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SCAR-Marine Biodiversity Information Network

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CHAPTER 5.6. BENTHIC HYDROIDS (CNIDARIA: HYDROZOA).

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.6. Benthic Hydroids (Cnidaria, Hydrozoa)

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1. Introduction

Hydrozoans constitute one of the most diversified and characteristic zoological groups of the Antarctic benthic ecosystem, widely represented in its different epibenthic communities, and characterised by a high degree of endemism at the specific level and the dominance of a few, monophyletic groups (see Peña Cantero & García Carrascosa 1999, Peña Cantero *et al*. 2010). Nevertheless, Antarctic hydroids are still inadequately known, especially because knowledge of the fauna is completely lacking over vast areas of the region.

The scientific study of Antarctic hydroids started, as also happened to other marine organisms, as a result of the large scientific expeditions to the Southern Ocean at the end of the 19th century and the beginning of the 20th century. Hydroid collections gathered from those expeditions were studied by a large number of scientists (e.g. Allman 1883, 1888, Hartlaub 1904, Jäderholm 1905, Billard 1906, 1914, Hickson & Gravely 1907, Ritchie 1907, Totton 1930). Afterwards, however, there were practically no new studies on Antarctic hydroids, with a few exceptions, such as those by Naumov & Stepanjants (1965) and Stepanjants (1979) or Blanco (1984) and Blanco & De Miralles (1972). At end of the last century, the study of the Antarctic benthic hydroids blooms again thanks, almost exclusively, to the work developed by the author, research that still continues today (see, for example, Peña Cantero 2008, 2009, 2010, 2012, Peña Cantero *et al*. 1997, 1997a-b, 2002, Peña Cantero & Vervoort 2003, 2004, 2005).

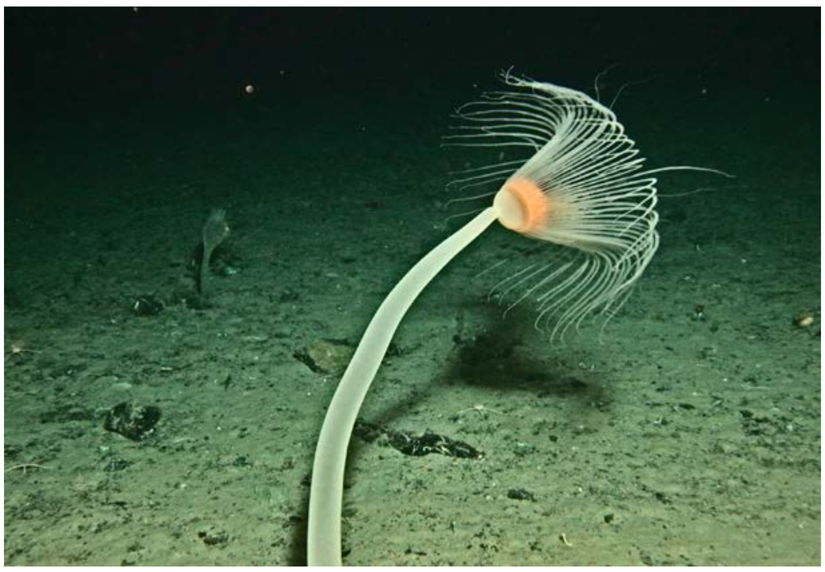


Photo 1 Athecate hydroid. Larsen B (*Polarstern* ANT-XXIII/8, st. 714-1). Image: J. Gutt © AWI/Marum, University of Bremen, Germany.

2. Methods

The study area considered herein is restricted entirely to the Antarctic Region. Knowledge of benthic hydroids in the sub-Antarctic is particularly limited, so that region has been excluded from consideration here.The Antarctic Region is quite well defined for the pelagic realm. Authors such as Hedgpeth (1969) or Knox (2007) have considered that it covers the whole area south of the Antarctic Convergence, whereas the sub-Antarctic region extends between the Polar Front and the Sub-Tropical Front. For the benthic realm the issue is not so clear and authors such as Andriashev (1964) and Picken (1985) considered the northern limit of the pack ice as the most valid limit for the Antarctic benthos.

