as they are advected northwards.



2.4. Sub-surface Antarctic endemics also found in the surface layer at or north of the Polar Front through upwelling

Species in this group tend to be associated with the Winter Water or are in any case usually confined to depths below the surface thermocline. Upwelling brings them into the surface layer at the Polar Front or in other upwelling regions. Examples of these species include the anthomedusa Calycopsis borchgrevinki (Browne, 1910) (Fig. 4, Map 4) and the polygastric stage of Diphyes antarctica Moser, 1925 (Fig. 5, Map 5a). The polyps of C. borchgrevinki presumably occur in the deeper waters of the continental slope and the medusa stage is unable to tolerate conditions in the surface layer, though it can often be found between the surface thermocline and 200 m depth - hence the "epipelagic" distribution in Map 4. Diphyes antarctica can tolerate conditions in the surface layer and remains there as it is advected northwards towards the Sub-Tropical Front. Its apparent absence in the epipelagic layer between 60° and 120°E appears to be an artefact due to a lack of taxonomic expertise rather than a real absence as many "siphonophore nectophores" were reported in the samples (AADC, 2013). The sexual (eudoxid) stage of D. antarctica appears to remain at lower epipelagic or mesopelagic depths as it is advected northwards (Map 5b).

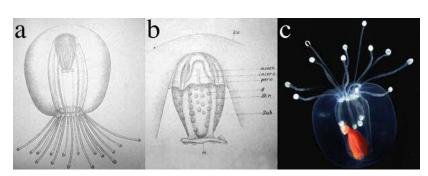
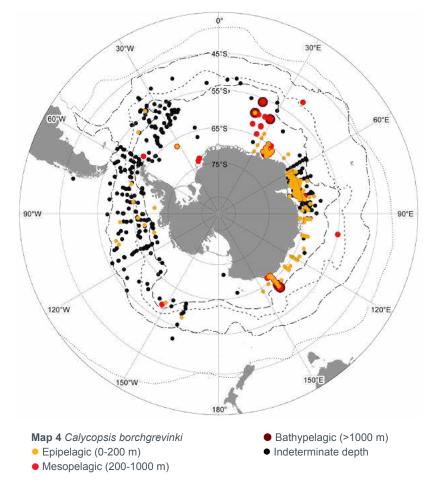


Figure 4 Original line drawing of *Calycopsis borchgrevinki* (Browne, 1910) (entire medusa (a), stomach and gonad morphology (b), and a photograph by Ingo Arndt of a living specimen in its natural orientation (c).



Gelatinous Plankton Map 4 Distribution of *Calycopsis borchgrevinki* based on available data, showing its epipelagic coastal distribution and subduction to meso- and bathypelagic depths as it is advected northwards.

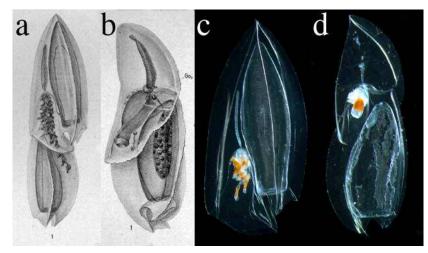
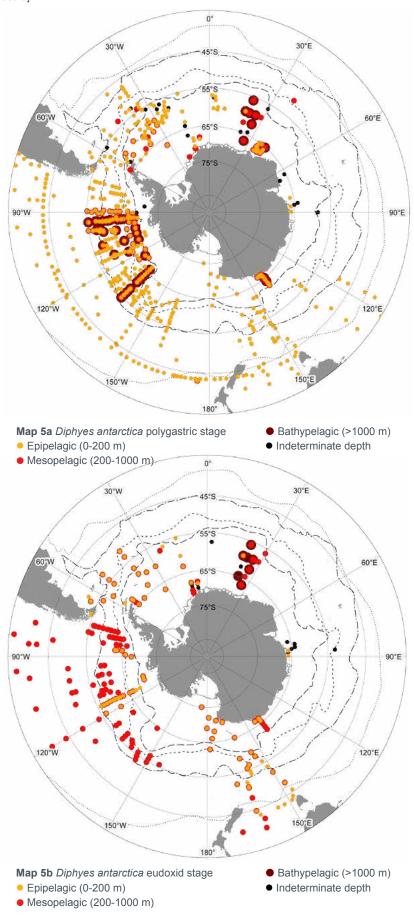


Figure 5 Original illustration of *Diphyes antarctica* Moser, 1925 (left), and photographs by Dr. Russell Hopcroft (right) of polygastric (a, c) and eudoxid (b, d) stages [not to scale]



Gelatinous Plankton Maps 5 Map 5a. Distribution of polygastric stages of *Diphyes antarctica* based on available data. — Map 5b. Distribution of eudoxid stages of *Diphyes antarctica* based on available data.

