

## 12. Conclusions: Present and Future of Southern Ocean Biogeography

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### 1. Introduction

The evolution of patterns in biodiversity, from genes to ecosystems, was the key topic of the Census of Antarctic Marine Life (CAML). CAML was the most successful comprehensive, multinational and multidisciplinary survey of Antarctic biota ever conducted (Chapter 1.2). It used standardised methodologies, both traditional and contemporary, for sampling and identifying specimens and also for managing and analysing data. This sampling effort added important new data on the presence of species to the online data portal SCAR-MarBIN (Scientific Committee on Antarctic Research - Marine Biodiversity Information Network; www.scarmarbin.be) and to the Barcoding of Life project. The compilation of these two data sets required the contribution of hundreds of taxonomists. These experts identified the substantial amount of specimens collected and revisited, with morphological and molecular techniques, the systematic classification of different taxa, in some cases providing new phylogenies.

The Biogeographic Atlas of the Southern Ocean has gathered scientists together to update our understanding of distributional patterns of biota in the Southern Ocean, which was previously based on publications such as the Antarctic Map Folio Series (Bushnell, 1964-1972) that included the zoogeographical classification of Hedgpeth (1969) (Chapter 1.1.). For the new Biogeographic Atlas, experts verified and used SCAR MarBIN data, along with results from CAML surveys and authenticated historical data. Some data, as yet unpublished, were contributed by different institutes and museums, and also by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) and the IWC (International Whaling Commission), to create presence maps of the different taxa: benthos (Part 5), pelagic and sea-ice biota (Part 6), fish (Part 7) and birds and mammals (Part 8).

Other similar initiatives exist in other oceans or globally (Part 1), demonstrating that marine macroecology is becoming an important topic for understanding how environmental changes will modify species biogeography. Due to its present-day characteristics, as well as its history, the Southern Ocean can be regarded as a natural laboratory to explore biogeographic patterns and processes (Part 10), evolutionary patterns and ecological and adaptive processes operating in relatively extreme conditions that were not frequently experienced during the last 500 My (Part 3). It is a key area for understanding species biogeography because of its important environmental gradients and topography (Part 4). The northern boundary of the Southern Ocean is not directly limited by any continents, so its extent to the north is sometimes difficult to delineate. It fluctuates with the position of frontal zones, themselves being far more complex in their structure than initially described. Scenarios of climate change indicate that the Sub-Tropical and Sub-Antarctic Fronts may shift further south, thus reducing the extent of the area south of the Antarctic Polar Front. This Atlas is released at a time when signs of important changes are being observed (Part 9), and when concerns about conservation of the Southern Ocean are increasing (e.g. see proposals for Marine Protected Areas, Chapter 9.4). The information provided in the Atlas will be useful as a baseline against which to assess future change, and also as a first step for developing a dynamic online version (Part 11), which will support a dataset for biogeographic modelling in a pro-active fashion for good management.

### 2. Data compilation and analysis

The data team associated with the Atlas provided experts with data that were mostly available at the level of occurrence only (i.e. presence-only data; Chapter 2.1). The data-cleaning process relied on the specialists working on each chapter; they completed the database, verified samples and species records and updated the taxonomy. The data used in this Atlas were primarily drawn from SCAR-MarBIN and ANTABIF (Antarctic Biodiversity Information Facility; www.biodiversity.aq); a few other sources were also used and made available for the first time. Parts of these distribution records were taken from pre-existing Antarctic databases, including those for molluscs (Griffiths *et al.* 2003), echinoids (David *et al.* 2005), amphipods (De Broyer *et al.* 2007), fish (CCAMLR), and whales (IWC), which integrate historic data. They were updated to include new records from recent cruises, information from specimens housed in museum collections, data from recent literature and from the CAML campaigns. Most additional data that were compiled by the chapter authors have now been included in ANTABIF by the data manager. The complete ex-

pert-validated database, including records to latitude 40°S, represents 1.07 million occurrence records for 9,064 validated species from about 434,000 distinct sampling locations.

#### 2.1. Spatial and temporal heterogeneity in taxa records

Chapter 2.2, covering “Data distribution: Patterns and implications”, clearly shows where the database is lacking information for some geographic areas (Map 1). These are in regions with high summer sea ice concentrations and/or an absence of scientific bases that are regularly supplied by ships; hence, transects in these regions result from dedicated cruises only and are therefore less frequent. In the portion of the Southern Ocean facing Marie Byrd Land, there are no national bases or islands, explaining why top predators, for example, are also poorly represented in this section despite their ability to cover long distances. As another illustration of this, benthic records are lacking for the Amundsen Sea and parts of the Bellingshausen Sea and most of the deep sea. At the opposite bathymetric extreme is the Antarctic intertidal zone which, until recently, was considered to be virtually devoid of life.

We have different levels of spatial knowledge for different taxa. The vast majority of samples from all taxa come from the top 500 m of the water column. Known hotspots reflect logistical routes and the location of national bases (Griffiths 2010). Exclusively benthic taxa are known mostly from shelf/coastal areas, whereas pelagic or mixed taxa have a more widespread distribution record. Pelagic records have a fuller ‘horizontal’ distribution due to the Continuous Plankton Recorder surveys (Chapter 10.3) and Antarctic krill estimation (Chapter 6.9), although there are low concentrations of records in the Pacific sector of the Southern Ocean and in the summer sea ice regions. The level of information decreases as we move from the epipelagic to the mesopelagic, bathypelagic and deeper layers. For birds and mammals (Part 8), there are also some limitations when using sightings to infer their distribution; however, the use of tracking devices may alleviate this. As a consequence, the region bordered by 100°W and 150°W and south of 60°S is less densely populated by the records shown in Map 1.

