

Census of Antarctic Marine Life  
SCAR-Marine Biodiversity Information Network

# BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

## ► CHAPTER 10.8. BIOGEOGRAPHIC PROCESSES

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SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

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## 10.8. Biogeographic Processes in the Southern Ocean

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### 1. Introduction

The long-term isolation of Antarctic biota coupled with the geodynamic history of the Southern Ocean has resulted in the evolution of original faunas with no equivalent in the Arctic, nor anywhere else in the world's ocean (Gutt *et al.* 2010). Antarctic fauna clearly evolved adaptations to polar conditions but adaptation alone does not account for the distinctiveness of Antarctic biodiversity. Antarctic life has been shaped by the unique tectonic, oceanographic, and climatic history of the Antarctic, in which speciation, adaptative radiations and diversification, selective extinction, and dispersal have all had a role (Rogers 2007, Pearse *et al.* 2009, Krug *et al.* 2010). The aim of this chapter is to put all these ecological and evolutionary processes together to explain the biogeographic processes at the origin of the distinctive biogeographic patterns described in this Atlas. Based upon the recent literature mostly, but not exclusively devoted to Antarctic biogeography of benthic invertebrates, biogeographic processes and resulting biogeographic patterns are documented with regards to major tectonic, climatic, and oceanographic events of Antarctic history since 70 Ma.

Looking for explanations and accounts of the biogeographic patterns featured by Antarctic marine life implies the identification of the ecological and evolutionary processes that have shaped the spatial distribution of taxa. The biogeographic distribution of taxa is driven by physical processes and biological interactions. Physical processes depend upon hydrographic and geographic changes induced by plate tectonics, climate and sea level changes (Futuyma 1997, Rogers 2007, Clarke 2008, Pearse *et al.* 2009), while biotic factors depend upon idiosyncratic dispersal and adaptation capabilities of species. Leaving aside the environmental parameters that control the spatial distribution of populations and individual species when current distribution is considered to be at equilibrium (Futuyma 1997, Briggs 2007, Colwell & Rangel 2009), speciation, extinction, and dispersal are the three fundamental processes usually invoked in biogeography and reviewed in this chapter.

Conceptual developments in cladistic and 'event-based' biogeography led to distinguish between vicariance and sympatric speciation (Futuyma 1997, Lomolino *et al.* 2005, Ebach & Tangney 2007). Vicariance is a case of allopatric speciation that is, speciation following the division of populations in separate, non-overlapping geographic areas when it is due to the fragmentation of an ancestral biota by emerging barriers (tectonic, climatic, or oceanographic). In the sympatric mode of speciation, reproductive isolation leads to distinct species arising within the same parent geographic area. It is driven by natural selection, in contrast to the allopatric process for which the initial division is physical. Identifying speciation processes comes down to explaining the origination, radiation (associated to the evolution of key innovations and adaptations), and diversification of Antarctic taxa. Extinction can be stochastic to selective, affecting those marine groups that cannot adapt to new conditions. It can be local, regional (e.g. extinction of durophagous predators after the Eocene-Oligocene cooling event), or global (e.g. extinction of ammonites after the Cretaceous-Paleogene biological crisis). Here, dispersal is taken in a broad sense, including all biogeographic processes associated with the mechanical (physical) movement of populations and species out of their initial distribution range. It is inclusive of emigration and immigration but it also concerns species distribution range expansion, contraction, fragmentation, and isolation. Long-distance dispersal is a special case of dispersal that is at the origin of disjointed biogeographic patterns. It can be direct, through dispersal of active propagules (larval stages or adults) or indirect, through passive rafting attached to floating substrates (Lomolino *et al.* 2005, Ebach & Tangney 2007, Rogers 2007, Clarke 2008, Pearse *et al.* 2009, Clarke & Crame 2010, Krug *et al.* 2009).

### 2. Distinctiveness, origin and fate of Antarctic marine diversity

Antarctic marine fauna is often considered to be characterized by unique biological and ecological characteristics including gigantism, slow metabolism and growth rates, late maturity and high longevity, high proportion of brooding species, relative scarce offspring release, eurybathy or at least wide ranging pressure and temperature tolerance, including for larvae of shallow-water species (such as *Sterechinus neumayeri* and/or polychaetes) (Brandt 2005, Brandt *et al.* 2007a,b, Kaiser *et al.* 2013). Some of these characters can be related to unique oceanographic features of the Southern Ocean and Antarctic continental shelf area. The Southern Ocean is vast, covering about 10 percent of the world's ocean (35 million km<sup>2</sup>). The Antarctic continental shelf (4.6 million

km<sup>2</sup>) accounts for 11 percent of the world's continental-shelf areas (Zwally *et al.* 2002, Gutt *et al.* 2010) and extends deep at about 450 m and deeper than 1000 m in some places (Clarke & Crame 2010). Antarctic ecosystems are strongly controlled by the extreme seasonality, low temperatures and variations of sea ice coverage (60% of the ocean's surface in winter and 20% in summer) and consequently of primary production (Gutt *et al.* 2010). It is also influenced by local ice disturbances due to iceberg scours and anchor-ice in shallow areas (Barboza *et al.* 2011).

The composition and levels of Antarctic marine diversity are notable as well. The overall diversity on the Antarctic continental shelf exceeds that of the Arctic (Clarke 2008), but is still relatively low (about 5 percent of the world's marine diversity) considering the shelf area (11 percent of the world's continental shelves). However, the level of diversity is highly variable depending on the taxa and taxonomic levels considered (Eastman & McCune 2000, Crame 2004, Clarke 2008, Clarke & Crame 2010, Krug *et al.* 2009, Ingels *et al.* 2012). The latitudinal gradient of diversity does not noticeably decrease with increasing latitude in the Southern Hemisphere, but patterns differ according to the taxonomic levels and groups analyzed (such as sharp demise in key benthic groups such as fish, decapod crustaceans, and bivalves compared to other groups like sponges, bryozoans, echinoderms, ascidians, hydroids, amphipods, isopods, which are highly diversified in Antarctica), and scale of analyses (low gamma versus high alpha diversity) (Crame 2004, Barnes & Griffiths 2008). The absence of common groups outside the Antarctic and conversely, the high level of endemism and prevalence of a taxonomically limited number of speciose groups is also a special trait of marine diversity in the Antarctic, and particularly on the continental shelf (Eastman & McCune 2000, Clarke & Crame 2010). Hence, durophagous predators are lacking (e.g. sharks) or rare (brachyuran crabs, lobsters, and rays). Diversity of teleost fish is low and dominated by notothenioids. The epifauna mostly includes sessile and particle feeders, while the vagile fauna is represented by echinoderms, pycnogonids, crustaceans, nermerteans, and gastropods (Kaiser *et al.* 2013). The uniqueness of Antarctic marine diversity can be explained partly by the specificities of Antarctic shelf habitats, including the rarity/absence of fluvial-terrestrial discharge, estuaries or deltaic environments, coral reefs, intertidal mudflats, and wave dominated shallow-water habitats. Moreover, shallow-water environments are typically covered with anchor ice to about 30 m depth.

