

Census of Antarctic Marine Life  
SCAR-Marine Biodiversity Information Network

# BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 10.5. PHYLOGEOGRAPHY AND POPULATION GENETICS.

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# THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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## 10.5. Phylogeography and population genetics

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### 1. Introduction

Simply put, phylogeography is a sub-discipline and extension of biogeography that looks at the distribution of taxa and their various degrees of relatedness simultaneously. One of the hallmarks of phylogeography as a discipline that differentiates it from biogeography is that the latter concentrates on patterns of distribution exclusively whereas the former also takes into account the processes that were involved in the creation of these patterns (Avice 2000). While many studies on biogeography will also discuss the implication of their findings for our understanding of the processes involved (Clarke 2008), phylogeography does this more explicitly so by making the evolutionary history of the taxon under study (e.g. a phylogenetic tree or network) part of the data input already. Not all authors have adopted the term 'phylogeography' for this approach but use others (e.g. historical biogeography) instead (Queiroz 2005, González-Wever *et al.* 2010, McGaughan *et al.* 2011, Sanmartín 2012, Sanmartín *et al.* 2008, Arbogast & Kenagy 2008).

Decades of internationally coordinated sampling have begun to fill in important geographical as well as taxonomic gaps in our knowledge about the identity and distribution of the fauna in the Southern Ocean. The advent and widespread use of molecular tools on the other hand have allowed us to tap into unprecedented resolution of heritable traits within as well as among species.

In concert, new tools and an increased availability of samples have led to a vastly increased knowledge about the species inventory and their distribution since the synopsis of Hedgpeth (1969).

One of the most popular applications of phylogeography that results from widespread generation of molecular barcodes are phylogeography networks that integrate intraspecific molecular variants, their relative abundances and the locations where they have been found into a single diagram. Since networks and geographical patterns inside of species are covered in detail in the two phylogeographic case studies that follow, the main focus of this chapter on phylogeography lies on how exactly the incorporation of spatial distributions into the context of molecular phylogenies has advanced our understanding of the processes that shaped the evolutionary history of Southern Ocean organisms.

### 2. Cryptic species and their implications

One of the most visible outcomes of the use of molecular tools in the Southern Ocean is the frequent discovery of genetically distinct species that have previously been classified as a single species on the grounds of their similar morphologies (Held 2003, Held & Wägele 2005, Janosik & Halaných 2010). What makes cryptic species different from the discovery of genuinely new species is the fact that they have been caught and handled before, some very often indeed, only the close resemblance to some seemingly well-known species has prevented recognising a species-level differentiation. Even before molecular barcoding became institutionalised, (pseudo)cryptic species were reported from the Southern Ocean using morphological evidence, but the increasingly widespread use of molecular methods has greatly increased the rate of discovery of new species and cryptic species.

Initially the splitting of well-known benthic species on the basis of the unfamiliar molecular data was greeted with skepticism and the first findings considered as exceptions, but since then numerous cryptic species complexes were discovered, many of them rather unexpectedly and as a result of ongoing barcoding efforts (Grant *et al.* 2010, Dettai *et al.* 2011, Linse *et al.* 2013). It is currently somewhat unclear if there are more such cryptic species discovered in the Southern Ocean than elsewhere. A large-scale global survey correcting for regional differences in sampling effort etc. suggests that there is currently no evidence for higher numbers of discoveries of cryptic species inside the SO than outside (Pfenninger & Schwenk 2007). Considering the logistic impediments to working in the Southern Ocean as well as the fact that this survey included data until the year 2006 thus limiting cryptic species reports to merely 15 (one order of magnitude smaller than for other zoogeographic regions), this result has to be considered preliminary for the SO.

But it is clear that by now the discoveries of cryptic species inside of known nominal species have graduated from an accidental finding that could be attributed to occasional oversights in taxonomy to one of the major sources of discovery of new species in the Southern Ocean and elsewhere (Bickford *et al.* 2007). Even though the most direct impact of the discovery that one species may in reality be two or more species concerns the taxonomy, in practice the refined taxonomic insight has many implications that extend far beyond taxonomy itself.

