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BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 5.26. ECHINOIDS.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.26. Echinoids

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1. Introduction

Eighty-two species of echinoids occur south of the Polar Front according to recent reviews (David *et al.* 2005a, Pierrat *et al.* 2012b). Most of these species are endemic to the Southern Ocean (ca. 68%). Although the Echinoidea has low species richness in the Southern Ocean compared to such other classes as the Gastropoda, Bivalvia, Malacostraca, Stenolaemata, and Gymnolaemata (Linse *et al.* 2006, Clarke *et al.* 2007, Griffiths *et al.* 2009), Antarctic echinoids still represent nearly 10% of the known echinoid species worldwide. This makes the Southern Ocean an enriched region for echinoid diversity considering that the Southern Ocean is now known to have about 5% of Earth's marine diversity for about 8% of the world's ocean surface area (Zwally *et al.* 2002, Linse *et al.* 2006, Griffiths 2010, Ingels *et al.* 2012). The diversity of Antarctic echinoids is also evidenced by the latitudinal gradient in taxonomic richness that increases poleward in echinoids. This is opposite to the global poleward decreasing gradient of overall marine diversity (Crame 2004). This pattern is found in only a few invertebrate groups, including pycnogonids (Clarke 2008). Antarctic echinoids are distributed among nine families and seven orders. Most species (ca 65%) belong to the two families Cidaridae (21 sp.) and Schizasteridae (30 sp.), which are highly endemic to the Antarctic continental shelf (81% and 67% of species respectively) (David *et al.* 2005a).

Echinoids are widely distributed throughout the Southern Ocean, from the shallows of the continental shelf to deeper waters of the slope, and down to the abyssal plains (Arnaud *et al.* 1998, Barnes & Brockington 2003, David *et al.* 2005b, Brandt *et al.* 2007, Linse *et al.* 2008). They include epifaunal and endofaunal species that display various feeding strategies (omnivorous, deposit-feeding, carnivorous, or phytophagous/algivorous), spawning modes (broadcasting or brooding), and developmental strategies (indirect development including a larval stage or direct development). They belong to numerous ecological guilds and are prominent members of benthic communities. In addition, echinoids include a large number of species (cidaroids) that provide suitable microhabitats for a varied range of sessile organisms (Hétier *et al.* 2004, Linse *et al.* 2008, Hardy *et al.* 2010), and therefore play a major role as key species in benthic communities.

Although few Antarctic species are strictly stenobathic, depth is an important parameter in constraining the distribution of species at large scales (Brey & Gutt 1991, De Ridder *et al.* 1992, Jacob *et al.* 2003, David *et al.* 2005a). In addition, biotic factors of the water column (seasonality of primary and secondary production) and physical parameters (depth and co-varying factors, currents, sea ice cover, iceberg scouring, sea-floor morphology, and sediment characteristics) may determine the abundance, richness, or diversity of echinoid assemblages (Saiz *et al.* 2008, Moya *et al.* 2012). The co-varying and interrelated contributions of these parameters to echinoid distribution might differ according to the habitat (shallow waters, deep continental shelf, or abyssal plains) and to the scale of the analysis being performed (in time, space, and taxonomy) (Pierrat *et al.* 2012a).



Photo 1 *Sterechinus neumayeri* (Meissner, 1900), King George Island. Image © B. David, Université de Bourgogne.

2. Methods

2.1. Occurrence data

Echinoid occurrence data were compiled from the Antarctic Echinoid Database (David *et al.* 2005a), which registers samples collected during oceanographic cruises led in the Southern Ocean until 2003, updated with records of new field samplings made in Antarctica since 2003 and supplemented with records collected as far northward as 35°S latitude (Pierrat *et al.* 2012b). This augmented database holds a total of 6163 occurrence data entries.