Despite the occurrence of peculiar physiographic traits, the distinctiveness and variability in Antarctic diversity also reflect different biogeographic histories (Crame 1999, 2004, Gray 2001, Griffiths *et al.* 2009). The age of the Antarctic continental shelf and deep-sea basins, the role of hydrographic barriers to dispersal that stimulated both allopatric and sympatric speciations (Gray 2001, Barnes & Griffiths 2008), and the evolutionary time over which species have evolved explain the distinctive and phylogenetically restricted diversity observed in the Southern Ocean in contrast to northern polar areas (Eastmann & Cune 2000, Brandt *et al.* 2007b).

Antarctic marine life has a complex origin. (1) A first source of taxa is represented today by a relict autochthonous fauna, which might have long evolved *in situ* and diversified with contrasted levels of speciosity. The origin of many lineages can be traced back to the Eocene, and as far old as the Late Cretaceous for some of them; for example, ancestors of struthiolarrid and buccinoid gastropods were identified in the Late Cretaceous (Zinsmeister 1982, Crame 1999, Stilwell *et al.* 2004, Beu 2009). A long *in situ* evolution and diversification that goes back to the Late Cretaceous-early Cenozoic has been invoked also for explaining the high diversity level of the Southern Ocean deep-sea fauna (Thatje *et al.* 2005). (2) A second source of taxa is considered derived by immigration from adjacent deep-sea basins and oceanic ridges. This second source has been formalized in the 'emergence' scenario (Knox & Lowry 1977), which is discussed below. (3) The third source of present-day taxa might result from dispersal from southernmost America along the Scotia Arc region (Hedgpeth 1970, Knox & Lowry 1977, Clarke & Crame 2010).

Finally, Clarke (2008) pointed out that some taxa originated in the Southern Ocean might have also migrated along the Scotia Arc in the reverse direction that is northward, out of the Antarctic. Conversely, many taxa such as brachyuran crabs, lobsters, ammonites, hyoliths, and many teleost fish went extinct following major environmental upheavals and cooling pulses occurred in the Southern Ocean at the Cretaceous-Paleocene and Eocene-Oligocene boundaries, during the late Miocene, and Pliocene-Pleistocene climatic cycles (Table 1) (Clarke 2008).

Table 1. Correspondence between Earth dynamics, its forcing factors, biogeographic processes, patterns, and corresponding taxa in the Southern Ocean (modified after Rogers 2007). Data from: Hessler & Thistle (1975); Knox & Lowry, 1977; Clarke & Crame 1989, 1992; Crame, 1999; Eastman & Cune 2000; Zachos *et al.* 2001; Page & Linse 2002; Lawver & Gahagan, 2003, 2011; Patarnello *et al.* 2011; Stilwell, 2003; Stilwell *et al.* 2004; Lee *et al.* 2004; Thatje *et al.* 2005; Baker *et al.* 2006; Linse *et al.* 2006; Scher & Martin 2006; Barker *et al.* 2007; Brandt *et al.* 2007a; Rodriguez *et al.* 2007; Rogers 2007; Strugnelli & Linse 2007; Clarke 2008; Clarke *et al.* 2008; Aronson *et al.* 2009; Beu 2009; Griffiths *et al.* 2009; Wilson *et al.* 2009; Pearse *et al.* 2009; Krug *et al.* 2010; Leese *et al.* 2010; Clarke & Crame 2010; González-Wevar *et al.* 2010; Göbbeler & Klusmann-Kolb 2010; Raupach *et al.* 2010; Díaz *et al.* 2011; Janosik *et al.* 2011; Dalziel *et al.* 2013. ACC: Antarctic Circumpolar Current; ACS: Antarctic Continental Shelf; ADW: Antarctic Deep Water; PF: Polar Front; SO: Southern Ocean. Colored cells symbolize the intensity of forcing factors. The interpretation of biogeographic responses of taxa relies on fossil data and/or molecular works. Digits indicated in parenthesis refer to the taxa given as examples in the "Marine Groups of Interest" box at the bottom of the table. ►