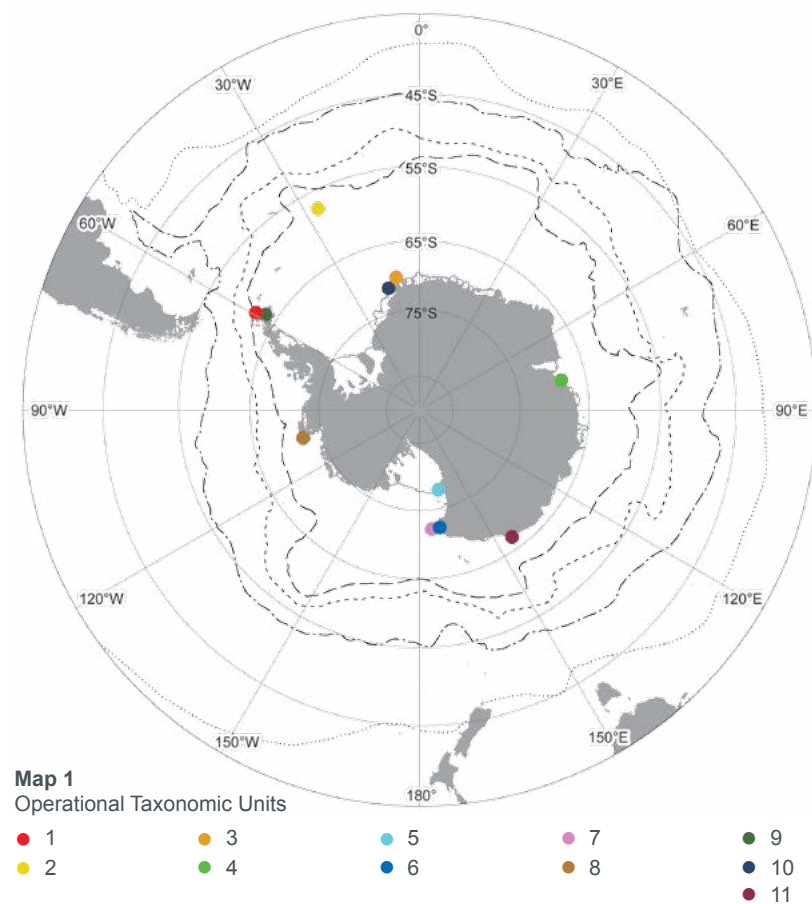
The pattern of new species discovery on the Antarctic shelf where cryptic species have been found in every higher taxon that has been investigated is rather different from the continental slope and the Southern Ocean deep sea where cryptic species discoveries are less common (Raupach & Wägele 2006, Raupach *et al.* 2007, Brökeland & Raupach 2008) and most new species tend to be first discoveries (Brandt *et al.* 2007) but this difference is most

likely due to the fact that for depths exceeding 1000 m very little knowledge existed to begin with (Ellingsen *et al.* 2007; Brandt *et al.* 2012).

On the Antarctic shelf, cryptic species do not appear to be randomly distributed across the tree of life or in space. A large number of the cryptic species that have been identified so far in the Southern Ocean divide one large distribution area of the more inclusive super taxon into several smaller ones, which are often allopatric (Held 2003, Held & Wägele 2005, Wilson *et al.* 2007, Linse *et al.* 2007, Leese *et al.* 2008a, Leese *et al.* 2008b, Krabbe *et al.* 2009, Mahon *et al.* 2010, Hunt *et al.* 2010, Smith *et al.* 2011). There is, however, no general pattern that is common to all newly delimited species and their distributions. Not all widespread species disintegrate into more regionally distributed species when put under molecular scrutiny, some are genuinely widespread on continental or global scales (Schiaparelli *et al.* 2008, Arango *et al.* 2010, Hemery *et al.* 2012, Allcock *et al.* 2011, Strugnelli *et al.* 2012, Brandt *et al.* 2012).



Photo 1 *Glyptonotus* sp. MOTU 3, Eastern Weddell Sea. Image © C. Held.



