CHAPTER 6.4. SOUTHERN OCEAN PTEROPODS.

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN


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1. Introduction

Pteropods are small free-swimming planktonic gastropods. Their informal name derives from the modified molluscan foot (‘poda’) to form paired swimming wings (‘pter-‘) in both the Thecosomata (‘covered’ or shelled pteropods) and the Gymnosomata (‘naked’ or shell-less pteropods). Both orders are found in the surface ocean to the deep sea, have a global distribution, although population densities are often highest in polar and sub-polar regions, and exhibit distinct biogeographic patterns in the Southern Ocean. It should be appreciated that the two orders are taxonomically distinct from each other within the gastropods (there are major differences in their morphologies, trophic levels, mode of predation and contribution to carbon export). Consequently, they should be cautiously lumped together under the general term ‘pteropod’, and ideally described as either Thecosomata (shelled) or Gymnosomata (naked) in order for there to be a clear distinction between the group under discussion.

Shell pteropods have a thin external shell composed of a form of calcium carbonate known as aragonite. They are the largest planktonic producer of aragonite in the world’s oceans (Orr et al. 2005) and contribute significantly to the carbon cycle of the ocean (Lalli & Gilmer 1989, Noji et al. 2007). The Southern Ocean south of the Polar Front in particular (Accemoro et al. 2003, Honjo 2004), where densities can be as high as 100–1000s individuals/m³ (Hopkins 1987, Pakhomov et al. 1997, Seibel & Dierssen 2003, Hunt et al. 2007).

Many of the thecosomous pteropods have a third internal shell only during their early life stage (Lalli & Gilmer 1989). They are specialised carnivorous feeders, do not tend to form swarms and not usually significant contributors to the zooplankton biomass of a region, except in some polar areas (van der Spoel & Dadon 1999).

All thecosomous pteropods are protandric hermaphrodites (i.e. change from male to female throughout their lives). However, details of the life histories of pteropods, and Southern Ocean pteropods in particular, remain a significant knowledge gap. It is assumed that most shelled species entire life cycles are of the order of a year with eggs released in gelatinous masses followed by veliger larval hatching, metamorphoses and development into juveniles. Limacina helicina varieties are thought to follow this cycle (van der Spoel & Dadon, 1999) whereas ovoviviparity (the maintenance of eggs within the mother’s body to hatch ‘live’ offspring) has been seen in some pteropods, especially those adapted to the deep-sea habitat such as Thielea helicoides (van der Spoel & Dadon 1999). Gymnosomus have a similar reproductive anatomy to thecosomes pteropods but may function as simultaneous hermaphrodites at times.

The number of generations per year appears to differ between Antarctic and sub-Antarctic populations. Antarctic pteropods are thought to produce just one generation per year. Seasonal density observations by Hunt et al. (2008) support this suggestion for Limacina retroversa although Bednarskii et al. (2012) have recently proposed that a small number of Limacina retroversa may live for more than 2 years in Southern Ocean waters. Note that Limacina retroversa is often referred to in the literature as Limacina helicina antarctica but the Southern Ocean species has recently been recognised as a distinct species (Thielea helicina Rang, 1834, the nomenclature of the World Register of Marine Species here). Sub-Antarctic pteropods have been proposed to have different generation modes and growth rates. Dadon & de Cidre’s (1992) work on the life history of Limacina retroversa in Australia remains the only detailed study of a Southern Ocean pteropod’s life history to date. They found this taxon survived for a maximum of one year, producing two generations: the first in spring and the second in late summer. The first generation has a high growth rate and matures early to reproduce in late summer while the second grows during autumn but not at all over winter, reproducing in the spring. This annual cycle matches the general primary production cycle of the sub-Antarctic zone.

Pteropods are thought to undergo diel migrations, residing in surface waters at night and descending to deeper waters during the day (typical distances travelled are species specific but of the order of 10–100 m) (Hunt et al. 2008, Lalli & Gilmer 1989, van der Spoel & Dadon 1999). They play important roles as both grazers and prey in the Southern Ocean community. Shelled pteropods feed on suspended phytoplankton using free-floating mucous webs (Lalli & Gilmer 1989) and can have a significant grazing impact, particularly in high latitude regions. In the Southern Ocean, they favour diatoms, dinoflagellates, tintinnids, copepods, silicoflagellates, polychaetes and other invertebrate larvae and can consume as much as 19% of the daily primary production when they are aggregated (Hopkins 1987, Hunt et al. 2008).