Geologic stages (ages)		Maastrichtian - Eocene (70-34 Ma)	Eocene - Oligocene boundary (ca. 34 Ma)	Miocene - Pliocene (23 Ma-5 Ma)		Pliocene - Present Day (5-0 Ma)
EARTH DYNAMICS	Tectonic/geographic history	Gondwana final breakup	Complete circum-Antarctic seaway (opening of Drake Passage and deep seaways between South Tasman Rise and East Antarctica; between Kerguelen Plateau and Broken Ridge)	Widening of deep circum-Antarctic seaways and ACS deepening (glacial isostatic adjustment); formation of the Macquarie Ridge		Glacial isostatic adjustments
	Oceanographic history	Establishment of Ross-Weddell trans-Antarctic seaways and South Pacific Current (ca. 50 Ma), proto-ACC (ca. 43 Ma)	Water cooling in SO and possible early onset of shallow ACC ; persistence of Ross-Weddell trans-Antarctic seaways into the Oligocene	ACC strengthening, deepening, and northward expansion with setting up of polar conditions over the continental shelf area (14-12 Ma)		Cycles of ACC and ADW latitudinal and intensity shifts, cycles of sea-level changes, re-opening of Ross-Weddell trans-Antarctic seaway (ca. 4 Ma)
	Climatic & glacial history	Long-term trend of climate cooling since 50 Ma and onset of glaciations (isolated ice-caps) in East Antarctica in late Eocene	Major climate cooling event including onset of continental glaciation (icesheets) in East Antarctica	Transient glaciation (ca. 23 Ma), warming (23-15 Ma) then climate cooling trend and expansion of East Antarctic icesheet (14-12 Ma); onset of continental glaciation in West Antarctica (8-5 Ma)		Orbitally-forced glacial cycles of icesheet extension and contraction on Milankovitch frequencies (including Last Glacial Maximum)
FORCING FACTORS	Antarctic Isolation	—	+	—	+	+++
	Transient ACS habitat fragmentation			+	+	++
	Climate cooling		+++	ca. 15 Ma		+
	Rhythmicity and intensity of glaciations		+		+	++
	Circum-Antarctic circulation	—	+	—	+	++
	Rhythmicity of circulation variations			+	+	++
PROCESSES	Speciation	In situ evolution (1); vicariance (2); origination and diversification (3)	Vicariance (7), origination and radiation (8)	Vicariance (12); radiation (innovation and adaptation) and diversification (13)		Vicariance (17), differentiation (18)
	Extinction	Global K-T boundary crisis (4); result of climate cooling and geographic isolation (5)	Selective and regional (9)	Local, stochastic to selective and regional (14)		Local, stochastic to selective and regional (19)
	Dispersal	Colonization of the deep-sea from the shelf (6)	Dispersal to the deep sea (submergence), dispersal over and onto (emergence) the shelf and to the north (emigration) (10); jump-dispersal (11)	Range-expansion to the deep sea (submergence), dispersal over and onto (emergence) the ACS and to the north (emigration) (15); jump-dispersal (recurrent long-distance indirect dispersal through passive rafting from Scotia Arc region downstream of ACC, and through direct dispersal as planktonic larvae between Patagonia and New Zealand) (16)		Range contraction/fragmentation and isolation to shallow refuges coupled with shifts in bathymetric distributions (slope) and subsequent colonisation/range expansion and coalescence (ACS and diversity pump hypotheses); transient emigration to vs immigration from the north along the Scotia Arc (4); transient jump-dispersal between Patagonia and New Zealand of planktonic larvae (21)
PATTERNS	Biogeographic patterns	Progressive endemism and isolation of faunas (2, 5); fragmentation of Weddellian province (2, 3)	Antarctic endemism (geographic, oceanographic and thermal isolation) (7-9)	Antarctic endemism (geographic, oceanographic and thermal isolation) and partitioning of SO into distinct faunal provinces (12-14)		Fragmentation of populations into distinct lineages and of species into complexes of sibling or cryptic species (17, 18)
		Faunal affinities between deep Antarctic and other ocean basins, including the Arctic (6)	Wide depth and circumpolar distribution ranges (10)	Wide depth and circumpolar distribution ranges (15)		Extended bathymetric and circumpolar distribution ranges; faunal affinities between the continental shelf and the slope; between Antarctic and sub-Antarctic faunas (20)
	Diversity patterns	Relict autochthonous fauna originated in Cretaceous (1)	Highest diversity values within and east of Scotia Arc (downstream of ACC) (7, 10, 11)	Evolution of species flocks in SO and over AS (12, 13, 16)		Decreasing species richness down the slope (17)
		Faunal replacement (Early Danian at species level; Late Danian at genus level) (4)	Original Antarctic fauna, including the deep sea (7, 8)	Highest species richness within and east of Scotia Arc for taxa with nonpelagic development; faunal similarities between Patagonia and New Zealand (16)		Faunal similarities between Patagonia and New Zealand (21)
			Low diversity values, especially at high taxonomic levels (> genus) (9)			
	MARINE GROUPS OF INTEREST	(1) Struthiolariid and buccinoid gastropods, deep-sea paraselloideans, Actiniaria, octocorals, hydrozoans	(7) Spheniscidae, isopods, amphipods, notothenioids, euphausiids, molluscs, schizasterids and echinids, Actiniaria, algae	(12) Spheniscidae, euphausiids, Limidae, cidarid and echinid-related echinoids, asteroids		(17) Foraminiferids, channichthyids, polychaetes, amphipods, isopods, bivalves, crinoids, (?) asteroids
		(2) Spheniscidae, gastropods, bivalves, notothenioids, schizasterid echinoids, peracarids	(8) Spheniscidae, isopods, amphipods, suspension-feeding ophiuroids and crinoids, Actiniaria, gastropods (Pleurobranchomorpha)	(13) Notothenioids, channichthyids, trematomes and Lepidotothen, cidarid and schizasterid echinoids, Actiniaria, Nacellidae		(18) Euphausiids, nemerteans, Teuthida, isopods, bivalves, nudibranchs, nacellids, notothenioids, pinnipeds, spheniscidae, cetaceans, echinoids, asteroids, ophiuroids
		(3) Spheniscidae, cetaceans, neogastropods (evolutionary burst after K-T boundary), bivalves, teleosts, hexactinellids	(9) Large-bodied Spheniscidae, stomatopods, balaniforms, durophagous predators (decapods, neoselachians & teleosts), derived bivalve clades, clypeasteroid and cassiduloid echinoids	(14) Macroalgae, cirripeds, bivalves, Patellidae		(19) Certain echinoids with planktotrophic larvae, certain shallow marine molluscan species, (?) decapods
		(4) Widespread/cosmopolitan and shallow-water benthos among which suspension-feeding bivalves (15/26 newly evolved molluscan species above K-T boundary), ammonites, hyoliths	(10) Spheniscidae, echinoderms, molluscs (bivalves, littorinids), bryozoans, pycnogonids, ascidians, peracarids	(12, 13, 16) Nototheniids (SO), Artedidraconidae (AS), pycnophryne (AS), Channichthyidae (SO), Trematominidae (AS); Epimeria (SO); Eusirus (SO); serolids (SO)		(20) Molluscs, isopods, decapods, echinids, asteroids, ophiuroids, pycnogonids, foraminiferans, nematodes, ostracods, polychaetes, hexactinellids
		(5) Widespread/cosmopolitan bivalves and echinoids	(11) (?) Peracarids	(15) Spheniscidae, echinoderms, molluscs (bivalves, littorinids), bryozoans, pycnogonids, ascidians		(21) Molluscs
		(6) Hexactinellids		(16) Peracarids, molluscs		



### 3. The role of adaptation and the importance of Antarctic history

This long and multiphased oceanographic and climatic history has shaped polar biodiversity that either went extinct or eventually adapted to polar conditions through morphological (e.g. plumage transformations in penguins), physiological (e.g. insulation in marine mammals and birds; fasting in penguins), biochemical (antifreeze glycoproteins in notothenioid fish) and ecological innovations (e.g. cryopelagic fish communities; breeding systems in penguins; entire food web conditioned by high seasonal primary productivity) (Eastman & McCune 2000, Rogers 2007, Clarke 2008, Patarnello *et al.* 2011). Adaptation allowed for survival and range expansion of individual species out of Antarctica into the Southern Ocean.

Adaptation to polar conditions is best evidenced in taxa from both poles that evolved independently convergent traits (Eastman & McCune 2000, Rogers 2007, Patarnello *et al.* 2011). Among the best illustrations of adaptation to extreme environmental conditions is the sea-ice fauna, which in the Southern Ocean comprises euphausiid and amphipod crustaceans, nudibranchs, foraminiferans, and micro-organisms. This fauna has adapted to the ephemeral pack ice, which implies the existence of a transient pelagic life style during summer months when sea-ice melts, to the high seasonal temperature variations at the air-ice surface, extreme salinity variations and high seasonality of food resources mostly composed of ice algae (Gradinger 2001). Whereas Arctic and Antarctic sea-ice fauna show similar physiological and ecological adaptations, community composition differs between the two poles. This might be in part related to the higher proportion of sea-ice that melts in the Antarctic during the summer, but it is also very likely related to contrasted clade and regional histories as well. The same pattern holds true for teleost fish from both poles, which evolved freezing resistance adaptations independently — although some clades are definitely present at both poles, such as liparids — and compose, at the undersurface of the pack ice different cryopelagic communities between the two poles as the result of distinct regional histories (Eastman & McCune 2000).

Penguins (Spheniscidae) have clearly evolved a number of key features including the transformation of wing morphology for swimming, skeletal modifications for locomotion on land, modifications of plumage for insulation at low temperatures and particular breeding systems (Rogers 2007, Smith 2011). In the Northern Hemisphere, the speciose family Alcidae evolved convergent morphologies with Spheniscidae, as best illustrated by the high resemblance between penguins and the North Atlantic great auk, *Pinguinus impennis*, which went extinct by the middle of the nineteenth century due to over-hunting. Convergence concerns morphological adaptations to wing-propelled pursuit diving for fish, which are at the origin of the evolutionary success of both families near the poles (Smith 2011). The origin of penguins goes back to the Late Cretaceous and their evolution pre-dates glaciation events in the Southern Ocean. This is exemplified today by penguin species from temperate areas (e.g. *Spheniscus* from South Africa and South America up to the Galapagos). However, divergence time estimates between Antarctic and sub-Antarctic species on the one hand and the extinction of large-bodied Antarctic forms on the other are dated to about the Eocene-Oligocene boundary when climate markedly cooled (Rogers 2007). Here again, adaptation allowed for the evolutionary success and expansion of the family in the Southern Ocean and farther north, but the diversity of the family was conditioned by climate history.