2.5. Sub-Antarctic inhabitants of the epipelagic zone

Some species such as the calycophoran siphonophore *Eudoxoides spiralis* (Bigelow, 1911) occur predominantly to the north of the Antarctic Convergence, only rarely occurring closer to the continent and presumably having been transported there in some eddy or the like (Fig. 6, Map 6b) where they undoubtedly perish. This group also includes the calycophoran siphonophores *Eudoxoides mitra* (Huxley, 1859), *Sphaeronectes koellikeri* Huxley, 1859, the physonect siphonophore *Agalma elegans* (Sars, 1846), and the rhopalonematid trachymedusa *Rhopalonema velatum* Gegenbaur, 1857. Most of these species probably inhabit the entire southern hemisphere temperate zone but appear not to occur there due to the dearth of surveys to the north of the Sub-Antarctic Front.

2.6. Bipolar species concentrated within the Polar Front

The calycophoran siphonophore *Muggiaea bargmannae* Totton, 1954 (Fig. 7, Map 7a–b) and the cydippid ctenophore *Dryodora glandiformis* (Mertens, 1833) belong to this group. They are basically epipelagic or upper mesopelagic and although they can be subducted and advected outside of the Polar Front they cannot survive there. The bathypelagic records for *M. bargmannae* have a good possibility of being due to contamination from shallower layers (e.g. Pugh *et al.* 1997).

2.7. Discontinuously-distributed boreal deep-water inhabitants

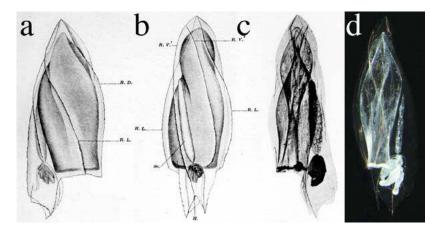
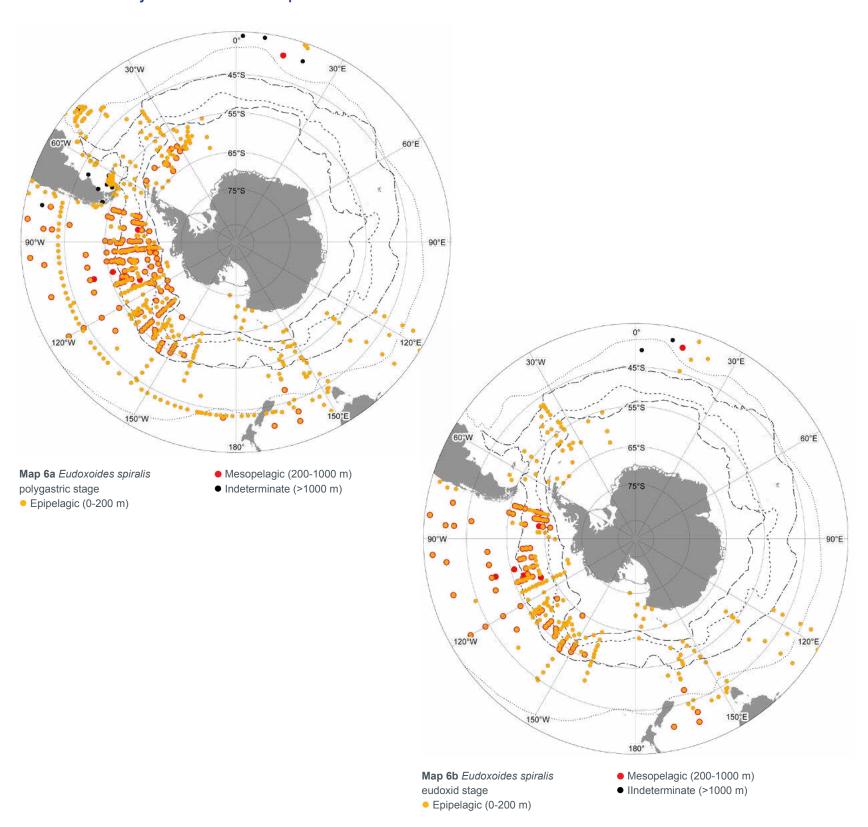


