

Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 10.4. BIPOLARITY.

Allcock A.L., 2014.

In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. 431-436.

EDITED BY:

Claude DE BROYER & Philippe KOUBBI (chief editors)

with Huw GRIFFITHS, Ben RAYMOND, Cédric d'UDEKEM d'ACOZ, Anton VAN DE PUTTE, Bruno DANIS, Bruno DAVID, Susie GRANT, Julian GUTT, Christoph HELD, Graham HOSIE, Falk HUETTMANN, Alexandra POST & Yan ROPERT-COUDERT



SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

The "Biogeographic Atlas of the Southern Ocean" is a legacy of the International Polar Year 2007-2009 (www.ipy.org) and of the Census of Marine Life 2000-2010 (www.coml.org), contributed by the Census of Antarctic Marine Life (www.caml.aq) and the SCAR Marine Biodiversity Information Network (www.scarmarbin.be; www.biodiversity.aq).

The "Biogeographic Atlas" is a contribution to the SCAR programmes Ant-ECO (State of the Antarctic Ecosystem) and AnT-ERA (Antarctic Thresholds- Ecosystem Resilience and Adaptation) (www.scar.org/science-themes/ecosystems).

Edited by:

Claude De Broyer (Royal Belgian Institute of Natural Sciences, Brussels)
Philippe Koubbi (Université Pierre et Marie Curie, Paris)
Huw Griffiths (British Antarctic Survey, Cambridge)
Ben Raymond (Australian Antarctic Division, Hobart)
Cédric d'Udekem d'Acoz (Royal Belgian Institute of Natural Sciences, Brussels)
Anton Van de Putte (Royal Belgian Institute of Natural Sciences, Brussels)
Bruno Danis (Université Libre de Bruxelles, Brussels)
Bruno David (Université de Bourgogne, Dijon)
Susie Grant (British Antarctic Survey, Cambridge)
Julian Gutt (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven)
Christoph Held (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven)
Graham Hosie (Australian Antarctic Division, Hobart)
Falk Huettmann (University of Alaska, Fairbanks)
Alix Post (Geoscience Australia, Canberra)
Yan Ropert-Coudert (Institut Pluridisciplinaire Hubert Curien, Strasbourg)

Published by:

The Scientific Committee on Antarctic Research, Scott Polar Research Institute, Lensfield Road, Cambridge, CB2 1ER, United Kingdom (www.scar.org).

Publication funded by:

- The Census of Marine Life (Albert P. Sloan Foundation, New York)
- The TOTAL Foundation, Paris.

The "Biogeographic Atlas of the Southern Ocean" shared the *Cosmos Prize* awarded to the Census of Marine Life by the International Osaka Expo'90 Commemorative Foundation, Tokyo, Japan.

Publication supported by:

- The Belgian Science Policy (Belspo), through the Belgian Scientific Research Programme on the Antarctic and the "biodiversity.aq" network (SCAR-MarBIN/ANTABIF)
- The Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium
- The British Antarctic Survey (BAS), Cambridge, United Kingdom
- The Université Pierre et Marie Curie (UPMC), Paris, France
- The Australian Antarctic Division, Hobart, Australia
- The Scientific Steering Committee of CAML, Michael Stoddart (CAML Administrator) and Victoria Wadley (CAML Project Manager)

Mapping coordination and design: Huw Griffiths (BAS, Cambridge) & Anton Van de Putte (RBINS, Brussels)

Editorial assistance: Henri Robert, Xavier Loréa, Charlotte Havermans, Nicole Moortgat (RBINS, Brussels)

Printed by: Altitude Design, Rue Saint Josse, 15, B-1210 Brussels, Belgium (www.altitude-design.be)

Lay out: Sigrid Camus & Amélie Blaton (Altitude Design, Brussels).

Cover design: Amélie Blaton (Altitude Design, Brussels) and the Editorial Team.

Cover pictures: amphipod crustacean (*Epimeria rubrieques* De Broyer & Klages, 1991), image © T. Riehl, University of Hamburg; krill (*Euphausia superba* Dana, 1850), image © V. Siegel, Institute of Sea Fisheries, Hamburg; fish (*Chaenocephalus* sp.), image © C. d'Udekem d'Acoz, RBINS; emperor penguin (*Aptenodytes forsteri* G.R. Gray, 1844), image © C. d'Udekem d'Acoz, RBINS; Humpback whale (*Megaptera novaeangliae* (Borowski, 1781)), image © L. Kindermann, AWI.

Online dynamic version :

A dynamic online version of the Biogeographic Atlas is available on the SCAR-MarBIN / AntaBIF portal : atlas.biodiversity.aq.

Recommended citation:

For the volume:

De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (eds.), 2014. Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, XII + 498 pp.

For individual chapter:

(e.g.) Crame A., 2014. Chapter 3.1. Evolutionary Setting. In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', *et al.* (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. xx-yy.

ISBN: 978-0-948277-28-3.



This publication is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License

10.4. Bipolarity

A. Louise Allcock¹ & Huw J. Griffiths²

¹Ryan Institute, School of Natural Sciences (Zoology), National University of Ireland Galway, Ireland.

²British Antarctic Survey, Cambridge, UK

1. Introduction

Stepanjants *et al.* (2006) trace the study of bipolarity back to Ross (1847). It is a phenomenon that has intrigued many biologists including both Darwin (1872) and Wallace (1880) and interest in the subject has not lessened over time. Over the course of more than 150 years of study, terms have been used in different ways and it is pertinent to begin with some definitions. Stepanjants *et al.* (2006) defined bipolarity as “the wide distribution of either the same, or closely related, or even unrelated taxa at the species and higher taxonomic levels, of flora and fauna having similar morphological characters, and inhabiting similar environments of the cold zones or cold waters of both hemispheres.” This definition does not specify either a latitudinal extent or a geographic/climatic zone (e.g., subtropical, subpolar, polar, etc) to which bipolar taxa should extend. But, unlike some definitions, it is also not limited to taxa with a disjunct distribution that are absent from the tropics. The differences between definitions raise two important points. The first is a biogeographical issue: how did disjunct distributions arise? The second is a physiological issue: how do taxa with a truly cosmopolitan distribution from one pole to the other survive in diverse environments? Although studies of bipolarity have been mainly concerned with the first point, both considerations are of interest to polar biologists.

Herein, the focus is on taxa which do extend to polar and subpolar regions, and which may, or may not, have a disjunct distribution. Despite the focus on polar taxa, some consideration of the literature on amphitropical (lit. ‘on both sides of the tropics’) distributions is essential since there are many such distributions in temperate waters and the body of literature investigating how such disjunct distributions arose is much greater.

Bipolarity and amphitropicality can be addressed to species, to genera, and to taxa of higher rank. However, the biogeographic origins of taxa at varying taxonomic ranks is likely to differ. Crame (1993), with reference to the marine mollusc fossil record, suggested there were three extended phases in the geological record that were particularly associated with amphitropical patterns. The first phase included several stages in the Jurassic and Early Cretaceous where taxa diverged into northern and southern lineages and he associated these with the breakup of Pangea placing the origin of such taxa in a vicariance framework. The second phase corresponded to the late Paleogene-early Neogene. Amphitropical taxa from this period might also have vicariant origins, although these origins are likely associated with global warming of the tropics in the Miocene (Crame 1993). A dated molecular phylogeny of patellid limpets provided evidence to support both these hypotheses (Koufopanou *et al.* 1999). Further supportive evidence of Paleogene-Neogene divergences are found in various amphitropical families and genera of fish (e.g., Burridge & White 2000; Burridge 2002). The third phase of the geological record that Crame (1993) suggested was particularly associated with amphitropicality is that marked by Pliocene-Pleistocene glacial cycles. Various authors have suggested that amphitropical patterns in genera of marine molluscs (Lindberg 1991; Vermeij 1992; Hilbush *et al.* 2000), crabs (Tam *et al.* 1996), and fishes (Stepien & Rosenblatt 1996; Bowen & Grant 1997; Burridge 2002; Mabuchi *et al.* 2004) stem from this period. Explanations may be vicariance based or dispersal based. Vicariant-based theories hypothesise a prior cosmopolitan distribution in cooler times isolated vicariously during interglacial periods. Dispersal-based theories hypothesise that lower temperatures in the tropics during glacial maxima may have been sufficient to facilitate transequatorial dispersal during these times (although temperature declines were probably only in the order of 1 or 2 degrees Celsius). In either case, gene flow may have occurred as recently as the Last Glacial Maximum suggesting there may be very little divergence between populations of the same species found in opposing polar regions.