**Phylogeography Map 1** Cryptic diversity in *Glyptonotus* Eight 1852. Sampling localities for molecular operational taxonomic units (MOTUs) in *Glyptonotus* Eight 1852; candidate species based on mitochondrial COI barcode data (Held 2005; Held & Agrawal unpubl.). MOTU 1 (red dot; South Shetland Islands) is the type locality and most likely represents *Glyptonotus antarcticus* Eight 1852 that was long considered a prime example of circumpolar distribution.





One of the biggest impacts of cryptic species is that their discovery makes literature data untrustworthy because species reported in earlier publications will refer to the previous, more inclusive taxon (wrongly) carrying a taxonomic name, which after the taxonomic revision rightfully belongs to only one of the newly delimited species contained within (e.g. Janosik *et al.* 2010). According to a literature and database survey carried out under the auspices of the Census of Marine Life ([www.coml.org](http://www.coml.org)) and utilising the data collected until and including the International Polar Year 2006/2007 (IPY), a total of 235 species were known to occur in both polar oceans ([http://www.coml.org/comlfiles/press/CoML\\_Ice\\_Oceans\\_Public\\_Release\\_02.15.2009.pdf](http://www.coml.org/comlfiles/press/CoML_Ice_Oceans_Public_Release_02.15.2009.pdf)). A small subset of these candidate bipolar species have been analysed in detail and evidence for reproductively isolated but cryptic species endemic to one polar ocean has been found in some (Hunt *et al.* 2010, Uriz *et al.* 2011) whereas evidence for a single species with bipolar distribution was found in others (Kuklinski & Barnes 2010, Pawlowski *et al.* 2007, Havermans *et al.* 2013). See Chapter 10.4.

### 3. Gene flow and the brooder vs. broadcaster debate

Even without divergent natural selection at work, genetic drift acting independently on isolated populations will over time result in growing dissimilarity of the two populations. Gene flow connecting the two populations, on the other hand, is the strongest antagonist of genetic drift in this scenario because each migrant acts as a vector transporting alleles from one population to the other, thus potentially reducing their uniqueness. For this reason, species with dispersal propagules in the form of pelagic larvae spending a long time in the water column are often expected to be genetically more homogeneous compared to species without such dedicated dispersal stages (brooders versus broadcasters debate).

During the early phase of Antarctic research it was commonly assumed that many if not most species are circumpolar and that gaps in their distribution were mostly due to incomplete sampling. Until the end of the last century it was commonly assumed that '...the distribution of most of the Antarctic fauna is circumpolar' (Arntz *et al.* 1994, Hedgpeth 1969, Clarke & Johnston 1996, Knox 1994, Dayton 1990).

This assumption was based on the many homogenising abiotic factors, most notably in the form of circumpolar currents (ACC and ACoC). Much of the detailed information about patchiness of geomorphology that makes sea-floor habitats appear less homogenous today and are now known to have a structuring effect on benthic communities (Post *et al.* 2011) was still unknown at the time.