Figure 6 Original illustration of anterior nectophore of *Eudoxoides spiralis* (Bigelow, 1911) in lateral (a) and lower (b) views, a photograph in lateral view from the original description (c), and a photograph in upper-lateral view of a formalin-preserved individual from the Kurose Hole, Ogasawara Islands, Japan, by MMG (d).

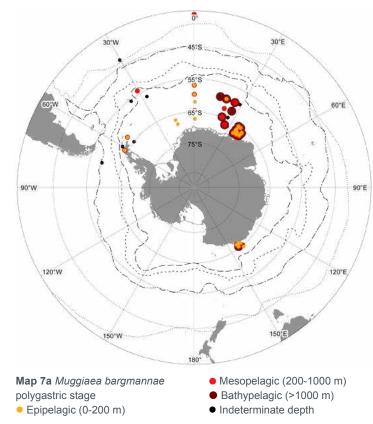


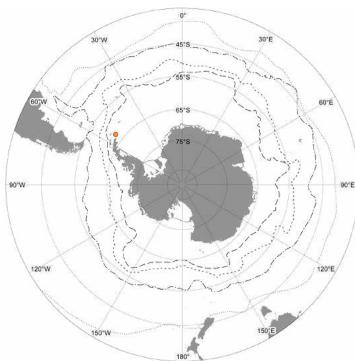
Gelatinous Plankton Map 6 Map 6a. Distribution of polygastric stages of *Eudoxoides spiralis* based on available data, showing its predominantly epipelagic distribution in subantarctic waters with occasional entrainment in warm eddies transporting it close to the Antarctic continent. — Map 6b. Distribution of eudoxid stages of *Eudoxoides spiralis* based on available data, showing its predominantly epipelagic distribution in subantarctic waters with occasional entrainment in warm eddies transporting it close to the Antarctic continent.



a

Figure 7 Original line drawing of *Muggiaea bargmannae* Totton, 1954 (a), and photograph by Dr. Russell Hopcroft (b) [not to scale].





Map 7b Muggiaea bargmannae eudoxid stage • Epipelagic (0-200 m)

- Mesopelagic (200-1000 m)

Gelatinous Plankton Map 7 Distribution of polygastric stages of *Muggiaea bargmannae* based on available data, suggesting that it is subducted into the mesopelagic layer as it is advected northwards.

extending south to the edge of the continental shelf

Some species are distributed in boreal waters of both the northern and southern hemispheres and penetrate into the deep water up to the Antarctic continental shelf. The anthomedusa *Pandea rubra* Bigelow, 1913 (Fig. 8, Map 8) has an asexual polyp stage that grows only on the shells of a certain species of pelagic snail, thought to be an epipelagic, cold-water species of the genus *Clio* (Lindsay *et al.* 2008)

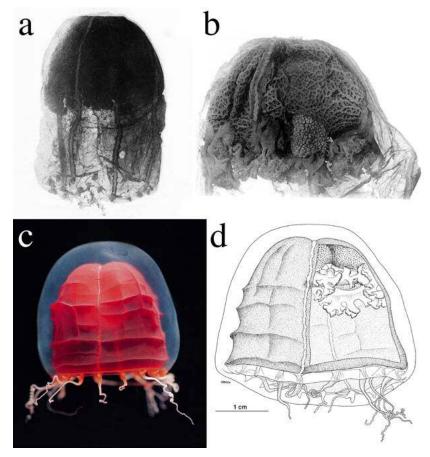
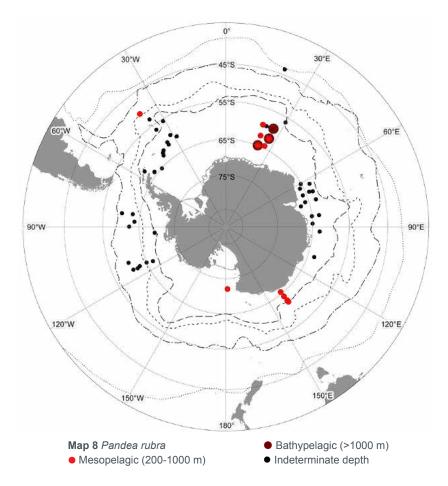


Figure 8 Original photographs of Pandea rubra Bigelow, 1913 (entire medusa (a), stomach and gonad morphology (b)), a photograph of a living specimen from off Japan by DJL (c) and a line drawing of the same (d).