Bipolar taxa (*sensu* Stepanjants *et al.* 2006) that do not have a disjunct distribution may maintain gene flow in a different manner. Stepanjants *et al.* (2006) discusses taxa that may also be found in sub-tropical and tropical zones, but at greater depths than in sub-polar and polar regions. Such equatorial submergence allows species to inhabit more similar environmental conditions throughout their range. Evidence for such species is hampered by a lack of sampling in deep tropical waters (e.g., Park & Ferrari 2009).

Molecular studies are particularly important for resolving the status of proposed bipolar species. Because many stem from extremely recent (Pleistocene) divergences, the time for morphological divergence may have been limited. Molecular data can provide evidence to support or refute specific status. Furthermore, the development of phylogenetic dating techniques can provide estimates of divergence times. The extensive number of cryptic species that have been discovered through molecular sequencing in recent years in the Southern Ocean (see summary in Allcock & Strugnell 2012) illustrates that morphological similarity is not necessarily evidence for conspecificity. Hence it is important that conclusions on bipolarity drawn from morphological comparisons are supported by molecular data.

2. Morphological discourses on bipolar species

Records of bipolar species can be found throughout the literature, but a comprehensive and meaningful list is hard to compile because of differences in definitions and interpretations. For example, some species described as bipolar may be amphitropical but may not occur in polar waters. Nonetheless, some figures may be drawn from species lists compiled over many years, but significantly expanded during the Census of Marine Life. For the Southern Ocean, the Register of Antarctic Marine Species (RAMS), available through the SCAR-MarBIN data portal (De Broyer & Danis 2011; Griffiths *et al.* 2011) provides the most comprehensive taxonomic list for the region. The equivalent for the Arctic Ocean is the Arctic Register of Marine Species (ARMS) (Sirenko *et al.* 2013). Both lists currently comprise mainly metazoans. Both are linked to the World Register of Marine Species and can therefore be examined at any taxonomic level. A comparison of the two lists suggests there are at least 600 metazoan families with representatives in both the Southern and Arctic Oceans and more than 800 metazoan genera recorded from both these oceans. A previous comparison of lists during the Census of Marine Life suggested that 230 metazoan marine species could be bipolar (Gutt *et al.* 2010). The species-based figure could be an overestimate because: a) specimens from Arctic and Southern Ocean populations have often been identified from keys and not directly compared with specimens from the other polar region; and b) morphological similarity may persist even when genetic divergences are large. But, although some authors have dismissed bipolar records as poor taxonomy (see references in Pearse & Lockhart 2004), and some studies highlight clear taxonomic issues (e.g., Uriz *et al.* 2011), new bipolar species continue to be described or redescribed. Recent examples include metazoan taxa such as anemones (Rodríguez *et al.* 2009; Rodríguez 2012), polychaetes (Parapar *et al.* 2011), bryozoans (Kuklinski & Barnes 2010), and non-metazoan groups such as dinoflagellates (Riaux-Gobin *et al.* 2012). Metazoan taxa whose biogeography has been considered in detail by taxonomists include Copepoda (Park & Ferrari 2009), Medusozoa (Stepanjants *et al.* 2006) and cidaroid sea urchins (Pearse & Lockhart 2004). Similar biogeographic reviews have been conducted for Foraminifera (Stepanjants *et al.* 2006) and dinoflagellates (Okolodkov 1999). These reviews suggest some contrast between taxonomic groups and embrace a variety of definitions of bipolar.

In a thorough review of the distributions of pelagic calanoid copepods, Park & Ferrari (2009) identified 13 species whose distributions include the Southern Ocean and the Arctic Ocean, another 30 whose distributions include the Southern Ocean and the sub-Arctic, one species that ranges from the sub-Antarctic to the Arctic, and ten species that occur in both sub-Antarctic and sub-Arctic waters. They are all deep-water species. A few have disjunct distributions. Park & Ferrari (2009) suggest that disjunct populations might be connected through populations in very deep tropical waters that simply haven’t been adequately sampled to date (i.e., the disjunct distribution is an artifact of limited sampling). In other words, they advocate equatorial submergence as a possible explanation. Alternatively however, they suggest that the disjunction of the populations may be relatively recent and that the morphological similarity currently seen may be transitory since speciation is at its very earliest stages. Although not specified by the authors, this is not dissimilar to the idea of a lack of gene exchange since the Last Glacial Maximum i.e., in line with the Pleistocene divergence seen in many amphitropical species.

Interestingly, Park & Ferrari (2009) found bipolar species pairs to be far more prevalent than bipolar species. They suggest this results from extinction in mid latitudes of a previously cosmopolitan species and subsequent divergence of the populations at each pole. An extension of this is that bipolar species are “transient natural phenomena” (Park & Ferrari 2009).

The life history of Medusa leads to different conclusions in this group. Stepanjants *et al.* (2006) estimate that there are around 20 species that occur at both poles. Connections between populations are maintained by migration of larvae/medusae in cold, deep-water currents in some species. In others, epibiotic stages maintain connections by drifting on organisms and objects. Probably ballast water has also played a role in recent times. The looser definition of bipolarity advocated by Stepanjants *et al.* (2006) means that the emphasis is on connection rather than disjunction. They also report genera and families that are present at both polar regions.

An analysis of Radiolaria allowed conclusions to be drawn about the timing of divergence events because of the good fossil record. Stepanjants *et al.* (2006) identified 19 species present at both poles but showing equatorial submergence in the tropics and 26 species with a disjunct bipolar distribution. They identified separation of populations in the Pleistocene due to temperature changes as one reason for divergence. However, they also note that such north/south divergences appear to have been a common phenomenon through geological time and point to bipolar species in Miocene and early Palaeogene deposits as well as in Jurassic and Cretaceous deposits, supporting the hypotheses of Crame (1993) which were framed from distributions of fossil molluscs.



Pearse & Lockhart (2004) in their analysis of cidaroid sea urchin distributions emphasise the importance of environmental factors such as cold-water currents in maintaining continuity between polar and/or sub-polar populations. They note the importance of the cold-water Pacific coastal current that extends along the west coast of the Americas. The continuous landmass and strong upwelling associated with it may also play a vital role in connecting the two polar seas. Although the route is different, the environmental continuity reflects that invoked by equatorial submergence.

These distributional studies have all been conducted by taxonomic experts but there is little doubt that, for some taxa, a proportion of proposed occurrences of bipolar species will be shown to comprise sibling species when examined closely. For example, Okolodkov (1999) examined the ranges of Arctic marine dinoflagellates by comparing Arctic collections from 17 research cruises with records from 400 literary sources. He concluded that although there were records of bipolar species, these should be treated with caution because of the unreliability of many old records where an identification may have been based on superficial morphological similarity to a well-known northern species. It is these taxonomic problems that make molecular sequence analysis particularly important to questions of bipolarity, not forgetting, of course, that dated phylogenies can also help determine the timing of divergence events.