#### 2.2. Numerical approach, including modelling, used for mapping

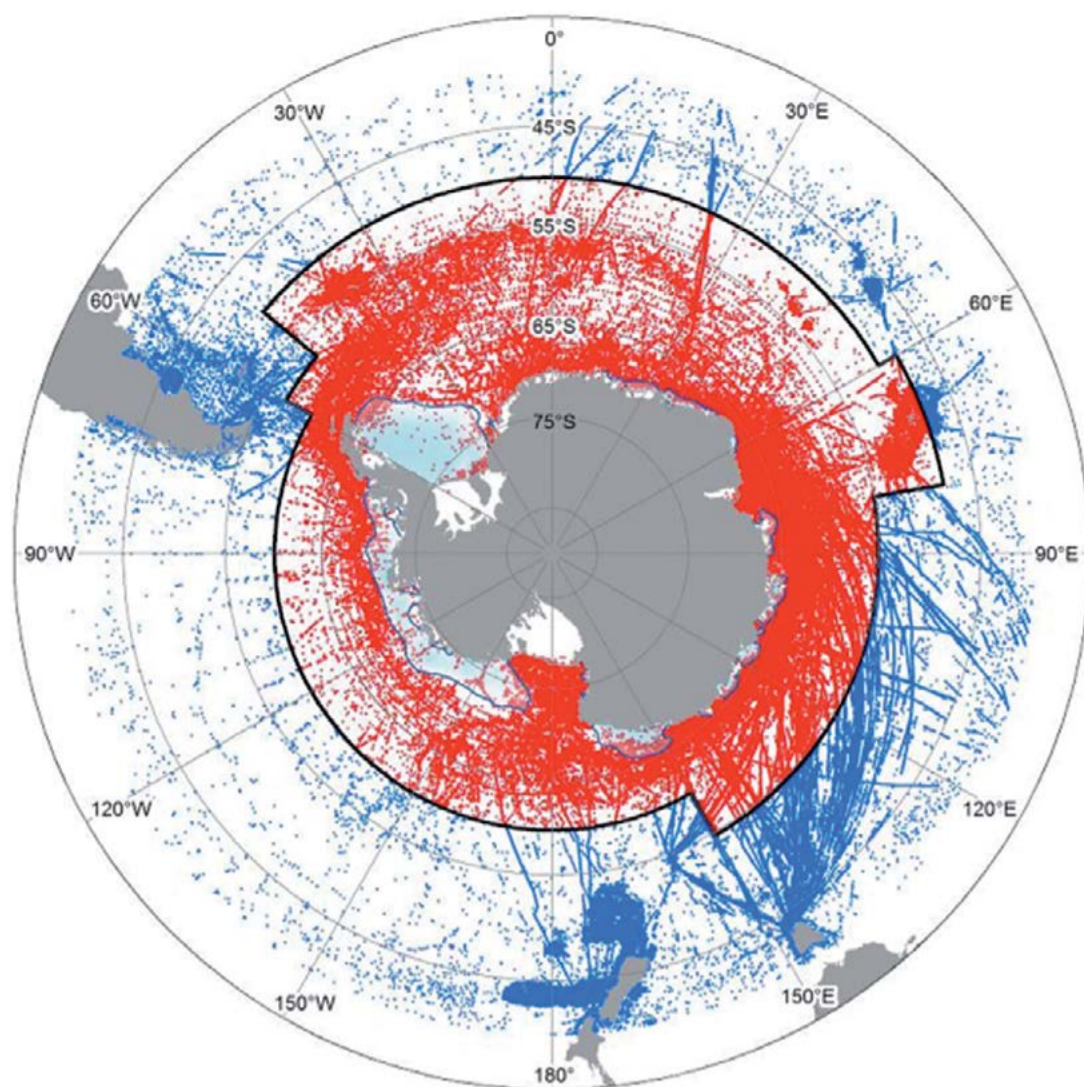
The Atlas provided new ideas for exploring marine biogeography. We followed four types of approaches:

- a taxonomic approach based on mapping species presence only for benthos (Part 5), pelagic and sea-ice organisms (Part 6), fish (Part 7) and bird and mammals (Part 8);
- a physiognomic approach used for the abiotic regionalisation that can be considered as a proxy of species assemblages. We provided a benthic regional classification (Chapter 10.1) and a pelagic regionalisation (Chapter 10.2);
- a mixed approach that is the “ecoregionalisation” process, which includes taxonomic, ecological and physiognomic data as it was used for zooplankton from the Continuous Plankton Recorder (Chapter 10.3) or, at regional scales, for fish (Koubbi *et al.* 2011a,b);
- a phylogeographic approach (Chapters 10.5, 10.6 and 10.7).

As a first step, it was important to update our knowledge on the Southern Ocean abiotic environment (Part 4) to delineate benthic regions based on geomorphological features (Chapter 10.1.), and pelagic regions based on sea-ice, water masses, currents, fronts or biogeochemical regions (Chapter 10.2). This information can help to define biogeographic regions, with the hypothesis that the abiotic environment can be used as a proxy for pelagic or benthic biodiversity when communities are not totally described. The environmental envelope of oceanographic and biogeochemical regions, such as defined by Longhurst (2007) for the world ocean or pelagic regions described in this Atlas (Chapter 10.2), were used to model the consequences of climate change on the extent of these provinces or bioregions (Chapters 9.1 and 9.2). Other promising approaches such as PHYSAT (Chapter 6.2) were used to estimate assemblages of phytoplankton, based on the analysis of remote sensing images. This allowed us to visualise monthly changes that occurred in the Southern Ocean.