Gelatinous Plankton Map 8 Distribution of Pandea rubra based on available data, showing its meso-bathypelagic distribution.

2.8. Deep-water inhabitants extending south to the edge of the continental shelf

Species that occur in deep waters worldwide can be entrained in southward-flowing deep water and can penetrate to the Antarctic continental shelf break. Some species such as the rhopalonematid trachymedusa *Pantachogon haeckeli* Maas, 1893 (Fig. 9, Map 9) and the calycophoran siphonophore *Vogtia serrata* (Moser, 1925) are confined to upper mesopelagic layers at their shallowest extent, while others such as the calycophoran siphonophore *Rosacea plicata* Bigelow, 1911 (Fig. 10, Map 10) and the coronate

scyphomedusa *Periphylla periphylla* (Péron & Lesueur, 1810) can penetrate the epipelagic (Fig. 11, Map 11), although only when surface temperatures are cold in the case of the latter. Other species inhabit the lower mesopelagic with their distributions becoming deeper as they approach the Antarctic continent. They include species such as the calycophoran siphonophores *Gilia reticulata* (Totton, 1954) (Fig. 12, Map 12a) and *Clausophyes moserae* Margulis, 1988, and the halicreatid trachymedusa *Botrynema brucei* Browne, 1908. The sexual eudoxid stages of *G. reticulata* have yet to be reported from epipelagic waters (Map 12b).

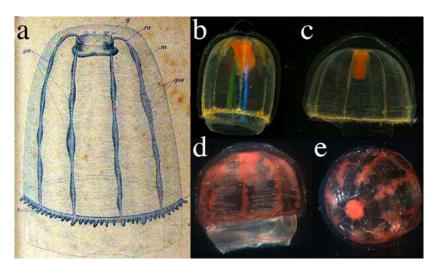
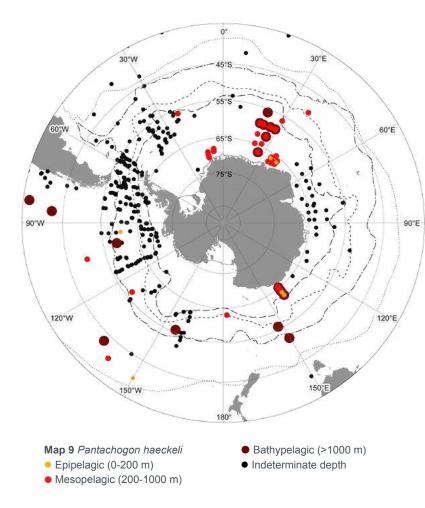


Figure 9 Original illustration of *Pantachogon haeckeli* Maas, 1893 (a), and photographs by DJL of individuals in various stages of development (immature: b, c; mature: d, e) [not to scale].



Gelatinous Plankton Map 9 Distribution of *Pantachogon haeckeli* based on available data, showing its meso-bathypelagic distribution encroaching on the Antarctic continent.

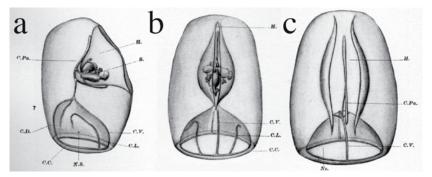
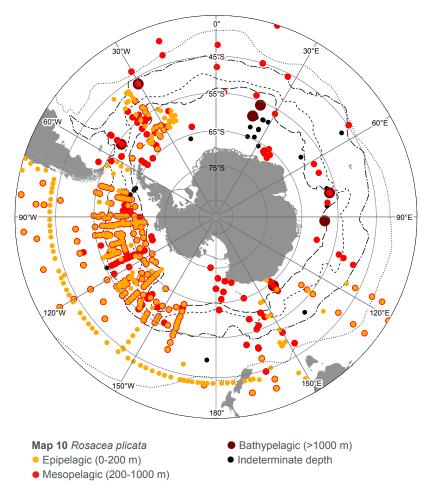


Figure 10 Original line drawing of *Rosacea plicata* Bigelow, 1911 with N2 nectophore in lateral view (a), and lower view (b), N3 nectophore in lower view (c).