For the biogeographic discussion the geographic distribution models considered by Peña Cantero & García Carrascosa (1999) have basically been followed. They included the following distributions: circum-Antarctic (distribution throughout the Antarctic region), Pan-Antarctic (present in Antarctic waters and throughout the sub-Antarctic region), Antarctic-Kerguelen (Antarctic waters plus the sub-Antarctic islands) and Antarctic Patagonian (Antarctic waters plus those of the Magellan area). There are also a few species with a West Antarctic-Patagonian distribution (restricted West Antarctic waters plus the Magellanic Zone).

Benthic hydroids exclusive of hydrocorals (family Stylasteridae), a group addressed in a separate chapter, are the subject of this report. Pelagic hydrozoans are also dealt with in another chapter.

3. Biodiversity

Antarctic benthic hydroids belong to the class Hydrozoa and are represented by members of the two hydrozoans subclasses, Hydroidolina and Trachylina, though the representation of the latter is minimal. Peak diversity among hydrozoans in Antarctic benthic communities exists in the subclass Hydroidolina, represented by the orders Anthoathecata and Leptothecata, with the later being much better represented.

Of 179 species considered, only two belong to Trachylina, in particular to the order Limnomedusae. The remaining 177 species are unequally distributed between Anthoathecata and Leptothecata. The former accounts for 33 species, whereas Leptothecata embraces the remaining 144 species. The biodiversity inside each order is similar for families (10 each), but distinctly different at the generic level, with Leptothecata practically doubling Anthoathecata in number (29 and 16 genera respectively).

Biodiversity patterns exhibited by Antarctic benthic hydroids clearly differ according to taxonomic level. Diversity is relatively high at the species level, with hydrozoans being amongst the top ten of all taxonomic groups in numbers of species (Clarke & Johnston 2003). At the generic level, however, diversity is relatively low. Peña Cantero & García Carrascosa (1999) reported 40 genera of leptothecate hydroids from the Magellan area but only 23 from Antarctic waters. A somewhat higher number of leptothecate genera (29) is now known from Antarctic waters, though numbers from Magellan waters could have also increased.

The Antarctic benthic hydroid fauna is characterised by concentration of species in only a few genera. This remarkable phenomenon is particularly true for Leptothecata. Almost 75% of species in the group are referable to six genera (*Antarctoscyphus*, *Halecium*, *Oswaldella*, *Schizotricha*, *Staurotheca* and *Symplectoscyphus*), constituting ca. 20% of the total number of genera. Approximately half of the species are assigned to *Oswaldella*, *Staurotheca* and *Symplectoscyphus* (i.e. 10% of the genera). Indeed, almost 20% of all leptothecate species belong to *Oswaldella*, the most speciose genus of hydrozoans inhabiting benthic communities in the Antarctic marine ecosystem. While species of Anthoathecata are more evenly distributed amongst genera, they nevertheless show the same tendency, with ca. 55% of the species being assigned to only four (25%) genera (*Clathrozoella*, *Eudendrium*, *Gymnogonos* and *Hydractinia*). *Eudendrium* is the most diverse anthoathecate genus, with eight species.

At family level, Sertulariidae is by far the richest in numbers of species. Of 179 species of benthic hydroids recorded from the Antarctic region, 61 of them (34%) belong to that family. Kirchenpaueriidae is another important family in the Antarctic benthic ecosystem, with records of 26 nominal species (ca. 15%), all belonging to *Oswaldella*. Other well-represented families are Haleciidae and Schizotrichidae, with ca. 7%, and Lafoeidae and Campanulariidae, with ca. 6% of the total number of species. The most speciose anthoathecate families are Eudendriidae (ca. 4.5%) and Corymorphidae (ca. 3.4%).

As at the generic level, hydroid diversity is also concentrated in a few families, though to a lesser extent, and again the pattern is most distinct in Leptothecata. Almost 80% of leptothecate species belong to four families, namely Sertulariidae, Haleciidae, Kirchenpaueriidae and Schizotrichidae, accounting for 40% of the families. In Anthoathecata, ca. 67% of species is concentrated in ca. 40% of the families (Bougainvilliidae, Corymorphidae, Eudendriidae and Hydractiniidae).