3. Molecular investigations of bipolar species

3.1. Bacteria

Although studies of bipolarity often focus on metazoans, or at least eukaryotes, there have been several attempts to elucidate the biogeographic distribution of bacteria using molecular techniques. An early study focusing on sea-ice bacteria supported the existence of bipolar genera, e.g., *Polaribacter*. Bipolar species were not identified, but this does not mean that they do not exist (Staley & Gosink 1999). Sea-ice bacteria present a particularly interesting case because their habitat requirements preclude a cosmopolitan distribution.

Shewanella frigidimarina has been shown to occur at both poles (Zeng *et al.* 2010) using molecular comparisons of samples taken from the Arctic and Southern Oceans. However, this bacterial species is not a true psychrophile and tolerates temperatures up to 30°C so, as acknowledged by the authors, its distribution could actually be cosmopolitan. Nonetheless, it illustrates that connections between the poles do exist for bacterial species. While, analyses of bacterial communities that have used molecular markers have shown that northern polar and southern polar marine bacterial communities may be highly divergent, these communities may also contain very similar bacteria (Hollibaugh *et al.* 2002; Brinkmeyer *et al.* 2003; Baldwin *et al.* 2005).

Ghiglione *et al.* (2012) used a pyrosequencing approach to sequence a portion of the SSU rRNA gene from bacterioplankton in 20 Southern Ocean samples, 24 Arctic Ocean samples and 48 samples from non-polar latitudes. They found operational taxonomic units (OTUs) which occurred at both poles, although the majority of the OTUs (85%) were unique to one or other of the poles. They also found they got different results depending on whether they compared shallow communities from each pole or deep communities. Interestingly they found that deep-water bacterial communities from the Arctic and Southern Oceans are potentially connected by deep cold water that flows as part of the global thermohaline circulation system.

3.2. Protists

There have been a number of molecular studies on polar foraminerans but the results are conflicting. The prevalence of genetically distinct lineages with many morphospecies led Darling *et al.* (2000) to suggest that a reassessment of the species concepts for Foraminifera might be required. Pawłowski *et al.* (2008) found a high number of cryptic species and no bipolar lineages in a study of benthic foraminerans with disjunct distributions from high latitudes. In contrast, genetic similarities have been found between Arctic and Antarctic populations of cosmopolitan deep-sea foraminiferal species (Pawłowski *et al.* 2007; Lecroq *et al.* 2009). Pawłowski *et al.* (2007) suggest that gene flow might be facilitated by the transport of juveniles or even small adults by the thermohaline circulation. In some bipolar morphospecies, bipolar lineages can be found, despite the presence of multiple lineages suggestive of the presence of cryptic species (e.g., Darling & Wade 2008).

A problem that is frequently encountered in studies where distinct genetic lineages exist among specimens with little or no morphological variation is that evolutionary rates differ between genes and across taxa and it is not possible to say how much sequence divergence is required between two lineages in order to infer that speciation has taken place. Montresor *et al.* (2003) encountered this problem when investigating Arctic and Southern Ocean samples of the marine dinoflagellate *Polarella glacialis* (Map 1). The Arctic and Southern Ocean strains differed by just 6 base pairs in 1794 bp of the SSU rRNA gene. Nonetheless, the authors were hesitant to confirm these lineages as a single species, since similarly small distances have been found among separate species of distantly related photosynthetic lineages. In the absence of a molecular clock, Montresor *et al.* (2003) were unable to suggest the age of this divergence, but they noted that the encysting ability of this species might enable it to endure unfavourable conditions, thus allowing dispersal between opposite polar regions.

3.3. Metazoa

Published molecular studies on potential metazoan bipolar species are scarce but revealing.

Govindarajan *et al.* (2006) found that the hydrozoan *Obelia longissima* lacked phylogeographic structure across its distribution. Although the study was focused on the evolution of Campanulariidae rather than on a particular species, and consequently only included five specimens of *O. longissima*, those specimens provided good coverage of the species' range, with specimens from the Antarctic Peninsula and New Zealand in the Southern hemisphere, and from Iceland and the White Sea in the north (Map 2).

More recently, Havermans *et al.* (2013) found evidence of homogeneity between Antarctic and Arctic lineages of a deep-sea morph of the amphipod *Eurythenes gryllus* (see Chapter 10.6.1). A 16S rRNA haplotype was found in both Antarctic and Arctic specimens, although COI haplotypes from the two locations differed by at least four base pairs.

Laakmann *et al.* (2012) targeted some of the species with relevant distributions highlighted by Park & Ferrari (2009) in their biogeographical review of calanoid copepods. They included five species from Park & Ferrari's list of 13 species occurring in both the Arctic and Southern Oceans. Three of these (*Gaetanus brevispinus*, *G. tenuispinus* and *Paraeuchaeta barbata*) are thought to have a cosmopolitan distribution: two (*Aetideopsis minor* and *A. rostrata*) are thought to have a disjunct distribution (Park & Ferrari 2009). Laakmann *et al.* found separate and divergent lineages from the Arctic and Southern Oceans in *A. minor* (Map 3) and *G. tenuispinus* (Map 4). They found a single homogenous lineage in each of *G. brevispinus* (Map 5), *P. barbata* (Map 6) and *A. rostrata* (Map 7). Interestingly, the species with divergent lineages were mesopelagic (500-1000 m depth) while those with a single homogenous lineage were bathypelagic (1000-2000 m depth). This suggests that gene flow can be more easily maintained between deep-sea polar environments than between shallower polar environments.