Brooding was first considered an adaptation to polar conditions, the high rate of brooding species (and species with non pelagic development) in the Southern Ocean being explained by extreme Antarctic conditions (Thorson 1950, Mileikovsky 1971). Taxa with planktotrophic development that are common elsewhere are thought to have gone entirely extinct in the Southern Ocean during glacial maxima, as a result of counter-selection (Poulin *et al.* 2002). However, as Pearse *et al.* (2009) pointed out, the fact that some extant Antarctic species have planktonic larvae and few taxa brood in the Arctic and in the deep sea (with the exception of peracarids, which are brooders but abundant in the Arctic and the deep sea) implies that brooding cannot be considered a unique adaptation to polar conditions (Poulin *et al.* 2002). It should instead be related to clade (Gallardo & Penchaszadeh 2001) and to Antarctic oceanographic and climatic histories that might have promoted vicariant speciation of brooders (Poulin *et al.* 2002, Pearse *et al.* 2009). Brooding behavior evolved a long time ago — e.g. brooding structures are known in Late Cretaceous echinoids, they pre-date climate cooling in Antarctica and appeared independently in different temperate parts of the world's ocean, from the Antarctic Peninsula to Madagascar and France (Poulin *et al.* 2002, Dudicourt *et al.* 2005) — and is now phylogenetically constrained in many groups (Pearse *et al.* 2009).

If part of Antarctic fauna clearly evolved key features that result from adaptation to polar conditions and allowed them to expand their distribution ranges in the Southern Ocean, as well-illustrated in cryopelagic communities and in penguins, adaptation alone does not account for the idiosyncratic structure and distinctiveness of Antarctic biodiversity (Eastman & McCune 2000, Poulin *et al.* 2002, Pearse *et al.* 2009). Characteristics of the Antarctic diversity with no equivalent in the Arctic, nor anywhere else in the world's ocean have been shaped by the unique tectonic, oceanographic and climatic history of the Antarctic continent that has played a determinant part in structuring the biogeography and diversity of modern faunas (Zinsmeister 1979, 1981, Zinsmeister & Camacho 1980, Beu *et al.* 1997, Del Rio 2002, Pearse *et al.* 2009, Krug *et al.* 2010, Patarnello *et al.* 2011), and in which adaptive radiations and diversification, selective extinction and dispersal have all had a role (Rogers 2007, Pearse *et al.* 2009, Krug *et al.* 2010). Based on current literature, major events of the Antarctic history, the corresponding forcing

factors, associated biogeographic processes and resulting biogeographic patterns are documented in Table 1 for several marine groups.

Major facts of Antarctic history that shaped modern marine diversity are the final break-up of Gondwana and subsequent physiographic isolation of shallow Antarctic waters during the Cenozoic. The full deep water separation from the South Tasman Rise and the opening of the Drake Passage allowed for the onset of the modern Antarctic Circumpolar Current and establishment of the Polar Front. Associated with and strengthening the major cooling event at the Eocene-Oligocene boundary, these tectonic, climatic, and oceanographic changes led to a profound transition in marine productivity patterns and a complete thermal and geographic isolation of the Antarctic marine biota. The onset of the ACC and establishment of the Polar Fronts as well as their reinforcement during the Miocene has promoted both vicariance and dispersal events (Crame, 1999). Finally, the numerous cycles of ice sheet extensions and retractions over the last five million years (Naish *et al.* 2009) strongly impacted polar habitats (intense iceberg scouring on the shelf and gravity flows down the slope, multi-year ice close to the shoreline, northward extensions of seasonal sea-ice and primary productivity limited in the summer season) (Clarke & Crame 2010), causing probable benthic faunal extinctions (Krug *et al.* 2010), but also stimulating speciation events (Patarnello *et al.* 2011, Near *et al.* 2012) by population fragmentation in isolated areas of the shelf or population displacement in refuges around sub-Antarctic islands (González-Wevar *et al.* 2013) or in the deep sea (Thatje *et al.* 2005, Clarke & Crame 2010).

Most scenarios and historical hypotheses that aim at explaining present-day biogeographic patterns in the Southern Ocean highlight the role played by the Antarctic Circumpolar Current and Antarctic Ice Sheet dynamics (Table 1), but they should be tested with regards to the precise timing and our current knowledge of the biogeographic processes involved: speciation, extinction, and dispersal (Pearse *et al.* 2009, Crisp *et al.* 2011). In this prospect, chronograms derived from molecular phylogenies may appear particularly relevant.

## 4. Speciation

In cladistic and event-based biogeography, the dissimilarities observed between inferred phylogenies and area cladograms are usually attributed to extinction, dispersal or sympatric speciation, whereas vicariant speciation can account for the correspondence between phylogenies and biogeographic patterns (Futuyma 1997, Lomolino *et al.* 2005, Ebach & Tangney 2007). Therefore, vicariant speciation is classically distinguished from non-vicariant, either sympatric or allopatric, due to dispersal (peripatric speciation) or dispersion limitations (parapatric speciation).

### 4.1. Vicariance

There is little evidence of vicariance over long-distance dispersal in southern temperate seas (Bowen *et al.* 2001, Waters 2008). In contrast, in the Southern Ocean there is a large body of evidence that the long and polyphase tectonic drift and isolation of once unified continental shelves (South Africa, South America, Antarctica, Australia and New Zealand) along with the onset of the ACC during the Cenozoic led to the emergence of distinct marine provinces by vicariance (Zinsmeister 1979, 1981, Zinsmeister & Camacho 1980, Beu *et al.* 1997, Del Rio 2002, Linse *et al.* 2006). Vicariance scenarios are supported by the congruence between time estimates of clade divergence and those of geographic, oceanographic and climatic events (Table 1). Hence, the Gondwana final breakup during the late Cretaceous and early Cenozoic was correlated to the fragmentation of the Weddellian province (Zinsmeister 1982). At the Eocene-Oligocene boundary, the opening of the Drake Passage and onset of the ACC is coeval with divergence time estimates (based on molecular data) between Antarctic and sub-Antarctic clades in many taxa such as notothenioid fish, echinoid genera *Loxechinus* and *Stereochinus*, crustacean genus *Euphausia* and marine alga *Phaeocystis* (Crame 1999, Lee *et al.* 2004, Pearse *et al.* 2009). In these taxa, vicariance was driven by both continental drift, as well as by oceanographic and thermal isolation and allowed for the diversification of endemic marine groups over the Antarctic shelf area (Eastman & McCune 2000). Phases of ACC reinforcement and northward extension during glacial maxima of the Miocene and Pliocene favored vicariant events as well (Baker *et al.* 2006, Rogers 2007, González-Wevar *et al.* 2012). Finally, the numerous cycles of icesheet extensions over the continental shelf during glacial maxima of the Pliocene and Pleistocene led to species range contraction and population isolation into transient mosaic refuges (Pearse *et al.* 2009, Clarke & Crame 2010). This resulted in the fragmentation of populations into distinct lineages and species into complexes of sibling or cryptic species in different groups (Table 1).

### 4.2. Diversification

In the Southern Ocean, the notable diversity of some taxa is the result of ecological differentiation and competitive exclusion between species (sibling and cryptic species) that can be also the reflection of true adaptive radiations (Futuyma 1997). Adaptive radiations might have been promoted by the prevalence of under-utilized environments and food resources that followed extinction events (Eocene-Oligocene crisis) and created favorable conditions for the diversification of surviving species (Eastman & McCune 2000). The ecological success of those taxa that survived extinction events was also promoted by key innovations (e.g. antifreeze proteins in fish) and adaptations to unique Antarctic environments: deep shelf habitats, near-freezing water temperatures, seasonality of pack ice, light regime, and primary productivity.