In Hedgpeth's (1969) folio, five Antarctic biogeographic maps were provided, each map depicting species occurrence records of cidaroids and

of the four genera *Sterechinus*, *Pseudechinus*, *Abatus* and *Amphipneustes*, a different symbol being used for each species. A sixth map was provided showing occurrence records of southern temperate schizasterid species. Recent genetic studies reveal a significant discrepancy in several echinoid groups between taxonomy and phylogenies both at species and genus level (Dettai *et al.* 2011, Diaz *et al.* 2011). Therefore, one may expect that systematics of Antarctic echinoids experience significant changes in the coming decade. For instance, it is noteworthy that no cryptic species has ever been reported in Antarctic echinoids by contrast with many other marine groups (Dettai *et al.* 2011). The biogeographic maps provided herein show both occurrence records and predictive species distribution models (SDMs) constructed using a GIS (ArcGIS version 9.3) and MaxEnt (version 3.3.2) for assessing species distributions based on presence-only data and selected environmental parameters (for details see Dudik *et al.* 2004 and Phillips *et al.* 2006). The technique aims at evaluating the probability distribution of a species over the whole study area. Among the set of environmental data, ten variables assumed to be ecologically significant to echinoids were selected (Table 1). These variables were checked for pairwise Spearman correlations of less than 0.85. The evaluation of the model was based on 10-fold-cross-validation, and the predictive performance of the model was tested as its ability to predict a "test subsample" from a "training subsample". Maps were performed for seven echinoid species selected from among the best-known and most common ones. However, certain maps could prove partly out of date in the near future.

A first set of two maps is devoted to the genus *Sterechinus*, which was previously considered a cluster of five species with contrasting geographic and bathymetric ranges. Recent genetic results (Diaz *et al.* 2011) challenge this view and lead us to reconsider the genus as composed of only three taxonomic units: one mainly Antarctic and shallow-water, *S. neumayeri* (Meissner, 1900), another found in sub-Antarctic, Antarctic and southern temperate deep waters of outer continental shelves, *S. antarcticus* (Koehler, 1901), and the third one, *S. dentifer* (Koehler, 1926) that is known from a few deep-sea records. Due to the scarcity of specimens collected, the taxonomic status of the latter is still pending and its distribution could not be modeled. The two other *Sterechinus* species are broadcasters and true omnivores. They are able to feed on sediments and on a variety of food items, and also harbor an opportunistic transient digestive microflora (Pearse & Giese 1966, Bosh *et al.* 1987, Brey & Gutt 1991, Tyler *et al.* 2000). A second set of five maps is devoted to cidaroids, a common and relatively diverse group in terms of taxonomy (21 Antarctic and sub-Antarctic species), ecology (contrasting depth ranges), and morphology (various spine morphologies). Because their spines provide microhabitats for a wide diversity of sessile macro-organisms (sponges, bryozoans, foraminiferans, molluscs, hydrozoans and similar "fouling" or encrusting organisms), cidaroids can be considered 'key' contributors to local benthic diversity, the contribution exceeding their own richness and abundance values. The five selected cidaroid species are well enough known to allow distribution modeling. Three species of the genus *Ctenocidaris* were selected: *Ctenocidaris gigantea* (Clark, 1925), *Ctenocidaris nutrix* (Thomson, 1876) and *Ctenocidaris perrieri* (Koehler, 1912). They are geographically different, from high Antarctic (*C. gigantea*) to Antarctic and Sub-Antarctic (*C. perrieri* and *C. nutrix*), genetically well-differentiated (Lockhart 2006), and show disparate spine morphologies upon which symbiotic associations partly depend (Hétier *et al.* 2008, Linse *et al.* 2008, David *et al.* 2009, Hardy *et al.* 2010). Two species of the genus *Notocidaris* were selected, *Notocidaris mortenseni* (Koehler, 1900) and *Notocidaris platyacantha* (Clark, 1925), distinguished by smooth, flat to shoehorn-shaped primary spines. The two *Notocidaris* species differ in reproductive pattern - brooder versus non-brooder (Gutt *et al.* 2011) - and different distribution ranges, one being endemic to east Antarctica (*N. platyacantha*) while the other is known all around the continent (*N. mortenseni*).

2.2. Coverage area

The area considered in the present chapter extends from latitude 45°S to the Antarctic shoreline at a maximum of 77°S latitude. The area covers the entire Southern Ocean, including the Antarctic continental shelf and sub-Antarctic islands, as well as the southern tip of South America and the Campbell Plateau south of New-Zealand. This large-scale study encompasses contrasting oceanographic areas and depth ranges, going from true polar to cold-temperate conditions and from shallow to deep-sea environments.