Species possessing larval dispersal stages (e.g. Matschiner *et al.* 2009, González-Wevar *et al.* 2010) demonstrate genetic connectivity on regional scales, which conforms to the expectations for broadcasting species. Some brooding species without planktonic larvae are also known to have large distributions and presumably strong genetic exchange, especially species that are good swimmers as adults (Baird *et al.* 2012, Havermans *et al.* 2013) although it should not be ignored that usually all species in these studies are roughly equally mobile but only some are widely distributed whereas others can contain cryptic species, sometimes on rather small geographic scales. In some species, the predictions based on larval or adult dispersal potential do not match the observed data and require additional processes to explain the observed connectivity patterns. Nominal species spanning the Drake Passage (DP) between South America and the Antarctic Peninsula were found to comprise cryptic species, each restricted to either side of the DP, irrespective of whether they were brooders (Hunter & Halanynch 2008) or broadcasters (Thornhill *et al.* 2008) indicating that dispersal is not the only parameter that determines genetic exchange across a major oceanic barrier. Janko *et al.* (2007) investigated benthic and pelagic Antarctic notothenioid fish and found a stronger signature of recent population growth in the supposedly more mobile pelagic species than among the benthic feeders that were assumed to be more affected by habitat loss during the glacial maxima. Further examples include significant local genetic differentiation in a species with a planktonic dispersal stage (Hoffman *et al.* 2010, Hunter & Halanynch 2010; Hoffman *et al.* 2012) or species integrity and gene flow over thousands of kilometers in benthic isopods and algae without any dispersal propagules or the ability to swim or float (Leese *et al.* 2010, Fraser *et al.* 2013). In both cases passive rafting on buoyant substrate in major ocean currents has been inferred as the most likely means of dispersal. Testing multiple hypotheses in a statistical framework and using fast-evolving microsatellite markers, Leese *et al.* (2010) showed that unidirectional gene flow in direction of the ACC was the model with the highest explanatory power, thus demonstrating that dispersal among sub-Antarctic islands in this immobile brooder happens in the upper water layers because the unidirectional ACC is predominantly a surface phenomenon. The means of dispersal in the direct-developing seaslug *Doris kerguelensis* is less obvious but it, too, shows genetic uniformity across thousands of kilometers despite lacking obvious dispersal capabilities (Wilson *et al.* 2009).

Developing fast-evolving molecular markers may be more difficult than using universal primers (Held & Leese 2007) but in turn it makes reconstructions of events possible that are too rare to make direct observation feasible (Leese & Held 2011) and for which purely biotic predictors can be very poor (see above).

The consequence of the widespread discovery of cryptic species in the Southern Ocean on the one hand and empirical studies of genetic connectivity on the other hand is that there is no distribution pattern that is a defining characteristic of all Antarctic benthos but rather a multitude of different distributions, ranging from extremely local differentiation to global genetic connectivity. Distribution patterns need to be demonstrated rather than assumed

keeping in mind that predictions based on dispersal potential (larval ecology) can be accurate for some taxa but can be amazingly misleading for others.

### 4. Eurybathy

A widely held opinion about the distribution of fauna on the Antarctic shelf that may deserve another look in the light of current phylogeographic and molecular methods is that eurybathy is more widespread in the Southern Ocean than elsewhere. In a classic study, Brey *et al.* (1996) demonstrated that species were indeed reported from a wider depth range in the Southern Ocean than comparative taxa in European waters. The assumption of a eurybathic benthic fauna of the Southern Ocean has never seriously been questioned since and is widely considered a defining characteristic of the Antarctic marine ecosystem as a whole. Most authors interpret the apparent eurybathy as a historical legacy of the glacial history during which the shallow-water fauna had to retreat partly or fully from the shelves to the continental slope or the adjacent deep sea (Thatje *et al.* 2005; Clarke & Crame 2010; Allcock & Strugnell 2012). The deeper waters ensured the survival of many species during the glacial maxima according to this interpretation of Antarctic eurybathy. The recolonisation of the shallow-water habitats took place from the refugia on the slope, however, only incompletely so, adding some of the deeper water habitats permanently to the species' vertical distributions even after the retreat of the ice on the shelves.

Another reason for the strong ties between Antarctic shallow and deep-water faunas might be the fact that around 70% of the world's deep-sea water is formed in the Antarctic especially under the great ice-shelves. From here the cold, well-oxygenated and saline water sinks into the deep sea forming the Antarctic Bottom Water (AABW) that covers much of the slope and deep-sea seafloor and reaches far into the Northern Hemisphere (Mantyla & Reid 1983). The thermohaline circulation creates both a vehicle for transportation and ensures strong physical similarities (e.g. salinity, temperature) from the Antarctic shelf to the deep sea that might make it easier for shallow-water fauna to descend and adapt to the conditions in the deep sea from the Antarctic shelf than from lower latitude shelves and vice versa.