Thecosomatous pteropods are the exclusive prey of the Gymnosomata (Lalli & Gilmer 1989) as well as food for higher trophic level predators such as krill, salps, fish, birds and marine mammals (Foster 1987, Kornosky et al. 2008). The carnivorous Gymnosomata have specialised hunting and feeding structures used for capturing thecosomatous pteropods and are themselves food for meso- and macronekton (Lalli & Gilmer 1989). Given the rate of environmental change the Southern Ocean is experiencing, we are faced with the question of whether or not pteropods will thrive, cope, adapt or decline. Pteropods are often referred to as ‘sentinel’ organisms as we expect them to be among the first organisms to be impacted by changing water chemistry, temperature, oxygen and nutrient deficiencies in our southern polar regions in the future. If pteropods undergo significant decreases in abundance, or even face a complete loss of species (Comeau et al. 2012), this could have significant implications for Southern Ocean biodiversity and the ecological services it is able to provide (Orr et al. 2005, Cooley et al. 2005).

2. Methods

Observations, biodiversity and biogeographic distributions of pteropods included in our Southern Ocean synthesis have been collated from general (Lalli & Gilmer 1989, van der Spoel et al. 1997) and regional (van der Spoel & Dadon 1999, Hunt et al. 2008, Howard et al. 2011, Roberts et al. 2011, Cantwell 2012, Hopcroft unpublished data) sources which incorporate distribution surveys of vertical or obliquely hauled plankton nets of various types (including bongo, trawl, IKT and Norpac) and mesh sizes (150 µm – 4.5 mm) — typically in the upper 500 m of the water column, continuous plankton recorder observations — typically in surface waters, sediment trap collections — to as deep as 2000 m, and literature collations. Source areas are summarised in Map 1 and taxa specific distributions from these areas represented in Maps 2–21. Our taxonomic classifications follow the World Register of Marine Species nomenclature.

3. Biodiversity & Biogeographic Distributions


3.1. Thecosomata

The Thecosomatous are distinguished by shell morphology, which includes coiled, curved, pyramidal and conical forms (Lalli & Gilmer 1989). Of the approximately 40,000 marine gastropod species, only about 140 are wholly planktonic (Lalli & Gilmer 1989) and 86 of these pteropods (van der Spoel et al. 1997). Whilst there are over 70 species of shelled pteropod known from the Southern Atlantic sector of the Southern Ocean alone (van der Spoel & Dadon 1999) the typical diversity in the Southern Ocean proper is much lower (Table 1, Photos 1–3).