The mixed approach consisted of modelling the potential preferred habitats of species and assemblages based on mathematical relationships between presence or presence/absence of species and environmental factors





**Map 1**

All records used for the Atlas

— SCAR-MarBIN primary area of interest  
— 20% Ice cover

- Within Area of interest
- Beyond Area of interest

% Summer Sea Ice Cover Value

High : 100  
Low : 20

**Conclusions Map 1** All samples used in the production of the Atlas. Red dots = samples taken within the SCAR-MarBIN primary area of interest, Blue dots = samples taken north of the primary area of interest

(Chapter 2.3) (Elith *et al.* 2006). This procedure allows for the prediction of species or assemblages in areas where no sampling has been carried out but where environmental information is available (from remote sensing, physical or biogeochemical modelling). Boosted regression trees (BRT) were tested on euphausiids (Chapter 6.9) and lantern fish (Part 7). Although most recently developed, the machine learning procedures such as Maxent and random forests (Chapter 9.1) have proved efficient for generating potential species distributions (Drew *et al.* 2011). Maxent was used for predicting species distributions from incomplete presence-only information (Elith *et al.* 2011) about crinoids (Chapter 5.25) and echinoids (Chapter 5.26), whereas 38 additional pelagic or birds and mammals species were modelled with random forests to evaluate their present distribution and that expected in 2100. Linking field data with Geographic Information Systems (GIS), the Internet, high performance data mining and machine learning could provide one of the best-possible approaches for conservation management (Huettmann 2012).

### 3. Importance of taxonomy in Southern Ocean biogeography

Taxonomy remains a fundamentally important component in biogeography, in the Southern Ocean as elsewhere. Taxonomy can contribute to “advanced” classifications of ecoregions based on bulk parameters, such as productivity, energy flux and complexity of interactions, since all these must be considered to be potentially species-specific (at least until across-species generality has been proven). Key taxa can be used for Southern Ocean biogeography if they are representative of a larger group of organisms in order either to decipher evolutionary and ecological processes behind the biogeographic structures or to learn more about ecosystem functioning. Key taxa are useful only if there are classifiable ecoregions, communities or assemblages for which they can be considered representative, and if assemblages do not only consist of a broad variety of individual gradients in occurrence. If such ecoregions exist *a priori*, a broad variety of, if not all, species occurrences have to be known in order to classify biogeographic regions before key species representing these regions can be identified.

of its neighbours, will remain true and even strengthen. Species numbers in the Antarctic are likely to increase with further sampling, taxonomic work and molecular data, helping to gain a better understanding of global diversity, distribution and evolutionary history (Griffiths *et al.* 2011).

## 4. Comparative biogeographic patterns for benthic and pelagic biota

Given the very different nature of the environments experienced by organisms at different depths in the water column the patterns observed in pelagic and benthic realms are often shaped by differing primary drivers.

### 4.1. General benthic biogeographic patterns

For the benthos, particularly those species with a large spatial distribution range, there appears to be a range of important physical environmental factors associated with the geomorphology of the Antarctic seafloor (Chapter 10.8). Geomorphological classification gives us a good insight into habitat forming features, such as the location of shelf basins, canyons, seamounts, etc., but mapping of smaller features is dependent upon high resolution maps of the seafloor. The biogeographic and species distribution patterns of benthos are largely driven by the Antarctic Circumpolar Current and the timing of past continental connectivity. The general patterns of relatively high species endemism and biogeographic isolation of the waters south of the Polar Front hold true for all groups. Depth is very often a key parameter in defining the range and distribution patterns of species; e.g. echinoids (Chapter 5.26). Most of our knowledge of the deep sea is restricted to the Weddell and Scotia Seas (Chapter 5.29). For species with a more restricted spatial range, sea surface temperature is another critical parameter, as is sea ice cover (of particular importance for strictly Antarctic shallow water species). At a more local scale the distributions of many benthic taxa are dictated by substrate type; e.g. the association of infauna with muddy sediments and sessile suspension feeders with hard substrates.

Key species can be abundant species with important roles in ecosystem function, such as Antarctic krill. Alternatively, rare species, for which taxonomic expertise is essential, often live in specific or unique environmental conditions and might be important for genetic diversity and ecosystem resilience. However, there has been much speculation about the representativeness of single species, especially within speciose systems in which the majority are rare species in the pelagic and benthic systems, particularly in the deep-sea. A truly rare species (not only due to a gap in information) can be a result of either occurrence or abundance. In the first case species can be locally very abundant but may occur only rarely. In the second case species are widespread but have low abundance per area. In both cases, rare species can contribute to a biogeographic classification but only if they can be associated with one specific biological province or assemblage and are largely absent in others.