However, the frequent discovery of cryptic species questions the basis upon which much of the support for a eurybathic benthic fauna in the Southern Ocean rests because an unknown number of the taxa included in Brey *et al.* (1996) study may be affected by this, i.e. be a collection of closely related species rather than a single species. Although in the last decade a lot of progress has been made, still only a small fraction of the taxa has been examined in enough detail. What we do know at this point is that, similar to the patterns of horizontal distribution discussed earlier, several species that were thought to be well-known and distributed vertically across a wide range of water depths, have been found to comprise several reproductively fully isolated species. There is some evidence that depth stratification is present at least in some of cryptic species (Held & Wägele 2005, Brandão *et al.* 2010, Schüller 2011, Havermans *et al.* 2013). Currently the number of well-studied cases is still low, hence it is too early to draw far-ranging conclusions, but if it turned out that more precisely delimited cryptic species frequently occupy a) different water depths and b) each species only a fraction of the depth range of the more inclusive taxon, then the status of eurybathy as an unquestioned characteristic of the Antarctic benthic fauna might be in danger just as circumpolarity may have already lost its role as the model of horizontal distribution pattern (see also Downey *et al.* 2012).

### 5. Submergence/emergence and connection to the deep sea

Despite the uncertainties regarding a wider depth range for single species in the Antarctic benthos (eurybathy; see above) there is strong phylogeographic support for a close connection between the Antarctic shelf and the adjacent deep sea in several higher taxa. Using molecular phylogenetics, Held (2000) found unequivocal evidence that deep-sea serolids were most closely related to shallow-water species on the Antarctic shelf. The occurrence of vestigial eyes in some of these deep-sea isopods in addition to completely blind species had already suggested that the deep sea was colonised by shallow-water ancestors (polar submergence) and not vice versa. However, the molecular phylogeographic approach established two new findings: the center of origin was the Antarctic shelf rather than shallow-waters of other continents and the deep sea was colonised by serolids several times independently since the deep-sea species are not each others' closest relatives, suggesting processes that promote or facilitate the transition from the Antarctic shelf into the deep sea. Strugnell *et al.* (2008) found a similar pattern of polar submergence for Antarctic octopus but in this lineage the deep-sea species formed a monophylum, supporting that submergence into the deep happened once in the ancestral lineage followed by subsequent radiation in deep waters rather. Strugnell *et al.* (2008) correlated the date for the ancestral submergence and the subsequent radiation with the opening of the Drake Passage and the large-scale production of AABW, respectively.

Molecular phylogeographic support for the opposite case, i.e. polar emergence, has also been found in several taxa independently (Strugnell *et al.* 2011, Riehl & Kaiser 2012). More recently, molecular data are appearing that suggest that refugia allowing survival at shallower depths might have been present even during glacial maxima (Rogers 2007; Allcock & Strugnell 2012). If so, continuous survival would not have been limited to taxa that were able to evade the ice by either taking refuge in deeper waters or lower latitudes. Even survival on the shelf at high latitudes might have been possible in geothermal refugia (Fraser *et al.* 2014).

## 6. Radiations and molecular clocks

The high rate of endemism in the SO (Griffiths *et al.* 2009) already indicates that the fauna of the Antarctic is fairly isolated from that of lower latitudes but phylogenetic and phylogeographic research has provided more detailed insight into how these differences evolved. The notothenioid fish are not only the dominant group of fish in the Southern Ocean today but they have also evolved as a group *in situ* (Eastman & McCune 2000; Near & Cheng 2008; Dettai *et al.* 2012). A similar pattern of a monophyletic group of Antarctic species that are more closely related to each other than any of them is to the more basal ancestors outside the SO has been found in a number of groups (see compilation in Lecointre *et al.* 2013 and references therein). These radiations have undoubtedly evolved in response to the drastically different environmental conditions in the SO but they can only be recognised fully if a phylogenetic tree is known. If only the biogeographic pattern without information of relatedness was known, any secondary exportations of derived taxa from inside the Antarctic radiation out of the Southern Ocean to lower latitudes (Held 2000; Strugnell *et al.* 2008; Göbbeler & Klusmann-Kolb 2010) would prevent the recognition of the radiation itself.