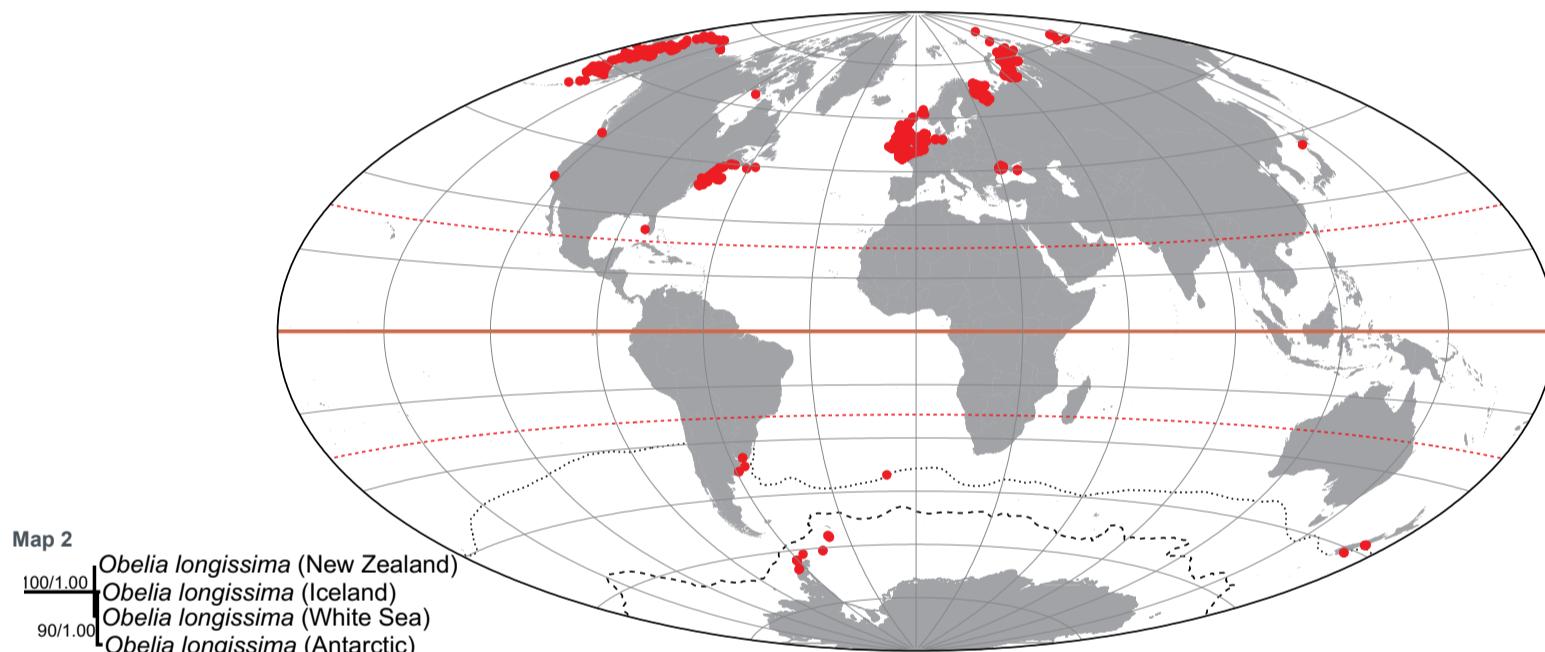
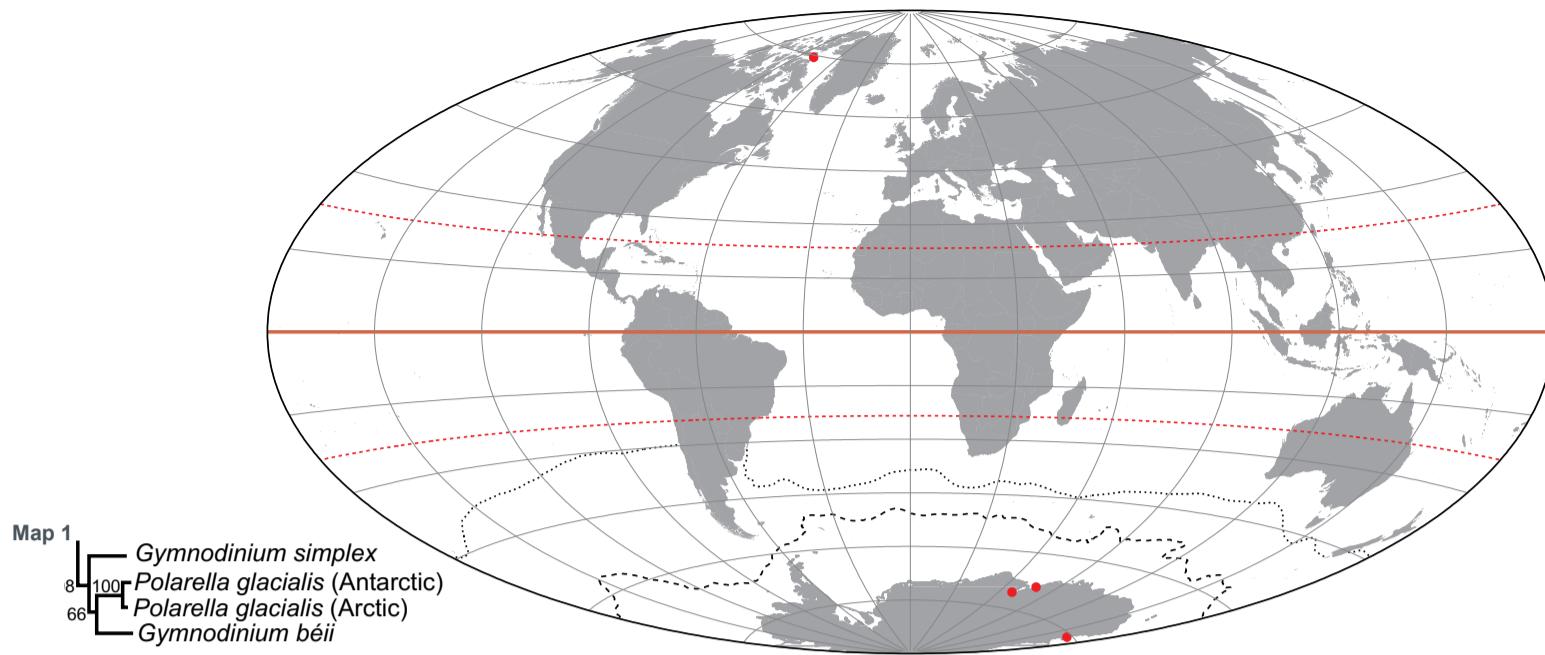
Molecular work on other copepod species whose distributions are extensive, although not necessarily extending to both poles, has simply shown clear evidence of the presence of cryptic species, e.g., *Metridia lucens* (Stupnikova *et al.* 2013), *Paracalanus parvus* (Cornils & Held 2014), *Rhincalanus nasutus* (Goetze *et al.* 2003), suggesting that further taxonomic work is required in many taxa.

Hunt *et al.* (2010), who considered the divergence between Arctic and Southern Ocean populations of the sea butterfly *Limacina helicina* (Map 8), reached similar conclusions. They found the Arctic and Southern Ocean populations to be extremely divergent. Using relaxed phylogenetics with nodes constrained by dates of Thecosomata fossils, they estimated that the Arctic and Southern Ocean lineages diverged around 31 Mya. Although such dates tend to have wide 95% highest posterior density intervals, in this case 12-53 My, the timing of this divergence clearly predates the Pliocene/Pleistocene glacial cycles and is associated with the Palaeogene-Neogene.

However, there is little doubt that some species can maintain panmixia over extremely long distances. Studies on the echinoderms *Hippasteria phrygiana* (Foltz *et al.* 2013) and *Ophiactis abyssicola* (O'Hara *et al.* 2014) have indicated a degree of genetic structuring, but also confirm these nominal species do indeed have truly cosmopolitan distributions, extending at the very least into temperate waters of both the northern and southern hemisphere. Although the studies did not include the full distributional range, it is likely that their full distributions will each be confirmed as single lineages when samples become available.