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**Map 1** Areas considered

**Map 2** *Clio piatkowskii*

**Map 3** *Clio pyramidata* f. *excisa*

**Map 4** *Clio pyramidata* f. *sulcata*

**Map 5** *Limacina rangii* f. *antarctica*
Antarctic shelled fauna include Clio piatkowskii, Clio pyramidalta f. excisa, Clio pyramidalta f. sulcata and Limacina range f. antarctica (Photo 1). Clio piatkowskii has been considered to be restricted to the deep Weddell Sea (van der Spoel et al. 1992, 1997, 1998) (Map 2) although in 2008 recorded it in small numbers in mesoplanktonic South Atlantic Polar Front waters and the Lazarev Sea. Dozens were also collected during the CEAMARC expedition in the East Antarctic (Hopcroft, unpublished data), thus lack of more numerous observations may simply reflect a lack of bathy-mesoplanktonic depth sampling rather than an actual absence of this taxa (which is able to migrate over 1000 m daily). We note here that we follow van der Spoel (1963) in referring to it as C. piatkowskii, which is typical of waters to the north of PF (Map 9) is typical of Antarctic coast and the range of C. piatkowskii f. antarctica where it can occur in mass blooms (van der Spoel et al. 1997). Hunt et al. (2008) reported Clio pyramidalta f. sulcata to be consistently present in their East Antarctic sector samples although not always in high abundances. This taxa is known to undergo pronounced diel migration (Hunt et al. 2008) found its range to be between 200 m and 1000 m during summer) and its lack of numbers in surface net and CPR samples may belie their true distribution in the Southern Ocean. Clearly molecular research is needed to determine if we have separate species or forms in southern waters. Forms of Clio pyramidalta, particularly f. sulcata, are common in Antarctic waters (Maps 3–4). Clio pyramidalta f. sulcata is typically found in the surface waters of the cold Southern Ocean between the Antarctic coast and the range of Clio pyramidalta f. antarctica which it can occur in mass blooms (van der Spoel et al. 1997). Hunt et al. (2008) reported Clio pyramidalta f. sulcata to be consistently present in their East Antarctic sector samples although not always in high abundances. This taxa is known to undergo pronounced diel migration (Hunt et al. 2008) found its range to be between 200 m and 1000 m during summer) and its lack of numbers in surface net and CPR samples may belie their true distribution in the Southern Ocean. Limacina range is one of the most common pteropods in the Southern Polar Ocean. Its cold water form — f. antarctica — is typical of waters to the south of the Polar Front (Map 5). van der Spoel et al. (1997) report Limacina range f. antarctica to be stenothermic (showing a clear preference for cold waters) while the sub-Antarctic Limacina range f. range is eurythermic (shows a preference for higher temperatures). Hopkins (1987) noted that densities of Limacina range can be as high as 300 individuals/m² in the Ross Sea, and other studies have report this pteropod to be a dominant component of the Ross Sea plankton and the dominant pteropod observed in waters south of the Polar Front (Hunt et al. 2008 and references therein). We note here that these researchers are likely referring to f. antarctica but have not attempted to determine between the two forms (as is unfortunately common in the pteropod literature due to the difficulty in identifying between forms in continuous plankton recorder collected samples) however, f. antarctica and f. range exhibit distinct morphologies and biogeographic patterns and should be separated where possible. Sub-Antarctic shelled fauna include Clio pyramidalta f. antarctica, Clio pyramidalta f. manteni, Limacina range f. range, Thielea helicoides, Limacina range retroversa australis and Peracle reticulata (Photo 2, Maps 6–11). Of the two sub-Antarctic forms of Clio pyramidalta, f. antarctica is typical of Intermediate Southern Ocean waters. Similarly, the sub-Antarctic form of Limacina range — f. range is particularly prevalent in warmer waters north of the Polar Front (Bé & Gilmer 1977, van der Spoel & Dadon 1999) (Map 8). This taxa accounted for at least a third of all shells collected to sub-Antarctic zone sediment traps (Roberts et al. 2011). Thielea helicoides (Map 9) is typical of deep-sea microplankton, although it never occurs in large numbers (van der Spoel et al. 1997). Again, its absence in East Antarctic collections may reflect the surface sample bias in collated research collections to date rather than an actual absence of the taxa in the region.

Table 1: Varities of shelled Southern Ocean pteropods. STF = Sub-Tropical Front (~43°S), PF = Polar Front (~55°S), ACC = Antarctic Circumpolar Current (~60°S). Distribution, biogeographic and depth affinity derived from van der Spoel et al. (1997) and van der Spoel & Dadon (1999) with supporting observations by Hunt et al. (2008), Howard et al. (2011), Roberts et al. (2011) and Hopcroft (unpublished data). Taxonomic nomenclature as per World Register of Marine Species database (2013).

<table>
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<tr>
<th>Species Authority</th>
<th>Typical Distribution</th>
<th>Biogeographic Affinity</th>
<th>Depth Range</th>
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<td>Cosmopolitan</td>
<td>Cosmopolitan</td>
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<td>Cosmopolitan</td>
</tr>
<tr>
<td>Clio recurva balantium Rang, 1834</td>
<td>Circumglobal</td>
<td>Cosmopolitan</td>
<td>Meso-Bathypelagic</td>
</tr>
<tr>
<td>Diacria trispinosa (de Blainville, 1821)</td>
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<td>Cosmopolitan</td>
<td>Epi-Mesoplagic</td>
</tr>
<tr>
<td>Helicinoides inflatus (d’Orbigny, 1834)</td>
<td>Circumglobal</td>
<td>Cosmopolitan</td>
<td>Epi-Mesoplagic</td>
</tr>
<tr>
<td>Limacina rangei (d’Orbigny, 1834)</td>
<td>Arctic</td>
<td>Epi-Mesoplagic</td>
<td>Arctic</td>
</tr>
<tr>
<td>Limacina retroversa australis (Eydoux &amp; Souleyet, 1840)</td>
<td>STF to PF</td>
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<td>Epi-Mesoplagic</td>
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<tr>
<td>Paracle reticulata (d’Orbigny, 1834)</td>
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<td>Sub-Antarctic</td>
<td>Mesopelagic</td>
</tr>
<tr>
<td>Peracle validiviae (Meiserhammer, 1905)</td>
<td>Circumglobal</td>
<td>Cosmopolitan</td>
<td>Meso-Bathypelagic</td>
</tr>
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</table>
Limacina retroversa australis (Map 10) has been described as one of the most common pteropods in sub-Antarctic waters (van der Spoel & Dadon 1999, Hunt et al. 2008). van der Spoel et al. (1997) report it most frequently between 50°S–60°S and this taxa was observed as the dominant pteropod in the vicinity of the Prince Edward Islands, reaching up to 800 individuals/m². South of the PF this species occurs at low densities or is completely absent (Hunt et al. 2008). Pararcaella reticulata (Map 11) has been reported to be a sub-Antarctic pteropod (van der Spoel & Dadon 1999) but hasn’t been reported in significant numbers in Southern Ocean studies. Again, this may be related to its mesopelagic habitat preference rather than an actual absence in Southern Ocean waters.