A phylogeographic approach has been used repeatedly to calculate the age of taxa as well as the speed of molecular substitution. Bargelloni *et al.* (1994) analysed a monophyletic group of Antarctic notothenioid fishes characterised by the possession of antifreeze glycopeptides in their blood that is absent in their relatives outside the Southern Ocean. The unexpectedly low level of divergence in the mitochondrial marker genes suggested either a radiation date that was much younger than the calibration date of 23 Mya for the age of the Drake Passage (Kennett 1977) or much slower accumulation rates of molecular substitutions than what was known from outside Antarctica. The 'molecular slow-down hypothesis' received support from physiology (Clarke & Johnston 1996) in view of the fact that the reduced metabolic rate of polar fish might also slow the production of oxygen radicals.

The assumption that interference of oxygen radicals with the fidelity of DNA replication during cell division directly might translate into reduced rates of evolutionary novelties at subzero temperatures where ROS production is low, has not materialised or at least turned out to be not universally true. In a two-cluster test (a variant of the relative rate test comparing groups of taxa rather than single species), Held (2001) found Antarctic serolid isopods to have mitochondrial substitution rates indistinguishable from their South American relatives. Notably, the use of phylogeographic data makes the results independent from assumptions about the absolute rate of molecular clocks and errors therein. It appears that the marked differences in temperature at which the two groups of invertebrates evolved for many millions of years have not resulted in measurably different rates of their molecular clocks, suggesting that a younger evolutionary origin of taxa including that of the radiation of notothenioids may be a more appropriate interpretation. More recent studies looking at the genetic divergence between pairs of species in South America and the Southern Ocean served to reinforce the impression that many Antarctic species have evolved much more recently than previously thought while estimates concerning the opening of the Drake Passage that separates the these species pairs physically today have shifted from around 23 Mya (Kennett 1977) to much older dates (Lawver & Gahagan 2003, Scher & Martin 2006, Barker *et al.* 2007).

## 7. Demography and genetic diversity

The size of a population is one of the most important parameters controlling its genetic diversity (Cutter *et al.* 2013) and clearly some taxa in the Southern Ocean have enormous population sizes, most notably in Antarctic krill (*Euphausia superba*). Extensive regional sampling and modeling of population genetics parameters demonstrates that the genetic diversity is exceptionally high in this species (Goodall-Copestake *et al.* 2010). Even when large sample sizes per replicate are considered thus eliminating a common error in diversity estimates in high abundance species, almost no genotypes are shared among 504 specimens (haplotype diversity 0.9981), indicating that its genetic diversity is not nearly adequately represented even in this large sample.

Despite the strong evidence for well-mixed krill populations on a regional scale, it is not inconceivable that on larger spatial scales even seemingly unrestricted pelagic species may depart from panmixia and show some geographic structure. Nevertheless, previous reports of significant population structuring on a continental scale in *E. superba* (Zane *et al.* 1998) may have been the result of sampling error and were not confirmed in a later study involving multiple markers and more samples (Bortolotto *et al.* 2011).

While the absolute population size may be hard to determine from genetic data without detailed knowledge about how many individuals actually contribute genetically to the next generation (effective population size vs census size), analysing the patterns how the genetic diversity is precisely distributed within and amongst the individuals yields information about the recent developmental trends of the population. A common pattern that is present in almost all Antarctic datasets is a signal of marked, recent population growth (e.g. Janko *et al.* 2007; Bortolotto *et al.* 2011; González-Wevar *et al.* 2013). Similar trends are known from Arctic datasets, which is consistent with a recovery of populations after the Last Glacial Maximum due to the vast increase of habitable shelf habitat following the retreat of the ice (Hewitt 2000). The relative increase or decrease of the population size can be modeled, but is expressed in terms of generations. Translating it into years before present requires additional assumptions about generation time to be made. Constraining the timing of the widespread population growth to last glacial maximum

(LGM) is therefore difficult and error-prone, especially if a single mitochondrial marker is used for inference, and usually assumed rather than explicitly verified. Besides the plausibility of a causal connection between ice retreat and population growth there is circumstantial evidence supporting a connection between growth and ice retreat (though not necessarily the last) in that shelf taxa tend to show more prominent signals of recent population growth than taxa inhabiting deeper waters on the slope or the adjacent deep sea, which have been less impacted by the glacial cycles than shallower habitats (Rau-pach *et al.* 2010).