However, adaptation to polar conditions is not the unique, necessary prerequisite for ecological success. The success of filter feeders such as bryozoans, sponges, ascidians, gorgonians, and hydroids is not limited to the Southern Ocean and was related to their capability to build efficient three-dimensional structures to feed (Crame 1999). Finally, it has been also postulated that high diversity levels might be the outcome of the long time-period over which extant taxa originated in late Cretaceous and early Cenozoic evolved and then diversified (e.g. gastropods and peracarids) (Crame 1999).

As the result of historical, ecological, and evolutionary processes diversity levels seem to vary spatially throughout the Southern Ocean, though the appraisal of diversity is highly dependent on sampling efforts (Griffiths 2010). Three biogeographic sectors have been identified as potential centers of diversification due to high levels of endemism and diversity: the Scotia Arc region (Linse *et al.* 2007), the Antarctic Peninsula (Griffiths *et al.* 2011), and the Atlantic sector of the Southern Ocean for the deep sea (Malyutina & Brandt 2007).

According to the taxonomic level considered, there seems to be two notable periods of intense diversification in the Southern Ocean: the Cretaceous-Eocene interval (1) and the end Miocene (2). (1) The Cretaceous-Eocene interval was a period of diversification of the predatory neogastropod families Buccinidae, Muricidae, and Turridae (Crame 1999). There is evidence of a Late Eocene diversification at species and genus levels in gastropods, bivalves, scaphopods, whales, and penguins in deposits of the La Meseta Formation on Seymour Island (Zinsmeister & Camacho 1982, Stilwell & Zinsmeister 1992, Crame 1999, Linse *et al.* 2006). (2) A major diversification of species also occurred during the strengthening of the ACC and climate cooling at the end of the Miocene, such as in the genus *Nacella* (Gonzalez-Wever *et al.* 2012).

Integrating divergence time estimates between clades and the historical, ecological and geographic conditions of their diversification, Pearse *et al.* (2009) thoroughly discussed the processes and scenarios of diversification of brooding species in the Southern Ocean. They concluded that two likely scenarios should be retained: the Antarctic Continental Shelf or ACS hypothesis, and the Antarctic Circumpolar Current or ACC hypothesis. The ACS hypothesis corresponds to a Milankovitch-cycle-driven species distribution range fragmentation and expansion on the continental shelf during the successive extents and retreats of ice caps in the Cenozoic. These cycles might have stimulated evolution through regional extinction and vicariance (Eastman & McCune 2000). It is analogous with Valentine's (1967) 'Climate-Driven Diversity Pump', the 'Orbitally Forced Species' Range Dynamics' (Dynesius & Janson 2000) for terrestrial communities, and the Antarctic marine 'Species Diversity Pump Hypothesis' of Brandt *et al.* (2007a). This process is considered to have enhanced speciation and diversification in molluscs such as philobryid bivalves, nudibranchs, and buccinoid gastropods (Pearse *et al.* 2009, Clarke & Crame 1989, 1992, 2010). According to the second scenario, the ACC hypothesis, the recurrent long-distance dispersal of brooding species with limited dispersion capabilities through the ACC would have generated high levels of diversity in the Scotia Arc region and downstream of the ACC in the Weddell Sea.

## 5. Extinction

Speciation and extinction can be closely linked. The availability of habitats and environmental resources after major extinction events appears to have facilitated adaptive radiations within some of surviving taxa (Brandt 2005). Hence, the extinction of decapods allowed for the emergence of new adaptive zones and the consequent radiation of peracarids (brooders), extinctions within teleosts favored the radiation of notothenioids (Near *et al.* 2012), and within gastropods this can explain the radiation of Buccinidae, Naticidae, and Turridae.

### 5.1. The K-T boundary event

The major extinction phase that Antarctic marine diversity has experienced for the last 70 million years is about at the Eocene-Oligocene transition and not at the K-T boundary (Krug *et al.* 2009, Clarke & Crame 2010). Interestingly, the same holds true for Arctic marine fauna (Krug *et al.* 2009). The effect of the K-T crisis on Antarctic marine diversity is still uncertain, although it might have had an effect on cosmopolitan and shallow-water benthic fauna (Clarke & Crame 2010). Overall, the K-T event led to a reduction of the Antarctic diversity in the Paleocene, but was compensated by the diversification of new taxa, among which neogastropods, penguins, and notothenioid fish (Clarke & Crame 2010).

The effect of the K-T boundary crisis on Antarctic marine fauna was best documented within the molluscs, which have a relative 'rich' fossil record compared to other phyla (Stilwell 2003, Linse *et al.* 2006, Clarke & Crame 2010). Of 26 late Cretaceous molluscan genera, only nine persisted into the Cenozoic. The mollusc fauna shows a transition from Cretaceous habitats dominated by ammonites, suspension-feeding bivalves, and hyoliths towards Cenozoic habitats with dominant carnivorous gastropods with planktotrophic development. Today, only one extant molluscan genus, the deposit-feeder bivalve *Malletia*, is known to have occurred in Antarctica since the Cretaceous and survived the K-T boundary crisis, whereas six genera and 13 families of bivalves originated in the early Cenozoic are still extant (Stilwell 2003, Linse *et al.* 2006).

## 5.2. Climate cooling and glacial cycles

Climate trends, rhythms, and events of the Cenozoic led to the replacement of Antarctic fauna, from sub-tropical cosmopolitan taxa with high taxonomic diversity to polar, taxonomically more restricted and endemic fauna (Eastman & McCune 2000). It is at the Eocene-Oligocene boundary (ca. 34 Ma) that a major climate cooling event, including the onset of continental glaciation in East Antarctica, impacted the most marine life, therefore triggering the regional (Antarctic) extinction and near-extinction of many marine groups such as large-bodied penguins, some decapods, stomatopods, balaniform barnacles, teleost fish, neoselachians, derived bivalve clades, clypeasteroid and cassiduloid echinoids (Table 1). Extinction was selective and affected those marine groups that could not adapt to new conditions, like durophagous predators (decapods, neoselachians, and teleost fish), for diverse physiological (e.g. regulation capacities in the cold) and ecological (e.g. reproductive strategies) reasons (Brandt 2005). However, there is no simple link between temperature decline and demise of those taxa. Hence, decapods are rare after the Eocene, but homolodromiid crabs are common in the Miocene Cape Melville Formation (Crame 1999). The same holds true for the bivalves of the *Chlamys* group that became extinct in the Pleistocene, albeit formerly present during the Cenozoic including glacial periods. Other factors, such as the availability of suitable habitats and quality of food resources would have been important as well.