Echinoid diversity is known from uneven sampling over this vast ocean area. While certain areas have long been regularly investigated: the Ross Sea, Campbell Plateau south of New Zealand, south-east Australia and Tasmania Adélie Land, Amery Basin, Weddell Sea, Antarctic Peninsula, Scotia Arc, and Tierra del Fuego, other areas such as the Bellingshausen and Amundsen Seas, the Enderby plain, or the South Indian Basin are still clearly under-sampled (Clarke *et al.* 2007, Saiz *et al.* 2008, Griffiths 2010, Moya *et al.* 2012) and constitute a limit to our knowledge of the Antarctic marine benthos (Gutt *et al.* 2004, Griffiths 2010, Ingels *et al.* 2012).

Table 1 Sources, value ranges and short description of the environmental parameters selected for generating SDM maps.

Environmental variables	Value ranges	Sources	Processing notes
Depth	0 m to 7958 m	ESRI © 2005	Global Digital Elevation Model (ETOPO 2) data set with 2 min resolution grid. Pixels above sea level set to « No Data ». Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Slope	0° to 5.69°	ESRI © 2005	Calculated with ArcGIS Spatial Analyst (ArcGIS procedure).
Sea ice coverage	0% to 100%	Spreen <i>et al.</i> 2008 http://iup.physik.unibremen.de:8084/amsredata/asi_daygrid_swath/11a/s6250/	Derived from AMSR-E satellite estimates of daily sea ice concentration at 6.25km resolution. Concentration data from 1-Jan-2003 to 31-Dec-2009 used. The fraction of time each pixel was covered by sea ice of at least 85 % concentration was calculated for each pixel in the original (polar stereographic) grid. Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Sea surface temperature (summer)	-1.83°C to 15.77°C	Feldman & McClain 2010 http://oceancolor.gsfc.nasa.gov/	Climatology spans the 2002/03 to 2009/10 austral summer seasons. Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Seafloor temperature	-2.26°C to 9.59°C	Clarke <i>et al.</i> 2009	Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Seafloor salinity	32.21 PSS to 34.89 PSS	National Oceanographic Data Center 2009 http://www.nodc.noaa.gov/OC5/WOA09/pr_woa09.html	Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Sea surface nitrogen oxides concentration (summer)	0.09 µmol l ⁻¹ to 34.85 µmol l ⁻¹	Oceanographic Data Center 2009 http://www.nodc.noaa.gov/OC5/WOA09/pr_woa09.html	Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Sea surface chlorophyll-a concentration	0 mg m ⁻³ to 16.79 mg m ⁻³	Feldman & McClain 2010 http://oceancolor.gsfc.nasa.gov/	Climatology spans the 2002/03 to 2009/10 austral summer seasons. Data interpolated from original resolution to 0.5-degree grid using « Spline with barrier » interpolation (ArcGIS procedure).
Granulometry	Clay, silt, sand / gravel, volcanic deposits	McCoy 1991 (modified by Griffiths 2007)	Derived from sediment types. Data interpolated from original resolution to 0.5-degree grid (ArcGIS procedure).
Biogenic component in sediment	Azooic, calcareous ooze, biosiliceous ooze McCoy 1991 (modified by Griffiths 2007)	McCoy 1991 (modified by Griffiths 2007)	Derived from sediment types. Data interpolated from original resolution to 0.5-degree grid (ArcGIS procedure).
Granulometry	Clay, silt, sand / gravel, volcanic deposits	McCoy 1991 (modified by Griffiths 2007)	Derived from sediment types. Data interpolated from original resolution to 0.5-degree grid (ArcGIS procedure).