Another remarkable feature of the benthic Antarctic hydroid fauna is that the dominant genera constitute monophyletic groups. This has been proved in phylogenetic studies using either morphological (Peña Cantero & Marques 1999) or molecular (Peña Cantero *et al*. 2010) data.

4. Biogeography

The benthic hydroid fauna of the Antarctic is highly distinctive at the species level. Stepanjants (1979) found that 44 (48%) of 91 species present were endemic to the region. Later, Peña Cantero & García Carrascosa (1999) found that approximately 70% of Antarctic benthic leptothecate hydroids were endemics. Studies carried out most recently have increased knowledge of this group considerably, and endemism has risen even further to ca. 80%.

The degree of endemism in the Antarctic benthic hydroid fauna is distinctly high amongst the different Antarctic zoological groups. Griffiths *et al.* (2009) suggested general species endemism rates of around 50%. Thus, for example, Hydrozoa endemism is higher than in Cheilostomata Bryozoa (55.6%, see Griffiths *et al.* 2009) and Pycnogonida (56.3%, see Munilla & Soler Membrives 2009), and closer to the species endemism in Gastropoda (73.7%, see Griffiths *et al.* 2009), Amphipoda (72.3%, see De Broyer *et al.* 2007) or Cumacea (80%, see Mühlenhardt-Siegel 2011).

Distinctiveness of the Antarctic hydroid fauna increases even more when it is combined with species also inhabiting sub-Antarctic waters. Several Antarctic species have Pan-Antarctic (3 species), Antarctic-Patagonian (9 species) or Antarctic-Kerguelen (6 species) distribution patterns. Thus, endemism reaches roughly 90% amongst species known from either the Antarctic region or from Antarctic and sub-Antarctic waters.

Few Antarctic species of benthic hydroids (16 species) are found beyond sub-Antarctic waters. In general, they are species with a multi-austral, bipolar, circumglobal or worldwide distribution.

Antarctic benthic hydroids are also characterised by the uneven distribution of species endemism within the Antarctic Region. Although a large part of endemic Antarctic species may be considered to have a circum-Antarctic distribution (49 species, ca. 29%, Map 3), there are many species restricted either to West Antarctic or to East Antarctic (Map 4). There are even species apparently restricted to very small geographic areas, especially South Georgia (Peña Cantero & García Carrascosa 1995, Peña Cantero *et al*. 1995) and the Balleny Islands (Peña Cantero 2009).

As for differences in endemism across Antarctica, Stepanjants (1979) found quite similar patterns within the hydroid faunas of East (ca. 14%) and West Antarctic (12%). Twenty years later, Peña Cantero & García Carrascosa (1999) found a clear bias to West Antarctic amongst endemic leptothecate hydroids, with ca. 64% of Antarctic endemism restricted to West Antarctic and only ca. 7% limited to East Antarctic. Differences between percentages reported by Stepanjants (1979) and Peña Cantero & García Carrascosa (1999) may be attributed to real differences between the two areas, but also by the unequal sampling and study efforts in East and West Antarctic since Stepanjants's investigation. In fact, research within the last decade has included study of more samples from East Antarctic, and the supposed higher level of endemism in West Antarctic has been reduced; several species of hydroids previously thought to be West Antarctic endemics have been found to be circum-Antarctic (cf. Peña Cantero & Vervoort 2003, 2004, 2005). Thus, nowadays 67 species (39%) are considered endemic in West Antarctic and just 21 species (12%) are restricted to East Antarctic. Future scientific surveys will probably increase the number of circum-Antarctic species even more.

In contrast to the high endemism at species level, Antarctic benthic hydrozoans show an almost nonexistent endemism at the generic level. Thus, among the 45 genera with representatives in the Antarctic region, only *Mixoscyphus* can be considered, at present, strictly endemic to the Southern Ocean. However, five genera (*Abietinella*, *Antarctoscyphus*, *Oswaldella*, *Staurotheca* and *Stegella*) have their species restricted to Antarctic (most) and sub-Antarctic waters and probably originated in the Antarctic region (Maps 1–2).