Gelatinous Plankton Map 10 Distribution of *Rosacea plicata* Bigelow, 1911 based on available data, showing its mesopelagic distribution around the Antarctic continent and its epipelagic distribution north of the Polar Front where it is upwelled and is advected northwards with surface water up to the Sub-Tropical Front.



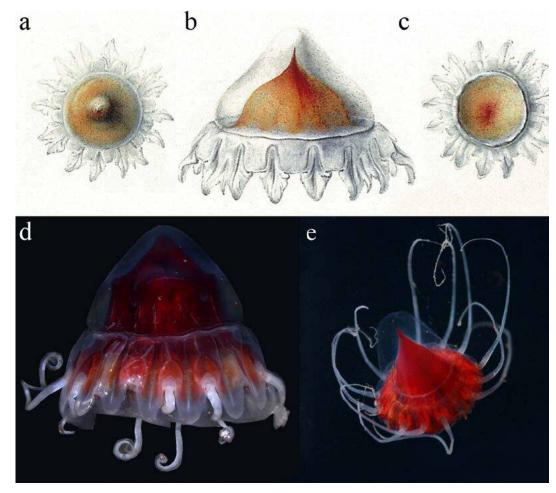
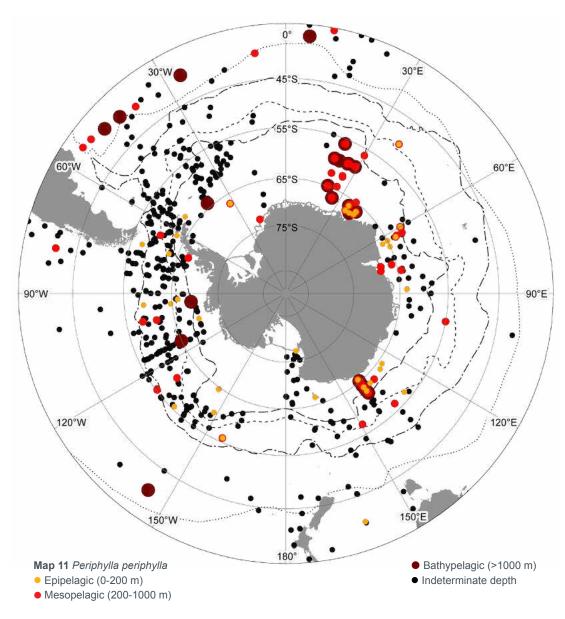


Figure 11 Original watercolour of *Periphylla periphylla* (Péron & Lesueur, 1809) in dorsal (a), side (b) and ventral (c) views, and photographs from the Lazarev Sea by Ricardo Giesecke (d) and from off Japan by DJL (e).



Gelatinous Plankton Map 11 Distribution of Periphylla periphylla based on available data, showing its bathypelagic distribution and encroachment on the Antarctic continent.

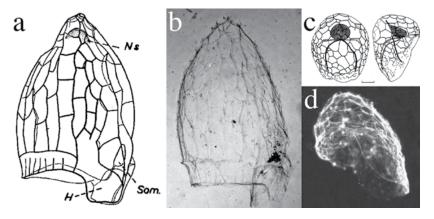


Figure 12 Original line drawing of anterior nectophore of *Gilia reticulata* (Totton, 1954) in lateral view (a), photograph of a fresh specimen from Pagès et al. 2006 (b), line drawings of upper [left] and lateral [right] views of a eudoxid bract from Pugh & Pagès 1995 [scale bar 0.5 mm] (c), and a photograph of a eudoxid bract in lateral view by MMG (d).

Map 12a Gilia reticulata Mesopelagic (200-1000 m) polygastric stage Bathypelagic (>1000 m) Epipelagic (0-200 m) • Indeterminate depth

Map 12b Gilia reticulata eudoxid stage

- Mesopelagic (200-1000 m)
- Bathypelagic (>1000 m)

Gelatinous Plankton Map 12a Distribution of polygastric stages of *Gilia reticulata* based on available data, showing its mesopelagic distribution in the offshore waters of the Antarctic continent and its epipelagic distribution north of the Polar Front where it is upwelled and is advected northwards with surface water up to the Sub-Tropical Front. — Map 12b. Distribution of eudoxid stages of *Gilia reticulata* based on available data, showing its mesopelagic distribution.