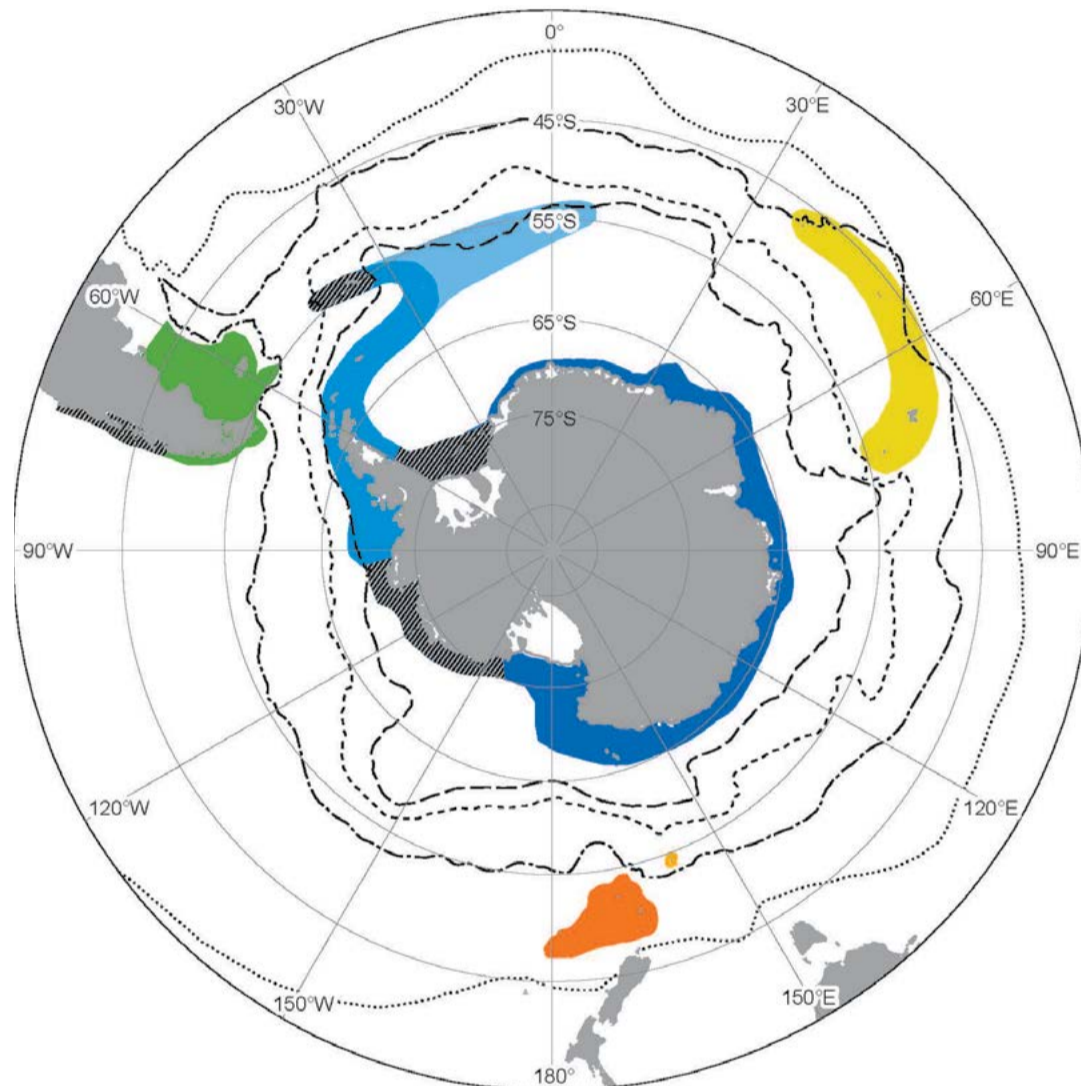
Given the high numbers of cryptic species complexes discovered, it has become clear that biodiversity in the Antarctic has been severely underestimated. Cryptic species complexes consist of closely related species with incomplete morphological differentiation, rather than distantly related species that have acquired a misleading degree of morphological similarity by other processes (convergent evolution). Besides raising species counts, the discovery of cryptic species has often resulted in a shift from a small number of widely distributed and morphologically variable species to a series of morphologically less variable species with smaller distributions, often allopatric ones. Notable exceptions of newly delimited species with larger distributions do exist, including truly circumpolar or even bipolar organisms. Besides the obvious relevance of studying cryptic species to taxonomy and systematics, there are less visible but nonetheless important ramifications in other fields, most notably those that put relatedness in the context of spatial distribution such as estimates of endemism, local and regional species diversity, size of distribution areas and latitudinal species diversity clines.

New molecular advances have started to change our understanding of circumpolar and cosmopolitan species, indicating the need for further, more detailed, taxonomic work on potentially cryptic species (Grant *et al.* 2010). Some of these biogeographic patterns may change with increased knowledge of diversity (both species and genetic). How much these patterns are likely to change is unclear, however it seems probable that the overall pattern, of a rich Antarctic fauna distinct from that



Several authors since Hedgpeth (1969) have attempted to summarise the general biogeographic patterns for the Southern Ocean benthos. Whole community studies are rare and only possible at the level of expert best knowledge (interpretation of data) and not by statistical methods (Chapter 5.28), therefore most biogeographic studies have focussed on individual taxonomic groups. Bivalvia (Chapter 5.11), Bryozoa (Cheilostomata and Cyclostomata; Chapter 5.23), Pycnogonida (Chapter 5.14), Porifera (Chapter 5.5), Ascidiacea (Chapter 5.27), Echinoidea (Chapter 5.26) and Tanaidacea (Chapter 5.19) show the Southern Ocean as a “single functional unit” with no evidence for a biogeographical split between East and West Antarctica, as previously described by different authors (Griffiths *et al.* 2009, Griffiths *et al.* 2011, Downey *et al.* 2012, Primo & Vázquez 2007, Pierrat *et al.* 2013). Gastropoda (Chapter 5.10.), Actiniaria (Chapter 5.8) and Amphipoda (Chapter 5.17), in contrast, display a level of differentiation between East and West, as described by Griffiths *et al.* (2009) and Rodriguez *et al.* (2007) (Map 2).

other groups (Pycnogonida, Ascidiacea, Bivalvia, Gastropoda, Cheilostomata) South Georgia displays an Antarctic nature (Griffiths *et al.* 2011, Griffiths *et al.* 2009, Primo & Vázquez 2007). The sub-Antarctic Islands of the Southern Indian Ocean (Bouvet Island, Prince Edward Islands, Crozet Islands, Kerguelen Islands and Heard Island) have varying degrees of faunal similarity with South America and Antarctica and the other sub-Antarctic Islands. The isolated and sparsely sampled Bouvet Island sits south of the mean position of the Polar Front and for the Pycnogonids, Actiniaria, Porifera and Bivalvia it groups with Antarctica, for the Cheilostomata with South America, and for the Cyclostomata with South Africa (Griffiths *et al.* 2009, Rodriguez *et al.* 2007, Downey *et al.* 2012). The other South Indian Ocean islands group with South America for the Bryozoa, Echinoidea and Bivalvia, and as a separate distinct group for the Pycnogonida and Gastropoda (Griffiths *et al.* 2009, Pierrat *et al.* 2013). For the Porifera the islands of Kerguelen and Heard have Antarctic characteristics (Downey *et al.* 2012), but in the Amphipoda they share many species with Macquarie Island (Chapter 5.7). The sub-Antarctic Islands of New Zealand exhibit strong affinities with the New Zealand shelf (mostly South Island), and share very little fauna with the other study regions (Griffiths *et al.* 2009, Griffiths *et al.* 2011, Downey *et al.* 2012, Chapter 5.7).