Antarctoscyphus, *Oswaldella* and *Staurotheca* are mainly Antarctic genera, with just a few species present in sub-Antarctic waters. At present, *Oswaldella* includes 27 formally described species (cf. Peña Cantero 2007) and four unnamed species. With the exception of *O. herwigi* El Beshbeeshy, 1991, present in the sub-Antarctic Patagonian Region, all species of *Oswaldella* have an Antarctic distribution (cf. Marques & Peña Cantero 2010). A similar predominance of Antarctic species exists in *Staurotheca*. Of 24 species unambiguously belonging to the genus (cf. Peña Cantero & Vervoort 2003), only six are found outside the Antarctic region: two have an Antarctic-Kerguelen distribution (*S. dichotoma* Allman, 1888 and *S. frigida* Peña Cantero, Svoboda & Vervoort, 1997), three have an Antarctic Patagonian distribution [*S. jaederhomi* Stechow, 1920, *S. nonscripta* Peña Cantero, Svoboda & Vervoort, 1997 and *S. vervoorti* (El Beshbeeshy, 1991)], and only one seems to be endemic to the Kerguelen area [*S. echinocarpa* (Allman, 1888)]. Of the 10 known species of *Antarctoscyphus* (cf. Peña Cantero *et al*. 1997), only *A. elongatus* (Jäderholm, 1904) is found outside the Antarctic Region, having an Antarctic-Kerguelen distribution; the remaining nine are endemic in the Antarctic. Finally, the single members of the genera *Stegella* [*S. lobata* (Vanhöffen, 1910)] and *Abietinella* [*A. operculata* (Jäderholm, 1903) (Map 5)] have an Antarctic-Kerguelen and an Antarctic-Patagonian distribution, respectively.

The high degree of endemism at the species level may be due in part to the predominant life cycle of Antarctic benthic hydroids, characterised by suppression of the free-swimming stage (Peña Cantero & García Carrascosa 1999). Highly seasonal primary productivity in the Antarctic region, and its restriction to open-water periods at most coastal sites, may favour groups of hydroids with reduced or even suppressed free-swimming stages. Most Antarctic hydroids have fixed gonophores, with only a few species having a free medusa stage. Nevertheless, as has been shown above, a large percentage of Antarctic endemic species is formed by those with a circum-Antarctic distribution, contrary to the *a priori* low dispersal potential of species with fixed gonophores. The uniform general conditions present throughout the Antarctic Ocean over a long time period may have made expansion of distributions possible in spite of the supposedly reduced dispersal capability provided by this type of life cycle.

The early hypothesis about subdivisions within the Antarctic Region, originally proposed by Hedgpeth (1969) and basically followed by subsequent authors (e.g. Dell 1972, Clarke & Johnston 2003), has been little modified even after extensive subsequent study in the region. Investigations on several different groups, including Amphipoda (De Broyer & Jażdżewski 1996) and Bryozoa (Barnes & De Grave 2000), have given support to the traditional model, although introducing a distinction between East and West Antarctic. It seems, however, that the Southern Ocean division is taxa-dependent (cf. Griffiths *et al*. 2009). Whereas some taxa (e.g. gastropods) apparently follow the classical model, including the separation between East and West Antarctic, others (e.g. Bivalvia) point to the Southern Ocean as a single biogeographic unit.

Benthic hydrozoans also seem to follow the classical hypothesis, although including the distinction between East and West Antarctic. In spite of the rise of circum-Antarctic species indicated above, both areas still keep their peculiarities. In addition, in a recent study on the delimitation of areas of endemism in the Southern Ocean using the Parsimony Analysis of Endemicity (PAE) and the species of the Antarctic genus *Oswaldella*, Marques & Peña Cantero (2010) also obtained support to the subdivision of High Antarctic into two regions: the *Western High Antarctic Zone*, embracing most of the western high Antarctic shore, extending from the eastern part of the Weddell Sea to the eastern part of the Ross Sea (including the Balleny Islands) and the *Eastern High Antarctic Zone*, which comprises a large area between the eastern marginal part of the Ross Sea and the Davis Sea (from 140° to 90°E). They also found two additional areas of endemism, namely the *Magellanic Zone*, outside the Polar Front, and the *Antarctic Peninsula Zone*, between 90°W and 90°E, including Peter I, the northern part of the Antarctic Peninsula, the Scotia Arc islands, Bouvet Island, the east part of the Weddell Sea, Princess Astrid Coast and the Davis Sea.