2.9. Southern Hemisphere extending south of the Polar Front

Some species such as the rhopalonematid trachymedusa *Crossota brunnea* Vanhöffen, 1902 (Fig. 13, Map 13) and the cydippid ctenophore *Bathyctena chuni* (Moser, 1909) seem to originate/flourish in the Deep Water of the Southern Ocean and penetrate northwards to replenish their populations in the Southern Hemisphere. *Crossota brunnea* is not synonymous with *C. rufobrunnea*, its northern hemisphere counterpart, contrary to the assertion of Navas-Pereira & Vannucci (1990).

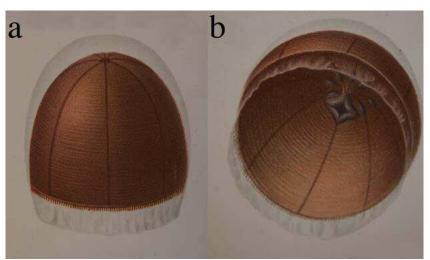
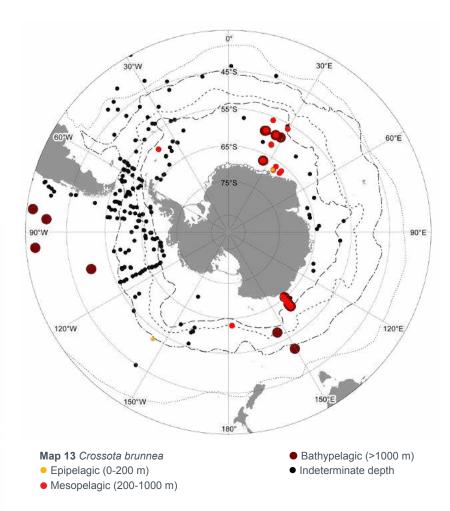


Figure 13 Original line drawings of *Crossota brunnea* Vanhöffen, 1902 (lateral view (a), ventro-lateral view (b).



Gelatinous Plankton Map 13 Distribution of *Crossota brunnea* based on available data, showing its predominantly bathypelagic distribution in the offshore waters of the Antarctic continent and occurrence north of the Sub-Tropical Front



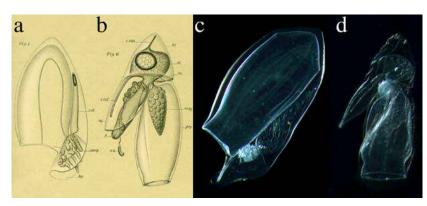
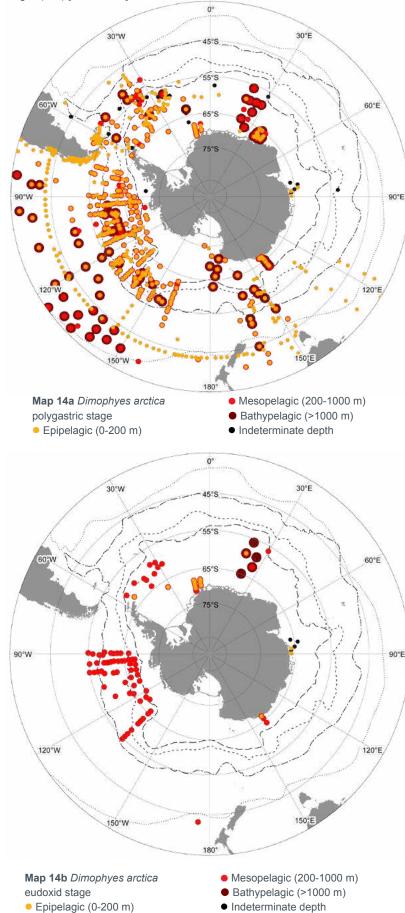


Figure 14 Original illustration by Chun 1897 (left), and photographs by Dr. Russell Hopcroft (right) of *Dimophyes arctica* (Chun, 1897) polygastric (a, c) and eudoxid stages (b, d) [not to scale].