4. Conclusions

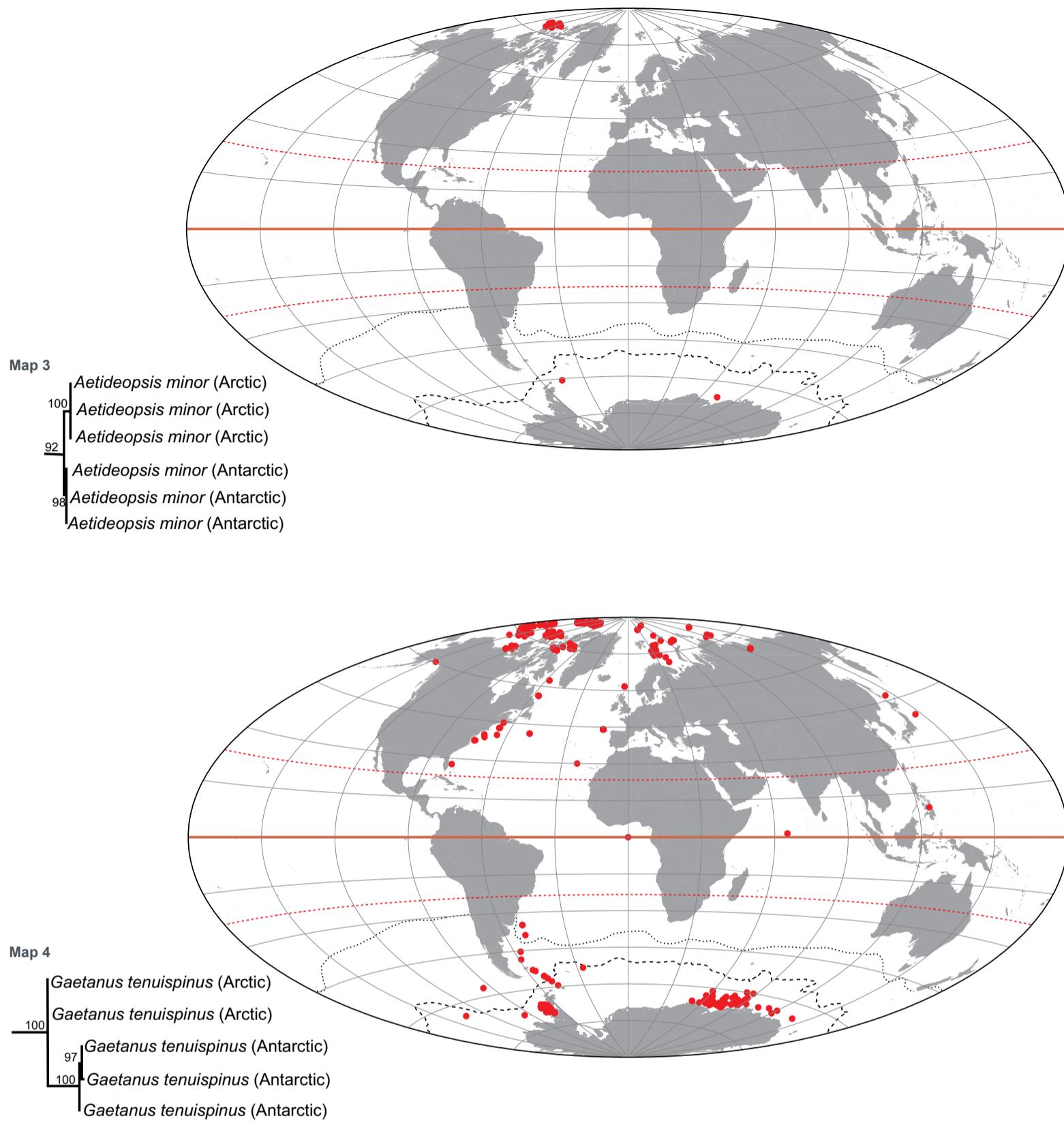
The available data suggest that bipolar divergences have taken place in multiple taxa throughout geological history as advocated by Crame (1993). Furthermore, the breakup of Pangea provides a satisfactory explanation for bipolar divergence in the Mesozoic. In the Cenozoic, although dispersal (from either north to south or vice versa) is a possible mechanism for the advent of disjunct bipolar taxa, most authors favour a scenario that involves a previous cosmopolitan distribution followed by subsequent extirpation from the tropics. Dispersal mechanisms are more highly favoured among terrestrial biologists (e.g., Popp *et al.* 2011). This is perhaps because dispersal from polar oceans often involves the thermohaline circulation (e.g., Strugnell *et al.* 2008) which is likely to provide a prolonged dispersal route (and therefore a route for gene flow) rather than the 'one off' dispersal required to form a founder population in the northern hemisphere. The extirpation scenario emphasises the need for suitable environmental conditions to facilitate gene flow and it appears to be clear that equatorial submergence facilitates gene flow between the poles in species with extended distributions. Although we still lack knowledge on the true distribution of many species, particularly rare, deep-water species, there is no overriding reason why bipolar species with disjunct distributions need to have diverged genetically or morphologically. If the origin of bipolar species occurs throughout geological history and is particularly associated with glacial cycles, then it is likely that there are populations at the poles that have diverged neither genetically nor morphologically yet, but which no longer exchange alleles. i.e., as Park & Ferrari (2009) suggested: bipolar species are transient natural phenomena.



Bipolarity Maps 1-2 Map 1 *Polarella glacialis*. It could not be determined whether Arctic and Southern Ocean strains comprised a single lineage on the basis of SSU rRNA sequence data. Superimposed tree redrawn from Montresor *et al.* (2003). Map 2 *Obelia longissima*. Limited geographic structuring exists between Arctic and Antarctic specimens according to COI sequence data (tree redrawn from Govindarajan *et al.* 2006).