## 8. Molecules and morphology

It is worth noting that although molecular data are not the only possible source for phylogeographically motivated studies, in practice their widespread use has given the field of phylogeography a major boost for various reasons. Although the information density may be lower than that of a phylogenetic tree or a genealogical network, information about relatedness is also contained in the delineation of higher taxonomic units (genera, families etc), which is still the main source of information about endemisms. What often muddles the use of taxonomy as a source of information for phylogeography, however, is the fact that this is only strictly true if the underlying taxonomy builds on the foundation of modern phylogenetic theory and more specifically on the identification of monophyletic groups rather than pragmatically identifiable units of similar-looking taxa. Frequently the modern taxonomic treatment of taxa is incomplete, leaving taxonomic 'collecting bins', i.e. para- or polyphyletic groups that are nevertheless united under a valid taxonomic label but one that does not express relatedness. A literature research that takes taxonomic composition of higher taxa for a statement of relatedness without making sure they consist of monophyla is thus conceptually flawed, but carefully constructed phylogenies based on morphology have been used successfully in phylogeographic studies (Wägele 1994, Brandt 1991; but see Held 2000).

At the intraspecific level, molecular data are almost required to prove that morphological variance is based on heredity and not on phenotypic plasticity within species.

## 9. Synopsis

The widespread use of molecular phylogenetics, phylogeography and population genetics have allowed putting many hypotheses about the common patterns in the Southern Ocean fauna and the driving forces behind them to the test. The growing consensus after more than a decade of molecular scrutiny is that there are far fewer defining characteristics that have proven true for all or even many Southern Ocean species than previously thought. Instead many different, taxon-specific responses have been identified. Species identities and non-identities can be (and need to be) demonstrated rather than assumed, which is a prerequisite upon which almost all subsequent inference critically depends. The distribution and evolutionary history of species in the SO and their response to the same environmental cues is much less uniform than previously believed and often a taxon-specific mix of more than one driving factor.

On the other hand, the application of molecular tools makes it possible to not only correlate observed patterns to general predictions but to formulate hypotheses in a statistical framework and to identify the one with the highest explanatory power among competing alternative hypotheses (Leese *et al.* 2010). In the near future, high-throughput next-generation sequencing and more advanced analysis techniques will become more widely used and help reduce the effect of sampling error and at the same time further expand the spectrum of questions that can be tackled (Moroz *et al.* 2014; Hoffman *et al.* 2014).

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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](http://www.biodiversity.aq).

## The Census of Antarctic Marine Life (CAML)

CAML ([www.caml.aq](http://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](http://www.scarmarbin.be), integrated into [www.biodiversity.aq](http://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](http://www.iobis.org)), under the aegis of SCAR (Scientific Committee on Antarctic Research, [www.scar.org](http://www.scar.org)). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with [biodiversity.aq](http://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



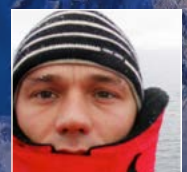
**Claude DE BROYER** is a marine biologist at the Royal Belgian Institute of Natural Sciences in Brussels. His research interests cover structural and ecofunctional biodiversity and biogeography of crustaceans, and polar and deep sea benthic ecology. Active promoter of CAML and ANDEEP, he is the initiator of the SCAR Marine Biodiversity Information Network (SCAR-MarBIN). He took part to 19 polar expeditions.



**Huw GRIFFITHS** is a marine Biogeographer at the British Antarctic Survey. He created and manages SOMBASE, the Southern Ocean Mollusc Database. His interests include large-scale biogeographic and ecological patterns in space and time. His focus has been on molluscs, bryozoans, sponges and pycnogonids as model groups to investigate trends at high southern latitudes.