In conclusion, although Antarctic benthic hydrozoans seem to follow Hedgpeth's classical scheme, including peculiarities between East and West Antarctic (Map 4), it is necessary to carry out a comprehensive study incorporating the data gathered during recent years and across all taxa to define more clearly the apparent subdivision of the Antarctic Region glimpsed by the study done with *Oswaldella*. Of course, it would be also necessary to fill the extensive gaps still existing around the Antarctic continent.

5. Bathymetry

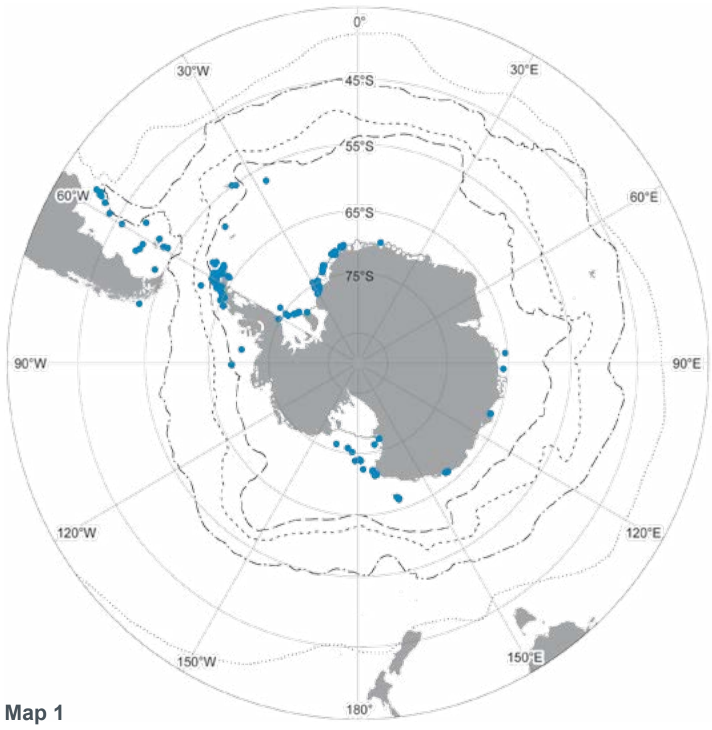
In relation to the bathymetric distribution of Antarctic benthic hydrozoans, only a comprehensive study has been carried out (cf. Peña Cantero 2004). It was restricted to the Antarctic Region as defined by Picken (1985) for the benthos, and considering the shelf break occurring at 500 m, a depth marked by the bathymetric distribution of benthic hydroids. The study, which included the bathymetric distribution of the 155 species known at the time (Stylasteridae excluded), allowed recognition of six groups of species. The *First group* was composed of species restricted to the shallowest 30 m, the lower limit marked by the maximum depth of anchor-ice formation. The *Second group* embraced species present on the continental shelf, except the shallowest subtidal. The *Third group* was formed by species occurring throughout the continental shelf. The *Fourth group* included those species extending from below the shallowest 30 m to beyond the shelf break, reaching bathyal or abyssal depths. The *Fifth group* was composed of strictly deep-sea species, occurring only beyond the continental shelf break. Finally, the *Sixth group* included species present along the whole bathymetric range, from shallowest to deepest waters. Most species of Antarctic benthic hydroids have extensive bathymetric distributions, but they are restricted to shelf waters [e.g. *Oswaldella shetlandica* (20–410 m) and *Symplectoscyphus cumberlandicus* (8–540 m)]. The dominant group with ca. 33% was the *Second group* (i.e. shelf species absent from the shallowest subtidal). However, the most remarkable fact is that 93% of the species are limited to or partially occur on the continental shelf. Only 7% of the species could be considered strict inhabitants of the Deep Sea, being found *only* beyond the continental shelf break. Of course, the *Fourth* and *Sixth* groups [e.g. *Symplectoscyphus curvatus* (49–2043 m) and *Schizotricha vervoorti* (50–1152 m), for the *Fourth* group, and *Antarctoscyphus spiralis* (6–1958 m) (Map 3) and *Symplectoscyphus plectilis* (7–1958 m), for the *Sixth* one] also contribute to the pool of inhabitants of the deep sea and, consequently, 43% of the species are found in the Antarctic Deep Sea.