Gelatinous Plankton Map 14a Distribution of polygastric stages of *Dimophyes arctica* based on available data, showing the wide range of its distribution. — Map 14b. Distribution of eudoxid stages of *Dimophyes arctica* based on available data, showing its predominantly mesopelagic distribution.

2.10. Cosmopolitan extending to south of the Polar Front

The calycophoran siphonophore *Dimophyes arctica* (Chun, 1897) is probably the only member of this group (Fig. 14, Map 14a). It occurs at both poles, mostly in epipelagic and upper mesopelagic waters, and in mesopelagic to bathypelagic waters worldwide. The sexual eudoxid stage seems to be distributed deeper than the polygastric stage when mapped (Map 14b) and some layered net samples have also reported that although habitat depth ranges largely overlap, population peaks for the eudoxids are deeper than the polygastric stages (e.g. Grossmann 2010).

3. Conclusions

In the majority of cases the distribution type of various gelatinous zooplankton species is unclear, due to a combination of limited taxonomic expertise and sampling artefacts. The sizes or life history stages are also seldom recorded though both depth distributions and environmental niche preferences could well vary according to these factors. Small calycophoran siphonophores slip through the mesh of large aperture nets such as the Rectangular Midwater Trawls (RMT) commonly used for plankton studies in the Southern Ocean and soft-bodied forms such as ctenophores are often destroyed to the point where species identification is impossible, if indeed any tissue remains at all. Although the ctenophores Callianira antarctica Chun, 1897 and large pink or brown Beroe species are conspicuous inhabitants of the Southern Ocean, their distributional type is not yet determined. Studies on gelatinous zooplankton in the Southern Hemisphere outside of the Southern Ocean are even fewer than within it, and as a result the true endemicity of many species has yet to be conclusively proven. In fact, the "endemic" species Leuckartiara brownei and Heterotentacula mirabilis have also been reported in recent years from the Mediterranean Sea (Pagès et al. 1999, Bouillon et al. 2000)! New species continue to be described from the Southern Ocean and its surrounding waters (e.g. Grossmann et al. 2012). The study of the gelatinous zooplankton fauna of the Southern Ocean would benefit greatly from the collection, photographic recording, and preservation for taxonomic study of pristine specimens of many of the species, preferably with some tissue preserved for DNA analyses and the voucher specimen fixed and preserved in buffered 4% formalin-seawater solution. The use of imaging technologies such as remotely-operated vehicles (ROVs) and in-situ photographic devices such as the Visual Plankton Recorder (VPR) or Underwater Video Profiler (UVP) would greatly augment the more traditional approach of SCUBA diving with a camera — still an invaluable tool for increasing our knowledge on this fragile but important component of the planktonic fauna of Antarctic seas.

4. Data Source

Data have been extracted from the following sources: Alvariño et al. (1990), Araujo (2012), Australian Antarctic Data Centre (accessed 2013), British Antarctic Survey (GBIF accessed 2013), Daniel (1985), Fuentes (2006), Fuentes et al. (2008), Grossmann (2010), Guerrero et al. (2013), Hardy & Gunther (1935), Hopkins (1985), Kramp (1948, 1949, 1957), Larson (1986), Larson & Harbison (1990), Leloup (1932, 1934), Lindsay & Fuentes (unpublished), Mackintosh (1934), Margulis (1992), Moser (1925), Museum Victoria (OBIS accessed 2013), Navas-Pereira (1992), Navas-Pereira & Vannucci (1990), National Museum of Natural History [U.S.] (accessed 2013), Ocean Genome Resource (accessed 2013), O'Sullivan (1982), Pagès & Gili (1989), Pagès & Kurbjeweit (1994), Pagès & Orejas (1999), Pagès & Schnack-Schiel (1996), Pagès et al. (1992, 1994, 1996), Palma (1985, 1994), Palma & Aravena (2001), Palma & Rosales (1997), Palma et al. (1999), Panasiuk-Chodnicka & Żmijewska (2010), Pugh et al. (1997), SCAR-MarBIN (De Broyer & Danis 2013), Southampton Oceanography Center Discovery Collections Midwater Database (accessed 2013), Toda et al. (2010), Totton (1954), Vanden Berghe (2007), Vanhöffen (1908, 1912). These publications are indicated with an asterisk in the references.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

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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.

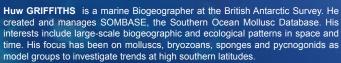
The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)
In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.biobis.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.

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