**Cédric d'UDEKEM d'ACQZ** is a research scientist at the Royal Belgian Institute of Natural Sciences, Brussels. His main research interests are systematics of amphipod crustaceans, especially of polar species and taxonomy of decapod crustaceans. He took part to 2 scientific expeditions to Antarctica on board of the *Polarstern* and to several sampling campaigns in Norway and Svalbard.



**Bruno DANIS** is an Associate Professor at the Université Libre de Bruxelles, where his research focuses on polar biodiversity. Former coordinator of the [scarmarbin.be](http://www.scarmarbin.be) and [antibif.be](http://antibif.be) projects, he is a leading member of several international committees, such as OBIS or the SCAR Expert Group on Antarctic Biodiversity Informatics. He has published papers in various fields, including ecotoxicology, physiology, biodiversity informatics, polar biodiversity or information science.



**Susie GRANT** is a marine biogeographer at the British Antarctic Survey. Her work is focused on the design and implementation of marine protected areas, particularly through the use of biogeographic information in systematic conservation planning.



**Christoph HELD** is a Senior Research Scientist at the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven. He is a specialist in molecular systematics and phylogeography of Antarctic crustaceans, especially isopods.



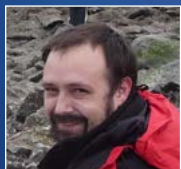
**Falk HUETTMANN** is a 'digital naturalist' he works on three poles (Arctic, Antarctic and Hindu-Kush Himalaya) and elsewhere (marine, terrestrial and atmosphere). He is based with the university of Alaska-Fairbank (UAF) and focuses primarily on effective conservation questions engaging predictions and open access data.



**Philippe KOUUBI** is professor at the University Pierre et Marie Curie (Paris, France) and a specialist in Antarctic fish ecology and biogeography. He is the Principal Investigator of projects supported by IPEV, the French Polar Institute. As a French representative to the CCAMLR Scientific Committee, his main input is on the proposal of Marine Protected Areas. His other field of research is on the ecoregionalisation of the high seas.



**Ben RAYMOND** is a computational ecologist and exploratory data analyst, working across a variety of Southern Ocean, Antarctic, and wider research projects. His areas of interest include ecosystem modelling, regionalisation and marine protected area selection, risk assessment, animal tracking, seabird ecology, complex systems, and remote sensed data analyses.



**Anton VAN DE PUTTE** works at the Royal Belgian Institute for Natural Sciences (Brussels, Belgium). He is an expert in the ecology and evolution of Antarctic fish and is currently the Science Officer for the Antarctic Biodiversity Portal [www.biodiversity.aq](http://www.biodiversity.aq). This portal provides free and open access to Antarctic Marine and terrestrial biodiversity of the Antarctic and the Southern Ocean.



**Bruno DAVID** is CNRS director of research at the laboratory BIOGÉOSCIENCES, University of Burgundy. His works focus on evolution of living forms, with and more specifically on sea urchins. He authored a book and edited an extensive database on Antarctic echinoids. He is currently President of the scientific council of the Muséum National d'Histoire Naturelle (Paris), and Deputy Director at the CNRS Institute for Ecology and Environment.



**Julian GUTT** is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board *Polarstern*. He is member of the SCAR committees ACCE and AnT-ERA (as chief officer). Main foci of his work are: biodiversity, ecosystem functioning and services, response of marine systems to climate change, non-invasive technologies, and outreach.



**Graham HOSIE** is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and biogeography of plankton species and communities, notably their response to environmental changes. He has participated in 17 marine science voyages to Antarctica.



**Alexandra POST** is a marine geoscientist, with expertise in benthic habitat mapping, sedimentology and geomorphic characterisation of the seafloor. She has worked at Geoscience Australia since 2002, with a primary focus on understanding seafloor processes and habitats on the East Antarctic margin. Most recently she has led work to understand the biophysical environment beneath the Amery Ice Shelf, and to characterise the habitats on the George V Shelf and slope following the successful CAML voyages in that region.



**Yan ROPERT COUDERT** spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.