Interestingly Peña Cantero (2004) found an inverse relationship in the bathymetric distribution between anthoathecate and leptothecate hydroids, with the former dominating in the upper levels and leptothecates being more frequent in the lower levels. For instance, only 2% of leptothecates were restricted to the shallowest waters, whereas 23% of anthoathecates occurred there. Stepanjants (1979) indicated that the larger representation of anthoathecates in shallow waters might be due to reduced salinities, since anthoathecates seem more tolerant of lower salinities while leptothecates supposedly require higher salinities. According to Peña Cantero (2004) other reasons (either ecological or evolutionary) could be behind this phenomenon, even bias related to sampling problems. Anthoathecates usually come in bad condition when using indirect sampling gears, making their identification extremely difficult or even impossible. As might be expected, most shallow-water records of anthoathecates are based on samples obtained by scuba-diving, thereby assuring better specimen condition.

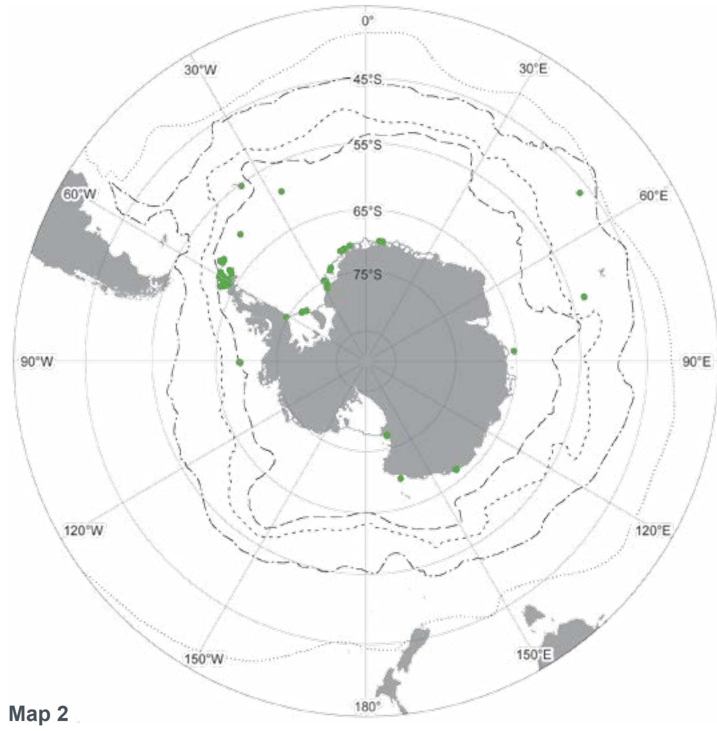
The low number of Antarctic benthic hydroids restricted to the shallowest levels (6%) could be related to the hardship of the environment due to the effects of ice in the upper subtidal (i.e. abrasion by sea-ice and anchor-ice formation). Nevertheless, there are also a number of species occurring in deeper waters that can also be found in the shallowest waters.