Map 2

■ Transition	■ Magellan, Magellan
<b>Benthic regions</b>	■ Sub-Antarctic Islands, Macquarie
<b>Region, Sub_divisi</b>	■ Sub-Antarctic Islands, New Zealand
■ Antarctic, Bouvet	■ Sub-Antarctic Islands, South Indian Ocean
■ Antarctic, East	
■ Antarctic, West	

**Conclusions Map 2** Summary of general benthic biogeographic regions in the Southern Ocean.

Biogeographical analyses indicate stronger faunal links between Antarctica and South America, than between Antarctica and South Africa, Southern Australia or New Zealand. Despite these general patterns, the biogeographical regions and connectivity in the Southern Ocean differ depending upon the class of animals and types of environment being considered. Recent results attest that oceanic islands are not only sinks for biodiversity (the flux is from the continent to the islands), but also sources for a reverse journey and colonisation toward the continents (Bellemain & Ricklefs 2008). The Southern Ocean holds a large number of archipelagos and islands of various sizes and origins. As such, it offers interesting possibilities to explore models of evolutionary radiation and extinction. Insularity is known to improve the probability of emergence of new species and to initiate high endemism (Presgraves & Glor 2010).

The biogeographic significance of the sub-Antarctic islands is more variable between different taxonomic groups and probably reflects their evolutionary and life history and dispersal capabilities. However, the proximity of some sub-Antarctic Islands to the strong current system around the Polar Front has resulted in extreme long-distance dispersal in some species with very low dispersal potential (Leese *et al.* 2010; Chapter 10.7). For the Porifera, Cyclostomata, Echinoidea and partly Amphipoda, South Georgia represents a true transitional zone between the Magellanic region and the Antarctic (Downey *et al.* 2012, Griffiths *et al.* 2009, Pierrat *et al.* 2013; Chapter 5.7). In

## 4.2. General pelagic biogeographic patterns

Planktonic and pelagic patterns are largely driven by the highly structured water masses and currents of the Southern Ocean, coupled with its extreme seasonality and seafloor characteristics (Chapter 10.4). Sampling in the water column is not uniform because the majority of samples come from the epipelagic zone, which includes the water column from the surface to 200 m. Our understanding of these upper waters is enhanced by remote sensing techniques, underway oceanographic studies and oceanographic data collected by top predators (Guinet *et al.* 2012). The distribution of sea birds and marine mammals is primarily explained by that of their prey and their diving capacity as air-breathing predators. For seabirds and seals, the proximity of suitable land habitats to breed represents an additional element that influences their horizontal distribution.

### Latitudinal gradients

As for benthos, frontal zones and bathymetry act as biogeographic barriers that segregate faunal assemblages or induce productive areas, enhancing primary productivity via fertilisation by nutrients (e.g. iron).

Historically, the Sub-Tropical Front and the Antarctic Polar Front were recognized as the main biogeographic barriers marking the limit between the Southern Ocean and the subtropical zones of the Indian, Atlantic and Pacific oceans. The results of the Continuous Plankton Recorder (Chapter 10.3) and the distribution of pelagic fish (Part 7) showed that the Sub-Antarctic Front is certainly the major biogeographic boundary in the Southern Ocean, confirming the results of Hunt & Hosie (2003, 2005, 2006a, b) based on a single transect of CPR and the results of Koubbi (1993) on fish larvae assemblages and Koubbi *et al.* (2011b) on mesopelagic fish assemblages.

The region between the Seasonal Ice Zone and the Sub-Antarctic Front is relatively uniform, with some variation between the permanent open ocean zone and the Polar Frontal Zone. Each of the biogeographic bands has distinct species compositions. However, differences between zones are based more on variation in the proportion of species abundances than complete differences in species. While there are consistent biogeographic bands of zooplankton assemblages around Antarctica (as shown in Chapter 10.3), the BRT modelling of *Oithona similis* (Pinkerton *et al.* 2010) and the CPR Atlas (McLeod *et al.* 2010) show some longitudinal variation. The BRT models show consistent hotspots of *O. similis* abundance. Similar results are shown for mesopelagic fish (Part 7) and euphausiids (Chapter 6.9), where latitudinal zonation of species or assemblages is observed but also changes according to basins or particular oceanographic or bathymetric features. Not all fronts act the same way, depending on species origin. The sub-tropical mesopelagic fish species seemed to be mainly limited to the south by the northern edge of the Polar Front, whereas the Antarctic species seemed to have their northern extent mainly linked to the Sub-Antarctic Front. However, interpretations are mainly driven from knowledge on the 0-400 m upper layer of the water column and few surveys have investigated deeper layers where some species might be found northward. Koubbi *et al.* (2011b) showed how the predicted assemblages of the mesopelagic fish in the Indian part of the Southern Ocean are influenced by the different branches of the major fronts, and also by the complex oceanography linked to the Kerguelen Plateau and its troughs influencing the Antarctic Circumpolar Current. This study, along with those from the CPR,



showed the importance of the Southern Boundary for separating permanently open ocean zone species from the more southern species. Top predators are also known to track frontal zones, the sea ice edge, eddies and polynyas for foraging (Bost *et al.* 2009).

Geomorphology is also important for the Southern Ocean pelagic species, as some of them are linked to shelves and shelf slopes. *Euphausia crystallorophias*, the ice krill, is known to occur only in the very cold neritic waters of the continental shelf, whereas *Euphausia superba*, the Antarctic krill, is mainly found in waters north of the continental shelf (Chapter 6.9). *Pleuragramma antarctica*, the Antarctic silverfish, is the only true pelagic fish species of the Antarctic shelf. However, many fish have pelagic larval stages and juveniles such as the other notothenioids.