Although not typical, occasionally cosmopolitan shell-less pteropods have been reported, collected or observed in Southern Ocean waters (Photo 3, Maps 12–17), likely introduced within eddies from northern waters. Cavolinia tridentata (Map 12), Clio cuspidata (Map 13), Clio recurva balantium (Map 14), Diacria tripirosa (Map 15), Helicocoides inflatus (Map 16) and Peraclea validviae (Map 17) have all been collected in sub-Antarctic zone nets (Howard et al. 2011) and deep sea traps (Roberts et al. 2011) as well as being observed during Census of Marine Life voyages (e.g. CEAMARC 2007/08: Hopcroft unpublished data).

Antarctic naked fauna include Clione limacina antarctica (Photo 4a) and Platybrachium antarticum (Photo 4b). Clione limacina antarctica is specific to the Southern Ocean, occurring in both Antarctic and sub-Antarctic waters but found predominantly south of the Polar Front (Hunt et al. 2008)(Map 18). This colourful taxa is a specialist predator on shelled pteropods, preferentially Limacina ranga in Antarctic waters and Limacina retroversa australis is sub-Antarctic waters (Lalli & Gilmer 1989) and its distribution and diet migration pattern accordingly tracks densities of Limacina pteropods in Southern Ocean waters (Hunt et al. 2008). Relatively little is known about Platybrachium antarticum although it is thought to have an Antarctic Ocean only distribution (Map 19) and we note that Hopcroft (unpublished data) recorded three sightings of this species during the CEAMARC cruise.

Sub-Antarctic naked fauna include Pneumodermopsis brachialis (Photo 4c) and Spongiosbranchaea australis (Photo 4d). Relatively little is known about Pneumodermopsis brachialis in the Southern Ocean and what we do know is restricted to van der Spoel & Dadon’s (1999) observations in the South-Atlantic Southern Ocean (Map 20). Conversely, Spongiosbranchaea australis is known to be both Antarctic and sub-Antarctic but particularly common in waters north of the Polar Front (Map 21). In East Antarctic waters, it tends to stay within the upper 150 m during both the day and night (Hunt et al. 2008). Observations indicate that Spongiosbranchaea australis is a specialist predator on Clio pyramidata (Lalli & Gilmer 1989, Hunt et al. 2008).

### 3.2. Gymnosomata

The Gymnosomata are distinguished by their shell-less adult forms. Whilst there are 45–50 species of naked pteropod (Lalli & Gilmer 1989), including 20 from the South Atlantic sector of the Southern Ocean alone (van der Spoel & Dadon 1999), the typical diversity in the Southern Ocean is much lower (Table 2, Photo 4, Maps 18–21).

### 4. Biogeographic processes and future research priorities

Pteropods (both shelled and naked varieties) are known to exist in epi- to bathypelagic waters in the Southern Ocean, although high abundances are only found in the epipelagic realm (van der Spoel & Dadon 1999). Accordingly, climatic influences on meso- (e.g. Perarcaella reticulata) to bathy- (e.g. Thielea helicoides) pelagic species are undetectable. However, species common in the epipelagic ocean layer are influenced by climate and climate change in addition to currents, water masses, prey and predators. For example: forms of Clio pyramidata are directly related to climatic belts including cold southern polar waters (f. sulcata), sub-polar waters (f. antarctica) and warmer waters in more temperate ecosystems (f. lanceolata) and Limacina species have a strong seasonal cycle and interannual variability in Southern Ocean waters. Regional and interannual variation in primary production has been proposed as the major determinant of spatial and temporal variability in thecosome pteropod population densities in the Southern Ocean (Comiso et al. 1993, Siebel & Dierssen 2003) and, for gymnosomes, the distribution and diet migration pattern of their prey (predominantly Limacina and Clio pteropods in Southern Ocean waters) dictates their distribution (Hunt et al. 2008).