It is not until the Miocene (ca. 23 Ma) that transient glaciations strongly impacted benthic communities due to changes in trophic conditions (drop in primary productivity) and habitat destruction and fragmentation, leading to the extinction of some species with small population sizes (Clarke & Crame 2010). This is especially the case for taxa now adapted to temperate waters (e.g. mytilids, ostreids, struthiolariids in molluscs) (Clarke & Crame 1992, Linse *et al.* 2006). The initial expansion of icesheets in East (14-12 Ma) and West Antarctica (8-5 Ma), then the orbitally-forced cycles of icesheet extension and contraction on Milankovitch frequencies (including the Last Glacial Maximum) led to the regional extinction of shallow marine taxa possibly due to the transient unaccessibility of their habitats (e.g. macroalgae, barnacles, mussels, limpets) and taxa with planktotrophic larvae due to reduced primary production (Pearse *et al.* 2009).

One may expect that a benthic fauna could not have survived these glacial cycles with their repeated grounding ice-sheet conditions on the continental shelf area (Eastman & McCune 2000, Thatje *et al.* 2005, Brandt *et al.* 2007a). However, the existence of lineages that extend back to the Cretaceous attests that some shallow-water benthic organisms survived glacial maxima (Clarke & Crame 2010). Of the five shallow water fossil species known from the Pliocene deposits of Cockburn island, three of them are still extant today, namely *Nacella concinna*, *Adamussium colbecki* and *Laternula elliptica*.

## 6. Dispersal

Dispersal processes form part of many scenarios that seek to explain present-day biogeographic patterns in the Southern Ocean (Sanmartin & Ronquist 2004, de Queiroz 2005, McGlone 2005). This can arise from many molecular-based estimates of divergence times between clades that post-date the age of the Gondwana final break-up so that vicariance alone cannot account for all allopatric speciation events. Recent molecular and ecological studies also have highlighted the importance of dispersal factors for promoting the wide distribution range of benthic invertebrates with limited dispersal capabilities like bryozoans (Barnes & Griffiths 2008), isopods (Brandt *et al.* 2009), and gastropods (Aldea *et al.* 2008). Taxonomic affinities between the Antarctic shelf, slope, and deep-sea faunas as well as between some Antarctic and sub-Antarctic faunas also point out the importance of migration events out of the Antarctic towards northern and deeper ocean areas (Table 1). Considering the profusion of speculative narratives in which dispersal processes have been invoked, some authors have stressed the need to test the robustness of dispersal hypotheses (Pearse *et al.* 2009, Crisp *et al.* 2011, Gillespie *et al.* 2012). Our increasing knowledge of the tectonic and oceanographic history of the Southern Ocean (e.g. Lawver & Gahagan 2003, Scher & Martin 2006, Lawver *et al.* 2011, Dalziel *et al.* 2013) now allows to test dispersal and vicariance hypotheses independently by relating ecological characteristics (i.e. dispersal and settling capabilities) and phylogenies to tectonic and oceanographical data, present and past (e.g. Pearse *et al.* 2009). The accumulation of congruent data across various taxonomic groups has increasingly supported the reliability of dispersal hypotheses, so that they should no longer be considered as secondary to vicariant hypotheses (Sanmartin & Ronquist 2004).

### 6.1. Dispersal vectors

In the Southern Ocean, dispersal vectors are represented by surface and deep-sea currents, which alternatively promote or limit dispersal in certain directions. The onset of currents, their variations in intensity and direction have deeply influenced the evolution of Antarctic marine life (Table 1).

For at least 14 Ma, the eastwards flowing Antarctic Circumpolar Current (ACC) and the nearshore westwards flowing Coastal Current have been the major dispersal vectors around the Antarctic continent including sub-Antarctic areas for the ACC (Dalziel *et al.* 2013). There is now a wide body of evidence (molecular, ecological, and oceanographic) that shows that the ACC in particular has had a major role in the long-distance dispersal of marine organisms throughout the waters of the Southern Ocean (Bargelloni



*et al.* 2000). Depending on the taxa (brooders versus broadcasters) and taxonomic levels analyzed, the ACC has promoted either allopatric speciation and diversification (Pearse *et al.* 2009) or long-distance connectivity between populations (Janosik *et al.* 2011) or closely related species (Barnes & Griffiths 2008, Waters 2008, Leese *et al.* 2010) in various invertebrates (e.g. echinoderms, bryozoans, nemerteans, crustaceans). The Antarctic coastal current may also be of some importance for explaining faunal similarities around Antarctica (Linse *et al.* 2006).

The northward movement of Antarctic deep waters, such as the Antarctic Bottom Water, may serve as a connection between deep waters of the Southern Ocean and those from other deep-sea basins across and below the Antarctic Polar Front (Brandt *et al.* 2007b, Barboza *et al.* 2011). For instance, Munnopsidae (Isopoda) are hypothesised to have dispersed to more northern Atlantic areas through the deep waters of the Weddell Sea (Malyutina & Brandt 2007). This also may have been the case for foraminiferans, polychaetes, and hexactinellids as well, whereas Antarctic isopods, ostracods, and nematodes are distinct from faunas in other oceans (Brandt *et al.* 2007a). A portion of Antarctic circumpolar deep waters flows northwards from the Antarctic Peninsula and joins the Malvinas Current. This deep current might have promoted the migration of Antarctic species (e.g. within the ascidian genus *Bathypeva*, crinoid *Florometra*, ophiuroid *Ophiacantha*, and cidaroid *Aporocidaris*) into the deep-sea and more northern areas (Barboza *et al.* 2011). The reverse direction of dispersal may be true as well. Hence, a water mass flows southward below the northern branch of Antarctic circumpolar deep waters from the Malvinas Current towards Antarctica (Barboza *et al.* 2011). Moreover, the low intensity of Antarctic Deep Waters during interglacial periods may have facilitated immigration from lower latitudes to the Southern Ocean (Brandt 2005).

Faunal affinities between now remote regions of the Antarctic shelf have already been reported for molluscs between the Ross Sea and the Weddell Sea (Linse *et al.* 2006, Brandt *et al.* 2007b, Barnes & Hillenbrand 2010) and for echinoids between the Weddell Sea and the Amundsen-Bellinghousen Seas (Pierrat *et al.* 2013). This may have been related to the existence of past trans-Antarctic sea-ways that used to extend between these areas across West Antarctic microcontinental blocks (Lawver & Gahagan 2003, Linse *et al.* 2006). They persisted prior to the outset of glaciations until the Oligocene, maybe mid-Miocene, and reopened during the Pliocene as the result of the collapse of the west Antarctic ice sheet (Pollard & DeConto 2009).

Eddies may have also contributed to the dispersal of propagules across barriers. For example, the eddy field observed in the southern southwest Atlantic (Scotia Arc region) has been invoked to explain transportation across and along the ACC between the Magellanic region and southern areas (Glorioso *et al.* 2005).

Benthic storms were also invoked as possible vectors of dispersal by resuspension of propagules, which might then be passively dispersed by bottom currents. This process was proposed for explaining the wide distribution range of deep-sea copepods (Gheerardyn & Veit-Köhler 2009).