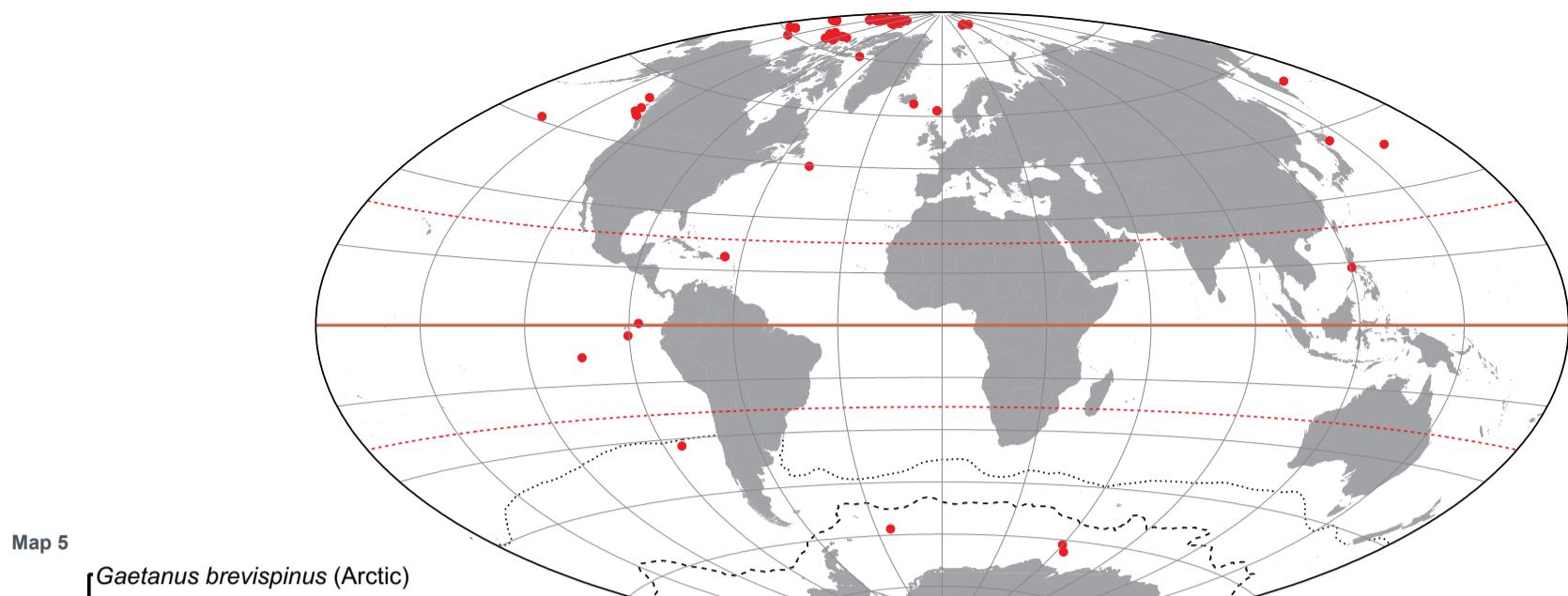
References

- Allcock, A.L., Strugnell, J.M., 2012. Southern Ocean diversity: new paradigms from molecular ecology. *Trends in Ecology and Evolution*, **27**, 520–528.
- Baldwin, A.J., Moss, J.A., Pakulski, J.D., Catala, P., Joux, F., Jeffrey, W.H., 2005. Microbial diversity in a Pacific Ocean transect from the Arctic to Antarctic circles. *Aquatic Microbial Ecology*, **41**, 91–102.
- Bowen, B. W., Grant, W. S., 1997. Phylogeography of the sardines (*Sardinops* spp.): Assessing biogeographic models and population histories in temperate upwelling zones. *Evolution*, **51**, 1601–1610.
- Brinkmeyer, R., Knittel, K., Jurgens, J., Weyland, H., Amann, R., Helmke, E., 2003. Diversity and structure of bacterial communities in Arctic versus Antarctic pack ice. *Applied Environmental Microbiology*, **69**, 6610–6619.
- Burridge, C.P., 2002. Antitropicality of Pacific fishes: molecular insights. *Environmental Biology of Fishes*, **65**, 151–164.
- Burridge, C.P., White, R.W.G., 2000. Molecular phylogeny of the antitropical subgenus *Goniistius* (Perciformes: Cheilodactylidae: Cheilodactylus): evidence for multiple transequatorial divergences and non-monophyly. *Biological Journal of the Linnean Society*, **70**, 435–458.
- Cornils, A., Held, C., 2014. Evidence of cryptic and pseudocryptic speciation in the *Paracalanus parvus* species complex (Crustacea, Copepoda, Calanoida). *Frontiers in Zoology*, **11**, 19.
- Crame, J.A., 1993. Bipolar molluscs and their evolutionary implications. *Journal of Biogeography*, **20**, 145–161.
- Darling, K.F., Wade, C.A., 2008. The genetic diversity of planktic foraminifera and the global distribution of ribosomal RNA genotypes. *Marine Micropalaeontology*, **67**, 216–238.
- Darling, K.F., Wade, C.M., Stewart, I.A., Kroon, R., Dingle, R., Leigh Brown, A.J., 2000. Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers. *Nature*, **405**, 43–47.
- Darwin, C., 1872. The origin of species. Murray, London.
- De Broyer C., Danis B., 2011. How many species in the Southern Ocean? Towards a dynamic inventory of the Antarctic marine species. *Deep Sea Research Part II: Topical Studies in Oceanography*, **58**, 5–17.
- Foltz, D.W., Fatland, S.D., Eleaume, M., Markello, K., Howell, K.L., Neill, K., Mah, C.L., 2013. Global population divergence of the sea star *Hippasteria phrygiana* corresponds to the onset of the last glacial period of the Pleistocene. *Marine Biology*, **160**, 1285–1296.
- Ghiglione, J.-F., Gland, P.E., Pommier, T., Pedrós-Alioé C., Maas, E.W., Bakker, K., Bertilson, S., Kirchman, D.L., Lovejoy, C., Yager, P.L., Murray, A.E., 2012. Pole-to-pole biogeography of surface and deep marine bacterial communities. *Proceedings of the National Academy of Science*, **109**, 17633–17638.
- Goetze, E., 2003. Cryptic speciation on the high seas: global phylogenetics of the copepod family Eucalanidae. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, **270**, 2321–2331.
- Govindarajan, A.F., Boero, F., Halanych, K.M., 2006. Phylogenetic analysis with multiple markers indicates repeated loss of the adult medusa stage in Campanulariidae (Hydrozoa, Cnidaria). *Molecular phylogenetics and evolution*, **38**, 820–834.



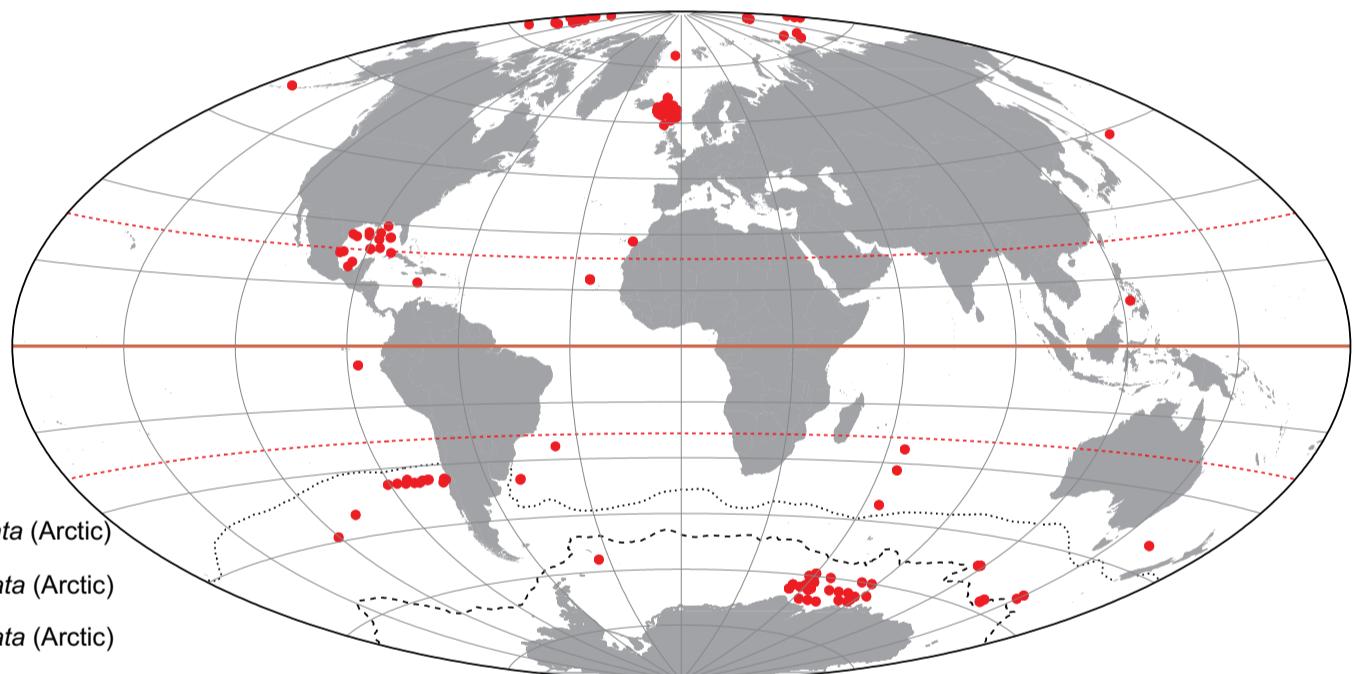
Bipolarity Maps 3–4 Map 3 *Aetideopsis minor*. Molecular work suggests two divergent lineages in this mesopelagic bipolar species. Maximum likelihood phylogram of concatenated ITS2 and COI redrawn from Laakmann et al. (2012) superimposed. Map 4 *Gaetanus tenuispinus*. Molecular work suggests two divergent lineages in this mesopelagic cosmopolitan species. Maximum likelihood phylogram of concatenated ITS2 and COI redrawn from Laakmann et al. (2012) superimposed.