### Table 2 Species and subspecies of naked Southern Ocean pteropods. STF = Sub-Tropical Front (~43°S). Distribution, biogeographic and depth affinity derived from van der Spoel et al. (1997) and van der Spoel & Dadon (1999) with supporting observations by Hunt et al. (2008) and Hopcroft (unpublished data). Taxonomic nomenclature as per World Register of Marine Species database (2013).

<table>
<thead>
<tr>
<th>Species</th>
<th>Authority</th>
<th>Typical Distribution</th>
<th>Biogeographic Affinity</th>
<th>Depth Range</th>
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<td>Clione limacina antarctica</td>
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<td>STF-Antarctic coast</td>
<td>Anti/Sub-Antarctic</td>
<td>Epipelagic</td>
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<td>Pneumodermopsis brachialis</td>
<td>Minichev, 1976</td>
<td>Sub-Antarctic waters</td>
<td>Sub-Antarctic</td>
<td>Epipelagic</td>
</tr>
<tr>
<td>Platybrachium antarticum</td>
<td>Minichev, 1976</td>
<td>Antarctic waters</td>
<td>Antarctic</td>
<td>Epipelagic</td>
</tr>
<tr>
<td>Spongiosbranchaea australis</td>
<td>d’Orbigny, 1834</td>
<td>STF-Antarctic coast</td>
<td>Sub/Antarctic</td>
<td>Epi-Mesopelagic</td>
</tr>
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</table>

### Photo 3

The major varieties of cosmopolitan shelled pteropods found in Southern Ocean waters. (a) Cavolinia tridentata (Forskal in Niebuhr, 1775). (b) Clio cuspidata (Bosc, 1802). (c) Clio recurva (Children, 1823). (d) Diacria tripirosa (de Blainville, 1821). (e) Helicocoides inflatus (d’Orbigny, 1834). (f) Peraclea validviae (Meesenheimer, 1905).

### Photo 4

The major varieties of naked pteropods found in Southern Ocean waters. (a) Clione limacina antarctica E.A. Smith, 1902. (b) Platybrachium antarticum Minichev, 1976. (c) Pneumodermopsis brachialis Minichev, 1976. (d) Spongiosbranchaea australis d’Orbigny, 1834. Scale bars: (a–d) and (f) 5 mm, (e) 0.5 mm. Images ©: (a–d) and (f) R. Hopcroft University of Alaska Fairbanks & CoML; (c) after van der Spoel & Dadon (1999). © Backhuys Publishers, Leiden, The Netherlands, (1999).
Unfortunately, we currently know very little about Southern Ocean pteropod population structures, production rates, metabolic rates, trophic relationships or the biogeographic processes that dictate distributions on the range of time scales required to make informed predictions about the fate of these important zooplankton in the future Southern Ocean ecosystem. For example, very little is known about the place of the gymnosomata in the Southern Ocean ecosystem. They are little reported from the gut contents of Antarctic organisms, likely due to their novel allomone compounds which have been shown to deter a number of fishes from feeding on them (e.g. Bryan et al. 1995, Phleger et al. 1999).

The final major gap in Southern Ocean pteropod research is regional shell production and calcification rates despite the shelled order providing significant ecosystem services to humanity: the production and export of calcium carbonate pteropod shells is an important regulating mechanism for the transport of both organic (Francois et al. 2002) and inorganic (Honjo 2004) carbon to the deep ocean. In fact, pteropod shells contribute at least 12% to the global carbonate flux (Berner & Honjo 1981) and may contribute as much as 50% in Polar Front waters (Honjo et al. 2000, Honjo 2004).

The general paucity of information on Southern Ocean pteropods is of particular concern, particularly in light of predictions for populations of marine calcifiers (shell makers) in polar regions in a future high CO$_2$ ocean. It is predicted that if CO$_2$ emissions continue unabated, Southern Ocean surface waters will become undersaturated with respect to aragonite (the material pteropods use for their shells) by 2100 (Orr et al. 2005) likely resulting in a decline in Southern Ocean pteropod densities and ultimately a northward shift in their distribution (Fabry et al. 2009). Impacts of this ongoing change in ocean chemistry, known as ocean acidification, may have significant ecological consequences for the Southern Ocean. There is an urgent need for targeted research on pteropods, and particularly the thecosomes, in order to quantify the likely ecosystem impacts of ocean acidification (in concert with other climatic stressors such as warming and freshening in the Southern Ocean).

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References


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 both 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.aiq) 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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