## 6.2. Biogeographic barriers

The Antarctic Polar Front (APF) represents the main biogeographic barrier for the dispersal of surface organisms, especially planktonic larvae (Barboza *et al.* 2011). Due to abrupt salinity and temperature variations between the two sides of the APF as well as high seasonality in primary productivity to the south, this barrier is considered to limit immigration of faunas from low latitudes and from the rich Eastern hemisphere towards the Southern Ocean (Griffiths *et al.* 2009). The congruence between biogeographic discontinuities and the position of the APF was observed for various taxa including pycnogonids (Griffiths *et al.* 2010), Limidae (Page & Linse 2002), brooding ophiuroids, nemerteans, and gastropods (Linse *et al.* 2006). It is a transient barrier though. The permeability of the APF on recent time scales was evidenced by faunal connectivity across the Drake Passage, the Scotia Arc acting either as a gateway or a filter and sub-Antarctic down-currents as dispersal vectors (Griffiths *et al.* 2009). However the APF permeability is species-specific (e.g. *Odontaster meridionalis* and *Sterechinus antarcticus* that have both planktonic larvae are distributed on both sides of the APF) and influenced by respective clade history, development (duration of larval stage), thermal (physiological constraints) and ecological (biotic interactions) tolerances (Janosik *et al.* 2011, Díaz *et al.* 2011).

South of the APF, the Scotia-Weddell confluence may constitute a secondary barrier to dispersal. It might be the cause of reduced faunal exchanges between the Weddell Sea and the Antarctic Peninsula. This barrier has been associated with recent differentiation between populations of the two regions in krill and nemerteans and even to allopatric speciation within channichthyid fish (Patarnello *et al.* 2011).

Both hydrographic and geographic barriers to dispersal have been also reported in the Antarctic deep sea. The Circumpolar Deep Water constitutes a hydrographic barrier to the connection between the Southern Ocean deep sea and other ocean basins, limiting latitudinal dispersal of deep-sea species (Brandt *et al.* 2007b). In the deep-sea Scotia Arc area, the South Scotia Ridge was interpreted as a geographic barrier to the dispersal of deep-sea copepods, which are otherwise widely distributed in deep ocean basins (Gheerardyn & Veit-Köhler 2009).

## 6.3. Long-distance dispersal

Long-distance or jump-dispersal has long been proposed as the default explanation when vicariance was not supported by the existence of a congruence between palaeogeography and clade history (Crisp *et al.* 2011). The historical context of long-distance dispersal is difficult to assess when successful. Usually thought to correspond to infrequent and stochastic events, leading to random speciation, it has long been considered unpredictable and therefore non-testable (Lomolino *et al.* 2005, Crisp *et al.* 2011). When successful, long-distance dispersal is promoted by hydrographic conditions (e.g. ACC, eddies or benthic storms as dispersal vectors) but also requires certain ecological situations. Propagules, either at the larval stage or as adults have to (1) withstand potentially unfavorable conditions during the dispersal process (lecithotrophic larvae can survive for very long periods in cold water around Antarctica and the deep sea, promoting long-distance dispersal; see Young *et al.* 1997); (2) withstand physical and biological stresses of the environment being colonized, which would favor species coming from disturbed or fluctuating environments; (3) find suitable habitats to settle upon arrival into the area being colonized, which implies suitable cues and mechanisms of habitat selection for the metamorphosis of larvae; and (4) establish viable colonies, which implies the existence of appropriate reproductive strategies and dispersal of propagules in flocks (Lomolino *et al.* 2005).

Despite all these ecological and hydrographic requirements, an increasing number of studies highlight the importance of long-distance dispersal to account for disjointed distribution patterns of benthic species, or clades of closely-related species in geographically distant areas of the Southern Ocean (O'Hara 1998, Waters 2008, Leese *et al.* 2010, Fraser *et al.* 2012, Gillespie *et al.* 2012, Pierrat *et al.* 2013). Several studies stress in particular the role played by indirect processes (e.g. by kelp or ice rafting) for dispersal of strictly benthic species with no planktonic larvae (Macaya & Zuccarello 2010, Nikula *et al.* 2010, Fraser *et al.* 2011). For instance, long-distance dispersal by passive rafting has been postulated to explain trans-oceanic affinities among strictly benthic isopods of South Georgia, Marion, and Bouvet Islands (Leese *et al.* 2010). Transient events of long-distance dispersal were proposed also to explain faunal affinities between Patagonian and New-Zealand molluscs and echinoids under cold periods and cycles of ACC intensification (Table 1) at the Oligocene-Miocene boundary, Miocene-Pliocene boundary, and during the Pleistocene (Beu *et al.* 1997, Crame 1999, Saucède *et al.* 2013). Finally, associated to subsequent allopatric speciation events, long-distance dispersal might partly account for the increasing richness in brooding species to the east of the Scotia Arc region, downstream of the ACC (Pearse *et al.* 2009).

## 6.4. Range expansion

The wide circumpolar distribution of many species (e.g. penguins, echinoderms, molluscs, bryozoans, pycnogonids, and ascidians) is a striking feature of Antarctic biogeography (Aldea *et al.* 2008, Barnes & Griffiths 2008, Brandt *et al.* 2009). Among them many are benthic invertebrates with limited dispersal capabilities (e.g. bryozoans, isopods and gastropods). Several studies have proposed the partition of the Antarctic shelf into distinct provinces or bioregions based on occurrence data across various taxa (Ekman 1953, Hedgpeth 1969, 1970, Clarke *et al.* 2007). Others, among which the most recent ones, attributed this former biogeographic partition of the high Antarctic to undersampling biases and stressed the circumpolar integrity of biogeographic patterns across taxa, and for the least the absence of clear-cut common boundaries (e.g. Dell 1972, Clarke 2008, Griffiths *et al.* 2009). If confirmed, this overall circumpolar distribution implies that range expansion of taxa with limited dispersal capabilities would have been favored by active dispersal vectors, namely the ACC and Antarctic coastal currents.

## 6.5. Migration and the importance of the deep sea

During the Pliocene, it has been hypothesised that cycles of icesheet extension and contraction on Milankovitch frequencies have had a major role in fragmenting species distribution ranges, leading to both extinction and speciation events (Clarke & Crame 1989, 1992, Pearse *et al.* 2009). The occurrence of taxa already present before the outset of glaciation argues against complete eradication of shelf fauna during glacial maxima. Benthic assemblages might have survived under floating ice-shelves (Littlepage & Pearse 1962, Heywood & Light 1975, Lipps *et al.* 1979, Riddle *et al.* 2007), but the migration of shelf faunas to refuges, either to sub-Antarctic islands, the Scotia Arc region and northern Antarctic Peninsula, as proposed by Griffiths *et al.* (2011) for pycnogonids, or to oceanic ridges (O'Hara *et al.* 2013) and the continental slope, as suggested by the wide bathymetric range of many benthic invertebrates (e.g. foraminiferans, nematodes, isopods, ostracods, polychaetes) and pressure tolerance of certain larvae (Brandt *et al.* 2007a, 2007b, Clarke & Crame 2010) was proposed as an alternative. This shift in bathymetric distribution might have been facilitated by (1) the low range of temperature variation of Antarctic waters with depth for recent periods of time at least, (2) the relatively deep extension of nearshore Antarctic waters as compared with other shelf areas of the world's ocean and (3) water masses that sink from the Antarctic shelf to deep areas (Gutt 1991, Brey *et al.* 1996, Brandt *et al.* 2007, Clarke 2008, Clarke & Crame 2010). However, the occurrence of stenobathic species in Antarctic ostracods (Brandão *et al.* 2010), isopods (Brandt *et al.* 2009), and gastropods (Aldea *et al.* 2008) implies a much more complex response of species during periods of icesheet extension.