Distance to the coast, and islands, also plays an important role in the pelagic system; e.g. some copepods are endemic to neritic habitats. The role of islands is extremely important for the life cycle of diverse species and the productivity of the pelagic zone. Island mass effects enable retention and support higher productivity than that observed in the high nutrient - low chlorophyll areas of the oceanic zone. The significance of this increased retention of phytoplankton biomass was demonstrated for different larval phases of fish around South Georgia and Kerguelen (Koubbi *et al.* 2009). Although not currently known, we can speculate that similar conclusions can be developed for some seamounts that are recognized as hotspots of biodiversity (Morato *et al.* 2010).

### Seasonal ice zone

The seasonal ice zone is a major feature influencing biogeographic patterns. By the end of winter approximately half of the Southern Ocean is covered by sea ice, yet at the height of summer coverage has reduced to less than 10%. The growth and retreat of sea ice, coupled with the extreme seasonality in the light regime, therefore act as major environmental forcings. Although many locations in Antarctica are currently experiencing little or no change in sea ice extent, complex ice-albedo feedback mechanisms mean that sea ice will both influence and be influenced by the climate. Unseasonal reductions (or increases) in sea ice thickness and area, irregularity in its growth cycle, and incidence of polynyas will affect primary production and carbon flux, thereby shaping the biogeography of pelagic and benthic species (Chapter 6.10). Nearshore benthic community composition is sensitive to snow- and ice-cover, which mediate the light reaching the sea floor. Even minor changes in the timing of sea ice retreat can have significant implications for benthic community composition, depending on the timing of that retreat within the annual solar cycle (Chapter 4; Clark *et al.* 2013).

Ice algae are adapted to low light conditions and can be a food source for some herbivorous species during times of winter scarcity. The ice algae that are released near the end of spring can either slough off in patches that sink to the benthos or become inocula for ice-edge phytoplankton blooms. Ice algae that sink to the benthos possibly trigger increased grazing and breeding activity in the benthos, as has been shown for the Arctic (Morata *et al.* 2011). In the pelagic zone, the increased light penetration that could result from decreased ice thickness might alter both composition and abundance of the phytoplankton bloom. This would have consequences for the distribution of many grazing species, including Antarctic krill. Understanding how reduction in krill biomass or retraction in their range will affect top predators requires a mix of modelling and observational studies. Additionally, species such as crabeater seals, *Lobodon carcinophaga*, or emperor penguins, *Aptenodytes forsteri*, which rely on sea ice as a platform to complete their life cycle, could be negatively affected by sea ice reductions due to decreased availability of breeding and birthing sites.

In the seasonal ice zone, polynyas are areas of open water surrounded by sea ice. They can be regions of high productivity, particularly in early spring when the absence of an ice cover means that sufficient light can get to the water column and trigger earlier blooms of phytoplankton. Some polynyas occur quite predictably at the same time and place each year, making them regions of enhanced secondary production. Grazing rates of copepods can be higher in polynyas than under sea ice, resulting in increased fecundity (Lee *et al.* 2013). Increases in the biomass of lower trophic level organisms make polynyas vital elements of the polar marine ecosystem, and are attractive foraging grounds for many predator species (e.g. Raymond *et al.* 2014). Changes in ice conditions lead to changes in the distribution and persistence of polynyas. Climate-driven collapses of the Larsen A and B ice shelves on the West Antarctic Peninsula have opened up new polynyas that are supporting increases in primary productivity in the region (Cape *et al.* 2014). This is likely to lead to changes in the regional marine ecosystem, as both the pelagic and benthic realms could benefit from the increased carbon fluxes.

### 4.3. What are the biogeographic corridors?

A key biogeographical question is whether the Antarctic is removed, or simply remote, from potential colonists. There are a number of mechanisms for potential exchange into and out of the Southern Ocean. Some indigenous species have been in the process of recolonisation since the Last Glacial Maximum (Clarke *et al.*, 2005; Barnes *et al.*, 2006). This could therefore imply that many species have entered the Southern Ocean since the establishment of the Antarctic Circumpolar Current and its apparent isolation.

The various water currents comprising the West-Wind Drift are responsible for affecting the faunal composition of the islands positioned downstream, mostly translocating fauna derived from South America further eastwards.

This not only includes broadcasting species with a high dispersal potential but also, rather surprisingly, species lacking any dispersal stages (as well as the ability to swim). By demonstrating highly asymmetrical gene flow in the direction of the current system, surface drift can nevertheless be established because the directionality of current flows is mainly a surface feature and is absent on the deep-sea floor (Leese *et al.* 2010). For South American species to reach the Antarctic requires crossing large distances of deep water, in some areas aided by the rapid (10 cm s<sup>-1</sup>) eastward flowing Antarctic Circumpolar Current in the direction of the Scotia Arc and sub-Antarctic islands. The West-Wind Drift and the Antarctic Circumpolar Current disperse organisms in the Southern Hemisphere in a clockwise direction from South America towards islands such as Bouvet, Crozet and the Kerguelen archipelago.

For Eastern Hemisphere species, the Antarctic appears both remote and cut off by the Polar Front and the Sub-Antarctic Front, which act as barriers to any species that could cross the deep water. From within the Polar Front the main route out of the Antarctic would be via Antarctic bottom water that flows northwards into neighbouring oceans but this (slow) route would be restricted to species capable of surviving at abyssal depths (Strugnell *et al.* 2008, Chapter 10.7). The above, of course, does not apply to species with large dispersal abilities like seabirds or marine mammals.