6. Conclusions

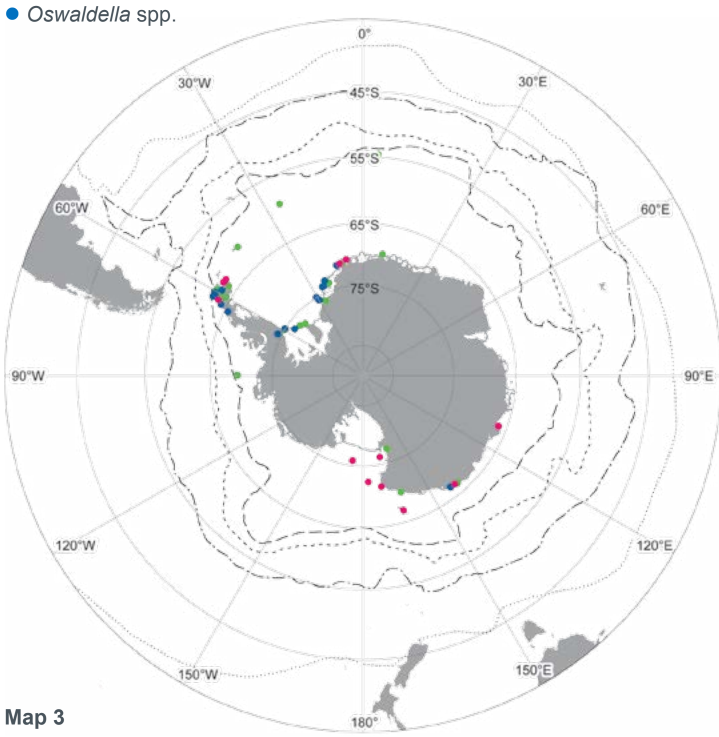
Biodiversity and both bathymetrical and geographical distributions of Antarctic benthic hydroids are analysed in light of information from recent studies. Benthic hydrozoans are relatively rich in terms of species and they are characterised by a remarkable concentration of that diversity within a few monophyletic genera. This pattern is particularly marked in Leptothecata, where *Oswaldella*, *Staurotheca* and *Symplectoscyphus* (which alone includes ca. 10% of the genera) account for approximately half of its diversity. Benthic hydroids are also remarkable for high endemism at the species level, reaching ca. 80%. Endemism rises to ca. 90% when considering species restricted in distribution either to Antarctic waters or to Antarctic and sub-Antarctic waters. High endemism in Antarctic benthic hydroids is due to an important contingent of species with a circum-Antarctic distribution (49 species, ca. 29%), but also



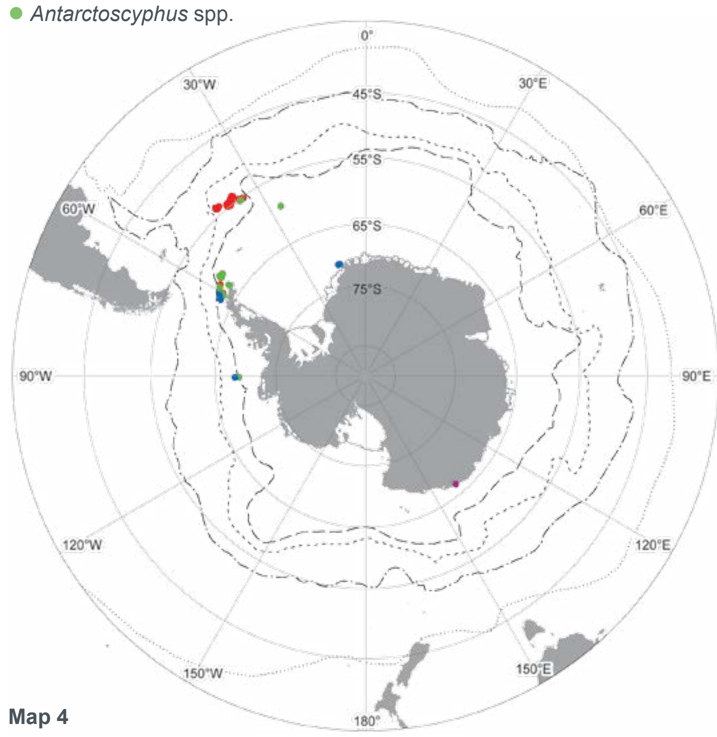
Map 1
● *Oswaldella* spp.



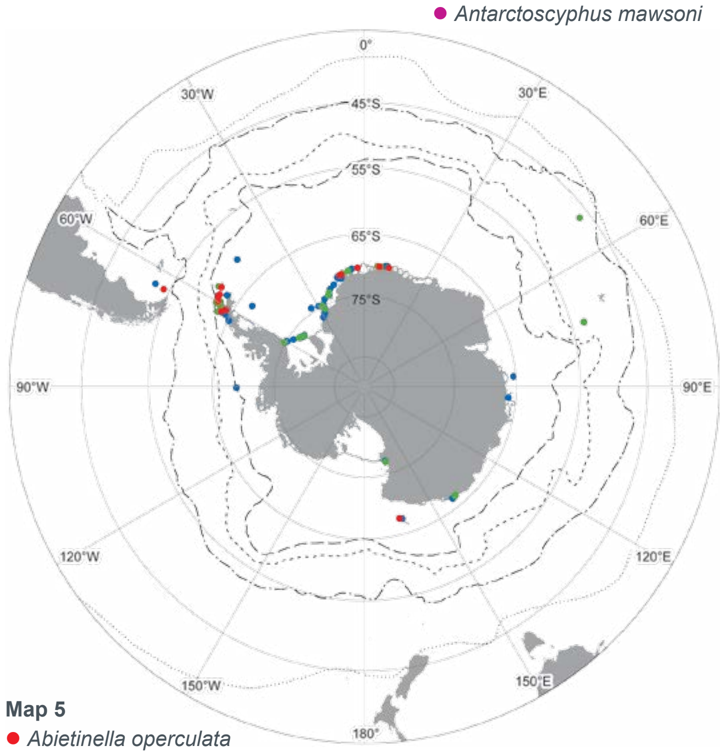
Map 2
● *Antarctoscyphus* spp.