- Griffiths, H.J., Danis, B., Clarke, A., 2011. Quantifying Antarctic marine biodiversity: The SCAR-MarBIN data portal. *Deep Sea Research Part II: Topical Studies in Oceanography*, **58**, 18–29.
- Gutt, J., Hosie, G., Stoddart, M., 2010. Marine Life in the Antarctic. pp 203–220 in McIntyre, A.D. (ed.) *Life in the world's oceans: diversity, distribution, and abundance*. Blackwell Publishing Ltd, 361 pp.
- Havermans C., Sonet G., Udekem d'Acoz C. d', Nagy Z.T., Martin P., Brix S., Riehl T., Agrawal S., Held C., 2013. Genetic and morphological divergences in the cosmopolitan deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species. *PLOS One* **8**(9), 1–15. e74218
- Hilbish, T.J., Mullinax, A., Dolven, S.I., Meyer, A., Koehn, R.K., Rawson, P.D., 2000. Origin of the antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of transequatorial migration. *Marine Biology*, **136**, 69–77.
- Hollibaugh, J.T., Bano, N., Ducklow, H.W., 2002. Widespread distribution in polar oceans of a 16S rRNA gene sequence with affinity to *Nitrosospira*-like ammonia-oxidizing bacteria. *Applied Environmental Microbiology*, **68**, 1478–1484.
- Hunt, B., Strugnell, J., Bednarsek, N., Linse, K., Nelson, J., Pakhomov, E., Seibel, B., Steinke, D., Würzberg, L., 2010. Poles apart: the “bipolar” pteropod species *Limacina helicina* is genetically distinct between the Arctic and Antarctic oceans. *PLoS ONE*, **5**, e9835.
- Koufopanou, V., Reid, D.G., Ridgway, S.A., Thomas, R.T., 1999. A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. *Molecular Phylogenetics and Evolution*, **11**, 138–156.
- Kuklinski, P., Barnes, D.K.A., 2010. First bipolar benthic brooder. *Marine Ecology Progress Series*, **401**, 15–20.
- Laakmann, S., Auel, H., Kochzius, M., 2012. Evolution in the deep sea: Biological traits, ecology and phylogenetics of pelagic copepods. *Molecular Phylogenetics and Evolution*, **65**, 535–546.
- Lecroq, B., Gooday, A.J., Pawłowski, J., 2009. Global genetic homogeneity in the deep-sea foraminiferan *Epistominella exigua* (Rotaliida: Pseudoparrellidae). *Zootaxa*, **2096**, 23–32.
- Lindberg, D.R., 1991. Marine biotic interchange between the northern and southern hemispheres. *Paleobiology*, **17**, 308–324.
- Mabuchi, K., Nakabo, T., Nishida, M., 2004. Molecular phylogeny of the antitropical genus *Pseudolabrus* (Perciformes: Labridae): evidence for a Southern Hemisphere origin. *Molecular Phylogenetics and Evolution*, **32**, 375–382.
- Montresor, M., Lovejoy, C., Orsini, L., Procaccini, G., Roy, S., 2003. Bipolar distribution of the cyst-forming dinoflagellate *Polarella glacialis*. *Polar Biology*, **26**, 186–194.
- O'Hara, T.D., England, P.R., Gunasekera, R.M., Naughton, K.M., 2014. Limited phylogeographic structure for five bathyal ophiuroids at continental scales. *Deep-sea Research Part I – Oceanographic Research Papers*, **84**, 18–28.
- Okolodkov, Y.B., 1999. Species range types of recent marine dinoflagellates recorded from the Arctic. *Grana*, **38**, 162–169.
- Parapar, J., Gambi, M.C., Rouse, G.W., 2011. A revision of the deep-sea genus *Axiokebuita* Pocklington and Fournier, 1987 (Annelida: Scalibregmatidae). *Italian Journal of Zoology*, **78**(S1), 148–162.
- Park, E.T., Ferrari, F.D., 2009. Species diversity and distributions of pelagic calanoid copepods from the Southern Ocean. pp. 143–180 in Krupnik, I., Lang, M.A., Miller, S.E. (eds.) *Smithsonian at the poles: contributions to International Polar Year Science*. Smithsonian Institution Scholarly Press, Washington, D.C.
- Pawłowski, J., Fahrni, J., Lecroq, B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen, T., Gooday A.J., 2007. Bipolar gene flow in deep-sea benthic foraminifera. *Molecular Ecology*, **16**, 4089–4096.
- Pawłowski, J., Majewski, W., Longet, D., Guiard, J., Cedhagen, T., Gooday, A.J., Korsun, S., Habura,



Map 5

Gaetanus brevispinus (Arctic)
 73
 Gaetanus brevispinus (Antarctic)
 94
 Gaetanus brevispinus (Arctic)
 91
 Gaetanus brevispinus (Antarctic)
 95
 Gaetanus brevispinus (Arctic)



Map 6

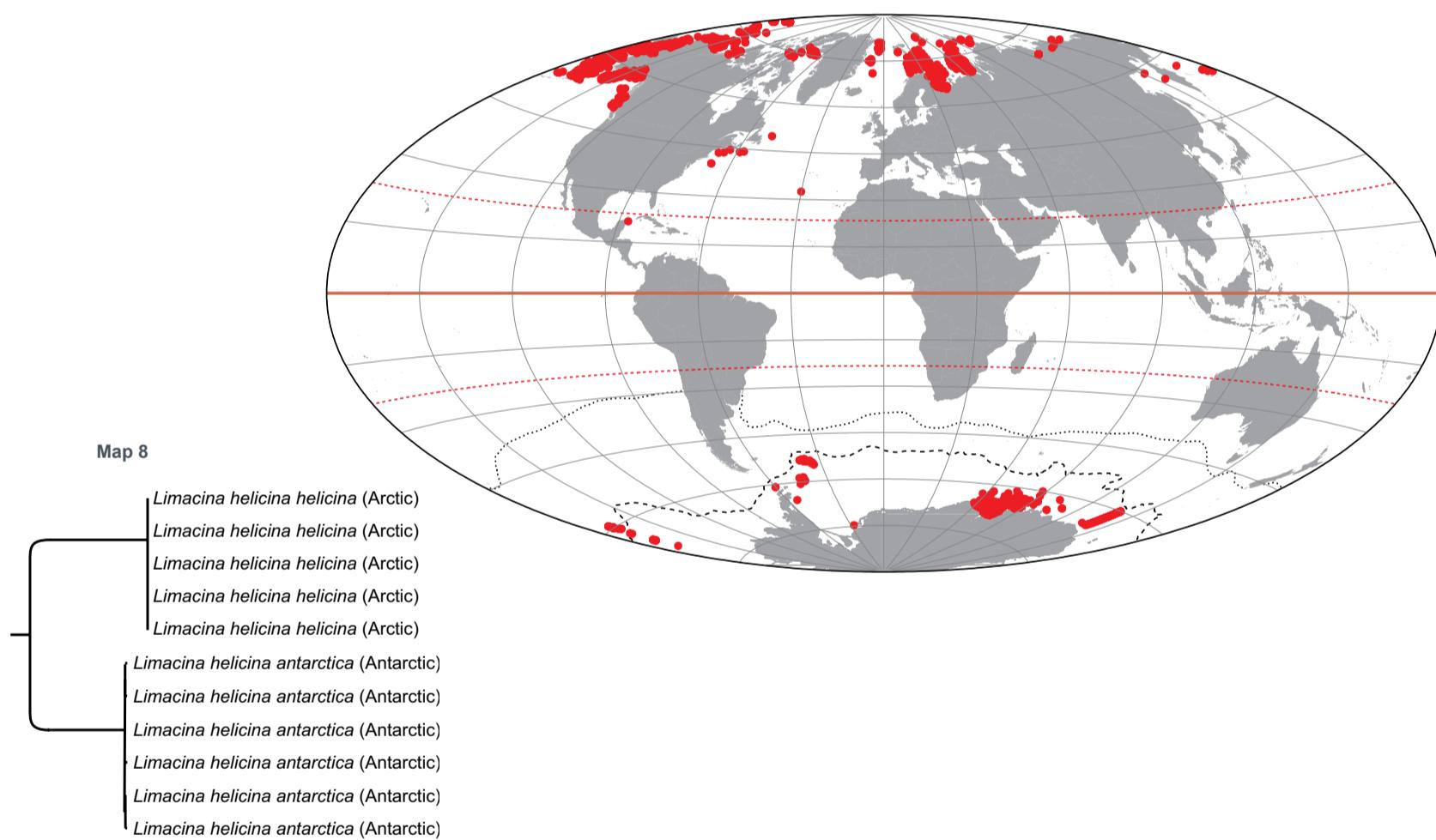
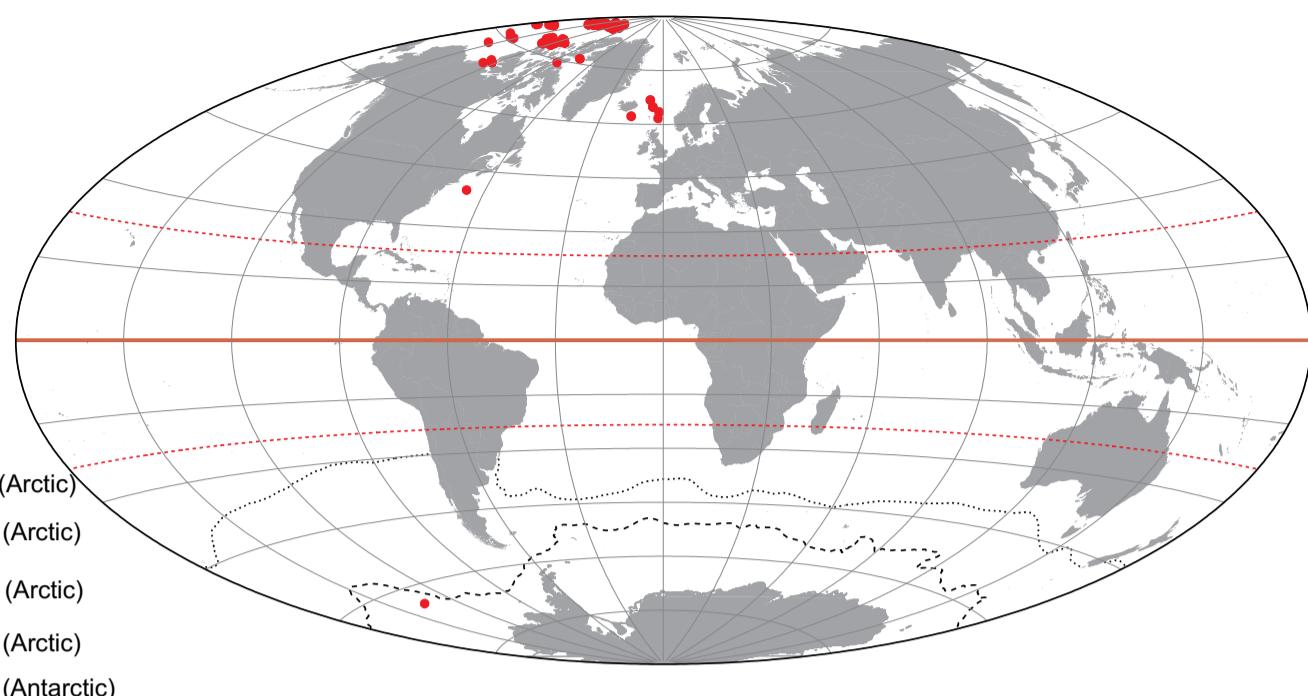
Paraeuchaeta barbata (Arctic)
 51
 Paraeuchaeta barbata (Arctic)
 100
 Paraeuchaeta barbata (Arctic)
 Paraeuchaeta barbata (Antarctic)
 Paraeuchaeta barbata (Antarctic)