### 4.4. Taxa-dependent patterns

Some biogeographical patterns depend on the evolutionary history of the taxa. Previous estimates of endemism in the benthos south of the Polar Front (Antarctic) by Arntz *et al.* (1997) and Barnes & De Grave (2000) suggested endemism of between 75% and 90% for many taxa. New data show that a generalised endemism value of around 50% holds true for bivalves (Chapter 5.11) and bryozoans (Chapter 5.23) (Griffiths *et al.*, 2009), ascidians (Chapter 5.27; Primo & Vazquez, 2007), pycnogonids (Chapter 5.14; Munilla & Soler-Membrives 2009), and some lower taxonomic levels, e.g. sea anemones (Rodríguez *et al.* 2007). These levels are comparable to other large isolated regions such as New Zealand. The gastropods (Chapter 5.10) showed a higher level of endemism (78%), but high regional endemism is a trait of this group (Griffiths *et al.* 2009). Endemism estimates may be affected by the discovery of cryptic species, which are expected to regionalise species inventories further. The spatial scale at which the transition occurs to species that are not shared depends strongly on the taxa and may range from regional to continental, or even global, scales.

Species flocks are sets of numerous closely related endemic species that are numerically abundant and ecologically diverse (Eastman & McCune 2000). Oceanographic (currents, water masses), physiographic (depth of the shelf) as well as climatic (low temperatures and glacial - interglacial historical sequences) characteristics of the Southern Ocean have triggered the occurrence of species flocks among the benthic fauna of the Antarctic shelf (Leconte *et al.* 2013). This particularly involves crustacean amphipods (Chapter 5.17) and teleostean fishes (Part 7). Echinoids (Chapter 5.26) and crustacean isopods (Chapter 5.18) have given rise to 'core flocks' that fit only three of the five criteria (species diversity, endemism, and monophyly).

## 5. Applications and future directions

### 5.1. The perspective of SCAR's Standing Scientific Group on Life Sciences

This Atlas can be considered as the first contribution to two Biology Scientific Research Programmes within the SCAR's Standing Scientific Group on Life Science: AntEco (State of the Antarctic Ecosystem) and AnT-ERA (Antarctic Thresholds - Ecosystem Resilience and Adaptation). SCAR's mission is to be "charged with initiating, developing and coordinating high quality international scientific research in the Antarctic region, and on the role of the Antarctic region in the Earth system" (www.scar.org).

AntEco has been designed to focus on past and present patterns of biodiversity across all environments within the Antarctic, sub-Antarctic and Southern Ocean regions. The broad objectives of the programme are to increase the scientific knowledge of biodiversity, from genes to ecosystems that, coupled with increased knowledge of species biology, can be used for the conservation and management of Antarctic ecosystems. Milestones and deliverables of AntEco are structured around three overarching interdisciplinary questions:

- How has Antarctic biodiversity evolved in response to past environmental change and what does this tell us about its capacity to respond to future changes?
- What are the systematic and environmental geographic features of Antarctic biodiversity, and what mechanisms underpin the current distribution and abundance of biodiversity?
- Given the evolved geographic distribution of diversity and forecast threats, what conservation actions are required for the preservation of biodiversity, and mitigation of, and adaptation to change?

The perspective of AnT-ERA is "to understand the current functioning of biological systems, to determine thresholds and predict upcoming ecosystem services" (Gutt *et al.* 2012a). Research projects that contribute to these challenges not only demand challenging research platforms but also manpower, sophisticated tools and advanced concepts. Most important for many of these is a robust data base of the occurrence, distribution, abundance and biomass of species. A sound knowledge of species is important to carry out studies



at the first of AnT-ERA's levels of biological organisation: the physiology of organisms, which includes the biomolecular processes. Biogeographic information helps to identify *in situ* species-specific tolerance limits, as well as thresholds, and to verify corresponding results from experiments and 'omic' analyses. Also the second level, covering species and populations, requires knowledge on environmental demands to identify species traits, which can be deduced from distribution patterns of species and environmental variables. The third level of ecosystems depends on all the approaches mentioned so far.

The overarching aim is a better understanding of Southern Ocean ecosystem functioning, enabling us to assess the future of Antarctic biota and ecosystem services in a changing environment, in the form of a continuation of the Antarctic Climate and the Environment report (Turner *et al.* 2009) and its regular up-dates (e.g., Turner *et al.* 2013).

## 5.2. Unknown and changing environments

Chapter 2 highlighted the gaps in our spatial knowledge, for some regions of the Southern Ocean, in the meso- and bathypelagic zone and in the deep environment (Chapters 5.29 and 5.30). Life under ice-shelves is certainly another gap in our knowledge, as demonstrated when the Larsen ice sheets collapsed. Scientific knowledge is also largely limited temporally to the spring and summer seasons. Winter is definitely one of the remaining frontiers to be explored because of the dominance of sea ice during that time (Part 4 and Chapter 6.11), and because of extreme weather conditions in the open ocean. For winter, scientific data are limited but not absent; fisheries and national programmes collect information, while recent developments in geolocation technology allow us to track top predators during their long and distant winter trips to reveal their wintering habitats, a supposedly undoable task only a decade ago. Progress in technology also enables the collection of additional parameters on the activity of these species and of the variability of the ocean during the winter.

It is clear from this Atlas that large changes to species' distributions can be expected as the climate changes (Chapters 9.1, 9.2 and 9.3). The Southern Ocean will be affected on local and regional scales, and overall, as it is a widely connected system. We can expect large-scale extinctions over time (sooner with stressed populations), as southward shifts of biogeochemical regions or ecoregions will reduce species' habitats. High future rates of species turnover in the Southern Ocean are also predicted with climate change (Cheung *et al.* 2009). Gutt *et al.* (2012) stressed the need for predictive models to study the effect of environmental changes on both benthic and pelagic systems in order to inform policy and decision making (Huettmann, 2012). However, we need systematic sampling and spatial coverage of both biological data and ecologically relevant physical parameters. Constable *et al.* (2014) hypothesized the consequences of climate change in the Southern Ocean ecosystem. For example, top predators that depend on frontal areas for foraging might have to cover greater distances to reach their feeding grounds as the frontal regions shift to higher latitudes (Péron *et al.* 2012).