Map 3
● *Symplectoscyphus naumovi*
● *Oswaldella stepanjantsae*
● *Antarctoscyphus spiralis*



Map 4
● *Antarctoscyphus asymmetricus*
● *Antarctoscyphus mawsoni*
● *Staurotheca undosiparietina*
● *Symplectoscyphus nesioticus*



Map 5
● *Abietinella operculata*
● *Antarctoscyphus elongatus*
● *Billardia subrufa*

Benthic hydroids Maps 1–5 Map 1. Distribution of the genus *Oswaldella Stechow, 1919* . Map. 2. Distribution of the genus *Antarctoscyphus Peña Cantero, García Carrascosa & Vervoort, 1997*. Map 3. Examples of species with a circum-Antarctic distribution: *Symplectoscyphus naumovi Blanco, 1969*, *Oswaldella stepanjantsae Peña Cantero, Svoboda & Vervoort, 1997*, *Antarctoscyphus spiralis (Hickson & Gravely, 1907)*. Map 4. Examples of species with a West-Antarctic distribution: *Antarctoscyphus asymmetricus Peña Cantero, García Carrascosa & Vervoort, 1997*, *Staurotheca undosiparietina (Stepanjants, 1979)*, *Symplectoscyphus nesioticus Blanco, 1987* and with an East-Antarctic distribution: *Antarctoscyphus mawsoni (Briggs, 1938)*. Map 5. Examples of species with an Antarctic-Kerguelen distribution: *ntarctoscyphus elongatus (Jäderholm, 1904)* and a Antarctic-Patagonian distribution: *Abietinella operculata (Jäderholm, 1903)*, *Billardia subrufa (Jäderholm, 1904)*.

to species restricted in distribution to either East (21 species, ca. 12%) or West Antarctic (67 species, ca. 39%). Antarctic benthic hydroids therefore provide support to the subdivision of the Antarctic Region into East and West Antarctic. Endemism may have been favoured by the predominant life cycle pattern of Antarctic benthic hydrozoans, characterised by the suppression of the free-swimming stage. As for bathymetric distribution, most species of Antarctic benthic hydroids are eurybathic, having very wide bathymetric distributions. However, most species (ca. 93%) are limited to or partially occur on the continental shelf. Only 7% of the species are considered strict inhabitants of the deep sea, though there are other species which include the deep-sea waters as part of their wide bathymetric range, so that ca. 43% of the species can be found in the Antarctic Deep Sea.

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Dr. Huw Griffiths (BAS, Cambridge) and Dr. Anton Van de Putte (RBINS, Brussels) prepared the maps. This is CAML contribution # 104.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

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

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

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

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

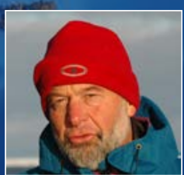
The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team



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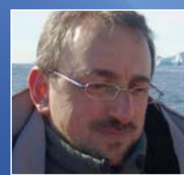

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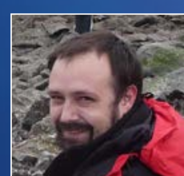

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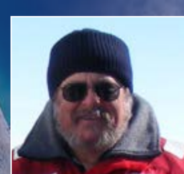

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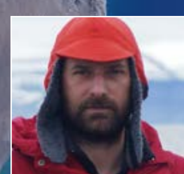

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