Bipolarity Maps 5-6 Map 5 *Gaetanus brevispinus*. Molecular work suggests a single homogenous lineage in this bathypelagic cosmopolitan species. Maximum likelihood phylogram of concatenated ITS2 and COI redrawn from Laakmann *et al.* (2012) superimposed. Map 6 *Paraeuchaeta barbata*. Molecular work suggests a single homogenous lineage in this bathypelagic cosmopolitan species. Maximum likelihood phylogram of concatenated ITS2 and COI redrawn from Laakmann *et al.* (2012) superimposed.

- A.A., Bowser, S.S., 2008. Genetic differentiation between Arctic and Antarctic monothalamous foraminifera. *Polar Biology*, **31**, 1205–1216.
- Pearse, J.D., Lockhart, S.J., 2004. Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep-Sea Research II*, **51**, 1533–1549.
- Popp, M., Mirré, V., Brochmann, C., 2011. A single Mid-Pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proceedings of the National Academy of Science*, **108**, 6520–6525.
- Riaux-Gobin, C., Witkowski, A., Ruppel, M., 2012. *Scalariella* a new genus of monoraphid diatom (Bacillariophyta) with a bipolar distribution. *Fottea*, **12**, 13–25.
- Rodríguez, E., 2012. Another bipolar deep-sea anemone: new species of *Iosactis* (Actiniaria, Endomyaria) from Antarctica. *Helgoland Marine Research*, **66**, 211–218.
- Rodríguez, E., López-González, P.J., Daly, M., 2009. New family of sea anemones (Actiniaria, Acontiarida) from deep polar seas. *Polar Biology*, **32**, 703–717.
- Ross, J.C.A., 1847. Voyage of discovery and research in the Southern and Antarctic regions during the years 1839–1843. John Murray, London.
- Sirenko, B.I.; Clarke, C.; Hopcroft, R.R.; Huettmann, F.; Bluhm, B.A.; Gradinger, R. (eds.) (2013) The Arctic Register of Marine Species (ARMS) compiled by the Arctic Ocean Diversity (ArcOD). Accessed at <http://www.marinespecies.org/arms> on 2013-04-04
- Staley, J.T., Gosink, J.J., 1999. Poles apart: biodiversity and biogeography of sea ice bacteria. *Annual Review of Microbiology*, **53**, 189–215.
- Stepanjants, S.D., Cortese, G., Kruglikova, S.B., Bjørklund, K.R., 2006. A review of bipolarity

- concepts: history and examples from Radiolaria and Medusozoa (Cnidaria). *Marine Biology Research*, **2**, 200–241.
- Stepien, C.A., Rosenblatt, R.H., 1996. Genetic divergence in antitropical pelagic marine fishes (*Trachurus*, *Merluccius*, and *Scomber*) between North and South America. *Copeia*, **1996**, 586–598.
- Strugnell, J.M., Rogers, A.D., Prodöhl, P.A., Collins, M.A., Allcock, A.L., 2008. The thermohaline expressway: Antarctica as a centre of origin for deep-sea octopuses. *Cladistics*, **24**, 853–860.
- Stupnikova, A.N., Molodtsova, T.N., Mugue, N.S., Neretina, T.V., 2013. Genetic variability of the *Metridia lucens* complex (Copepoda) in the Southern Ocean. *Journal of Marine Systems*, **128**, 175–184.
- Tam, Y.K., Kornfield, I., Ojeda, F.P., 1996. Divergence and zoogeography of mole crabs, *Emerita* spp. (Decapoda: Hippidae), in the Americas. *Marine Biology*, **125**, 489–497.
- Uriz, M.-J., Gili, J.-M., Orejas, C., Perez-Porro, A.-R., 2011. Do bipolar distributions exist in marine sponges? *Stylocordyla chupachups* sp. nov. (Porifera: Hadromerida) from the Weddell Sea (Antarctic), previously reported as *S. borealis* (Loven, 1868). *Polar Biology*, **34**, 243–255.
- Vermeij, G.J., 1992. Trans-equatorial connections between biotas in the temperate eastern Atlantic. *Marine Biology*, **112**, 343–348.
- Wallace, A.R., 1880. Island Life. MacMillan and Co., London.
- Zeng, Y., Zheng, T., Yu, Y., Chen, B., He, J., 2010. Relationships between Arctic and Antarctic *Shewanella* strains evaluated by a polyphasic taxonomic approach. *Polar Biology*, **33**, 531–541.

► Bipolarity



Bipolarity Maps 7-8 Map 7 *Aetideopsis rostrata*. Molecular work suggests a single homogenous lineage in this bathypelagic bipolar species. Maximum likelihood phylogram of concatenated ITS2 and COI redrawn from Laakmann *et al.* (2012) superimposed. Map 8 *Limacina helicina*. Molecular work suggests two highly divergence lineages. Superimposed tree redrawn from Hunt *et al.* (2010).

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

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

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

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

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

The Census of Antarctic Marine Life (CAML)

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

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

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

The Editorial Team



Claude DE BROUER 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'ACOZ 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 and antabif.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 KOUBBI 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. 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.