In this changing environment, another Census of Antarctic Marine Life will be necessary soon. In the meantime new surveys should take place in unknown or less-studied environments, using standardised methods, so we can assess changes to the presence of species, and evaluate any changes in their abundances and in their ecological roles. Modelling provides an excellent option for assessing the performance of sampling methods, criticizing existing results and driving new sampling strategies. Further, modelling will help to test hypotheses that are generated from the *in situ* biogeographic data. Based on biogeographic information, the environmental envelope models need to be further developed and completed by dynamic elements (Gutt *et al.* 2012b). Also concepts and meta-analyses focussing on trophic and other interactions (Chapter 5.31) demand detailed knowledge, since corresponding life performance such as consumption, production, and remineralisation must *a priori* be assumed to be species-specific.

Another major tool to detect climate-induced changes in ecosystem functioning and separate these from background variation is ecological long-term observations and time-series analyses (Rintoul *et al.* 2012), which might be all the more sensitive to changes, depending on how detailed the available information is at the organismic level. In this context, monitoring is essential on condition that it specifies the temporal resolution, which depends on taxa characteristics, accessibility and logistics. It also depends on choosing standard gear, sampling procedures and protocols that can be shared among scientists as we did during the Census of Antarctic Marine Life. One of the best examples is certainly the SCAR Southern Ocean Continuous Plankton Recorder Survey (Chapter 10.3). Monitoring programmes such as the Southern Ocean Observing System will be promising when more biological data are included (Chapter 9.3). However, other regional initiatives are continuing as a result of years of commitment by national programmes.

## 5.3. New molecular methods

Using high-resolution molecular markers can provide more detailed feedback about the state of a system than is possible with presence-only data at the level of species. The latitudinal shifts of species distributions that are anticipated as a response to ongoing climate change may be expected to happen on shorter timescales and in larger numbers for the lineages inside a species. This may compensate at least in part for the problem of the short baseline of long-term studies that have been initiated in recent years.

In the Southern Ocean, single locus, mitochondrial markers have featured prominently in the first phase of molecular research. New methods are on the horizon that may help to overcome inherent biases in our molecular

tools that would impede future progress. None of the traditional model organisms that have fully sequenced genomes at present are polar, so, for some time to come, the vast majority of molecular studies in the Southern Ocean will be carried out without the opportunity of resorting to fully annotated databases of close relatives to guide marker development or direct future research. For this reason, the promise of next-generation sequencing techniques to make the generation of sequences both faster and cheaper is particularly relevant to future work in the Southern Ocean. Firstly, higher throughput will allow larger sample sizes to be analysed making molecular studies less assumption-driven and, secondly, more markers will become available from unknown genomes, thus reducing the dependency on single markers with potentially idiosyncratic representations of the evolutionary past of the organism under study. Both effects combined will help make the sampled animals more representative of the real population, as well as the markers studied more representative of the genome. This will reduce the effect of sampling bias with regard to both the sampled population and the sampled genome.

Preserving and analysing RNA rather than DNA offers the unique opportunity to study which fraction of genes are not only present in the genome but also expressed at any point in the organism, allowing unprecedented insights into metabolic pathways, stress responses and unique adaptations. While currently rare, with ever decreasing prices and increasing standardisation of kits and protocols, transcriptomic studies will become more widespread in the near future; however, the availability of suitably preserved tissue samples may become a limiting factor unless sampling strategies are adjusted now to ensure adequate materials for future use.

## 5.4. Conservation

The data compiled in this Atlas are a valuable resource for the development of conservation policy based on the best available scientific information and approaches (Chapter 9.4.). Depending on the extent of its coverage in a given region, biogeographic data can help to inform the design of spatial conservation measures to achieve the objective of protecting representative examples of marine ecosystems, biodiversity and habitats (as defined by CCAMLR Conservation Measure 91-04, 2011). Even where few data are available, information on the extent of previous sampling may help to guide future research and monitoring, and to focus scientific effort in areas that may be under threat from human activities, but where knowledge is limited.

In addition to informing the design of new proposals for conservation policy and spatial protection, the provision of up to date biogeographic information is critical for supporting ongoing management. In particular, the CCAMLR requirements for research and monitoring within established MPAs will be enhanced by the availability of baseline data. Existing distribution data can also be used to identify future survey requirements, including defining candidate monitoring areas. However, it is important to recognise that different regions or protected areas may have different requirements for research and monitoring, depending on their particular characteristics or management provisions. Designated MPAs should be periodically reviewed to evaluate whether their objectives are still relevant, to assess the impacts of activities upon these objectives, to update plans for research and monitoring, and to develop proposals for any new or adapted management measures if required. All of these activities would benefit from readily available biogeographic data (e.g. globally provided online and with associated metadata).

## 6. Conclusion

This Atlas represents the culmination of nearly a decade long international effort and has highlighted a need to consider taxa on a case-by-case basis, depending on the environmental envelope that prescribes their presence, such as their bathymetric and oceanographic ranges. The compilation of biogeographic data, as in this Atlas and in information networks like SCAR-MarBIN/ANTABIF and other databases or portals, provides a fundamental basis to reduce future research efforts by nominating key taxa instead of the full biogeographic information of a region for various purposes in applied or fundamental science. However, we need to include taxa-related characteristics such as reproductive strategy, life history and evolutionary history to understand how environmental changes have occurred and will modify species distribution. For many groups we are yet to acquire the amount of high-resolution, georeferenced knowledge needed to draw meaningful conclusions regarding biogeographic provinces. However, the advent of new environmental data, species or assemblages modelling and molecular markers offers new possibilities for adding to knowledge that has been generated by traditional species-centric approaches. The online dynamic Biogeographic Atlas (Chapter 11) will be a living resource that will increase in functionality and data over time and will allow the continued effort and collaboration of the network of Antarctic scientists who contributed to the printed version.

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