At larger time scale, based on taxonomic affinities between the Antarctic shelf, slope and deep-sea faunas, it was proposed that some isopod families might have originated on the continental shelves of Gondwana then have migrated to the deep-sea (submergence scenario), while others might have moved from the deep sea onto the Antarctic shelf (emergence scenario) (Knox & Lowry 1977, Brandt 1992). The northward movement of deep water formed in the Weddell Sea might have promoted faunal connections between the Southern Ocean and other ocean-basins, as evidenced in foraminiferans, polychaetes, hexactinellids, whereas Antarctic isopods, ostracods, and nematodes show strong contrasts with faunas of other ocean basins (Brandt *et al.* 2007a). This could be due to respective (1) dispersal capabilities, isopods are brooders, whereas foraminiferans easily dispersed as propagules or larvae, and polychaetes as free-swimming trochophorae, as well as (2) physiological plasticity to important temperature and pressure changes (Brandt *et al.* 2007b).

Taxonomic affinities between the Antarctic continental shelf fauna and faunas of the Scotia Arc region and southern South America have been interpreted as the result of immigration from southernmost America along the Scotia Arc region (Hedgpeth 1970, Knox & Lowry 1977, Clarke & Crame 2010). Some taxa originated in the Southern Ocean might have also migrated along the Scotia Arc in the reverse direction that is northward, out of the Antarctic (Clarke 2008). Deep ocean basins of the Drake Passage and islands of the Scotia Arc combined with circulation patterns may have enabled faunal exchanges of eurybathic species and account for connectivity between southern South America and the Antarctic Peninsula, as shown in echinoderm species (Barboza *et al.* 2011). Díaz *et al.* (2011) also proposed an evolutionary pathway (secular migration with evolution) between shallow areas of the sub-Antarctic zone to deep-sea areas of the Antarctic via the Scotia Arc region. Finally, migration routes from Antarctica to southern South America via the deep sea (Clarke *et al.* 2005, Thatje *et al.* 2005, Barboza *et al.* 2011) or the Scotia Arc (Clarke 2008) seems to have occurred as well during glacial maxima of the Neogene (Table 1).

The existence of faunal affinities between deep-sea hexactinellids of the Southern Ocean and those from other ocean basins, including the Arctic (*e.g.* *Caulophacus*) could result from the ancient colonization of the deep sea from shelf areas in the early Cenozoic after the group radiated and diversified (Brandt *et al.* 2007a). Such an evolutionary scenario has been proposed for other marine taxa that colonized the deep sea at about the same time-period, such as holasteroid echinoids in the late Cretaceous and early Cenozoic (Solovjev 1974, David 1988, Saucède *et al.* 2004, Smith 2004, Smith & Stockley 2005).

## 7. Concluding remarks

The relationship between the timing of geodynamic events and evolution of clades highlights the close links that tie Antarctic biogeographic processes to the geographic, climatic and oceanographic history of the Southern Ocean (Table 1). In the Cenozoic, periods of high extinction rates corresponded to the phases of accelerated climate cooling and intense glaciation (ecosystem destabilization and habitat diversity loss) combined with increased Antarctic isolation (limited immigration from northern areas) (Krug *et al.* 2009). Speciation rates might have been enhanced by cycles of repeated icesheet advances and retreats over the continental shelf (ACS and diversity pump hypotheses) and variations in ACC intensity and expansions (ACC hypothesis) (Pearse *et al.* 2009, Patarnello *et al.* 2011). The evolution of Antarctic climate has both triggered extinction and stimulated speciation and diversification (Lomolino *et al.* 2005, Linse *et al.* 2006, Briggs 2007). The long-term isolation of Antarctic biota coupled with the geodynamic history of the Southern Ocean has resulted in the emergence of unique biogeographic patterns and original faunas that are readily distinguishable from the Arctic fauna.

A good knowledge of Earth dynamics including the timing of major geodynamic events that have affected the Southern Ocean is crucial to assess the reliability of biogeographic hypotheses and test the congruence between Earth history and biogeographic events (Pearse *et al.* 2009, Crisp *et al.* 2011, Gillespie *et al.* 2012). Table 1 gives a broad overview of the timing, duration, intensity, and rhythmicity of geodynamic processes along with major biogeographic events and resulting patterns. The achievement of biogeographic patterns has been strongly influenced by the chronology of biogeographic and geodynamic processes. Hence, Linse *et al.* (2006) interpreted differences in biogeographic patterns between bivalves and gastropods in part as the consequence of different timings in range expansion. They occurred under contrasted hydrographic conditions (*i.e.* permeability of the APF) and has resulted in different levels of endemism around Prince Edward and Kerguelen Islands. The duration and rhythmicity of geodynamic processes has to be considered as well, as biogeographic processes may extend over a wide variety of temporal scales, ranging from millions (*e.g.* emergence and submergence hypotheses) to thousands of years (*e.g.* downslope-shelf migrations on Milankovitch orbital cycle frequency) (Clarke 2008). On a Cenozoic time-scale, outcomes of the Gondwana's final breakup led to the isolation of Antarctic waters and overall limitation of dispersal out and into the Southern Ocean (Barnes *et al.* 2006). Yet, on a Quaternary time-scale, immigration into the Southern Ocean can be more precisely constrained in time and dated to periods of interglacial minima that represent only about 10% of the time elapsed since the last 430 ky (Barnes *et al.* 2006). Biogeographic interpretations should also take into account the rhythmicity of geodynamic processes (Gheerardyn & Veit-Köhler 2009). Long-term effects of geodynamic

processes such as Antarctic isolation due to plate tectonics, climate cooling, and circumpolar ocean circulation that intensified progressively during the Cenozoic would differ from the impact of time-limited events such as the K-T biological crisis or climate cooling at the Eocene-Oligocene boundary. They would also differ from recurrent environmental changes such as cycles of habitat fragmentation and destruction due to glaciations during the Pliocene or variations in intensity of oceanic circulation during the Neogene (Table 1).

Certain sectors of the Southern Ocean and events of the Antarctic history are still insufficiently known to allow testing the reliability of biogeographic hypotheses. Uncertainties partly depend on the quality and availability of palaeontological, molecular, sedimentologic, tectonic, and geochemical data. For instance, the sparse Antarctic fossil record results in speciation, extinction and migration events being poorly dated and chronograms inadequately constrained (Brandt 2005, Krug *et al.* 2010). Likewise, the history of glaciations in Antarctica is not known in detail enough to assess their precise impact on Antarctic marine faunas (Clarke & Crame 2010). If the timing of the tectonic split between Antarctica and the South Tasman Rise is relatively well-established today, the isolation of Antarctica from southern South America is far less constrained (Lawver & Gahagan 2003, Scher 2006, Rogers 2007, Lawver *et al.* 2011). The opening of the Drake Passage is currently dated from about the same time-period as the onset of the ACC, major cooling event, and glaciation of the Eocene-Oligocene boundary. However, the age of the full-establishment of deep waters between the Antarctic Peninsula and southern South America seems to have been over-estimated according to a recent study (Dalziel *et al.* 2013). This should help testing more precisely the congruence between clade divergence time estimates and the age of biogeographic isolation.

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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



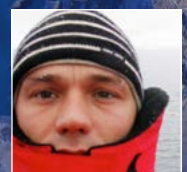
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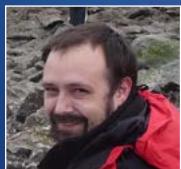
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