3. Echinoid diversity

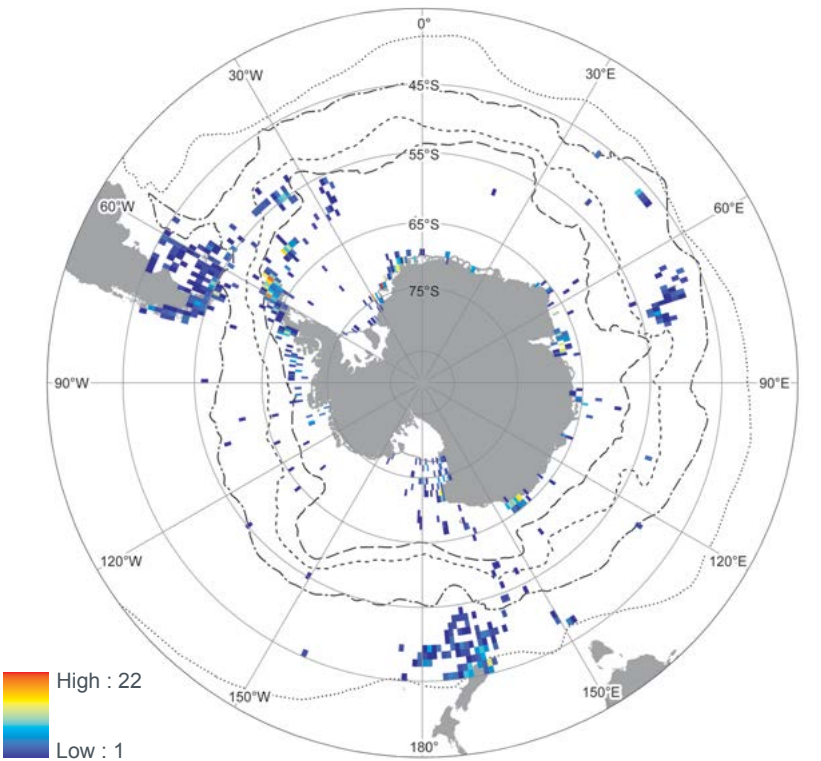
3.1. Richness pattern (Map 1)

Map 1 highlights sectors of high species richness over the Antarctic continental shelf as compared to South America and New Zealand and eastern sub-Antarctic islands (Kerguelen Archipelago, Crozet, etc.). The highest values are in the Antarctic Peninsula and southern Scotia Arc, in the eastern Weddell side and in the sectors of East Antarctica (Enderby Land and Adelie Land). However, the uneven sampling effort in the Southern Ocean (Griffith 2010) implies that richness patterns should be considered with caution, especially regarding potential centers of origin. Areas such as the Ross and Weddell Seas were cited as potential centers of origin and radiation for molluscs and pycnogonids (Linse *et al.* 2006, Griffiths *et al.* 2011). This does not seem to be the case for echinoids, especially in the Ross Sea. An outward-decreasing gradient of species richness from centers of origin toward adjacent areas is the first and most obvious criterion for identifying centers of origin. However, the age of taxa, dispersal tracks, phylogenetic relationships, genetic diversity, extinction rates, and speciation rates should be considered as well (Briggs 2004).

3.2. Latitudinal gradient (Fig. 1)

The echinoid species richness decreases from 45°S to 60°S latitude, it increases between 60°S and 70°S, and decreases again south of 70°S latitude (Fig. 1). This latitudinal gradient in echinoid richness does not match the global latitudinal gradient in taxonomic marine diversity that decreases continuously from the tropics to the poles (Crame 2004). The apparent mismatch between the two gradients could be due to the different scales at which gradients are considered, or regional characteristics such as Antarctic oceanography modulating the global decreasing gradient. Hence, the reversal of the richness trend south of 60°S latitude matches both the southern boundary of sub-Antarctic waters and the southernmost position of the Polar Front that constitutes an oceanographic barrier for many marine species. The increase in richness south of the Polar Front is much more significant at the species than at the genus level. The comparison of species and genus richness values shows that the number of echinoid species is less than twice the number of genera north of the Polar Front, while it is more than twice this number south of the Polar Front. Therefore, the Southern Ocean appears particularly enriched in echinoid species. However, this gradient in echinoid richness results from the averaging of longitudinal inequalities and regional peculiarities (Crame 2004)

so that there is a strong longitudinal inequality between the continental shelf of southern South America, where only 36 echinoid species and 23 genera are recorded and waters south of New Zealand and Australia in which 113 echinoid species and 62 genera were registered. If Antarctica appears as an enriched 'spot' in echinoid diversity, Australasia is definitely a hotspot (Barnes & Griffiths 2008). Finally, the decrease of echinoid richness south of 65°S latitude can be linked to the narrowing of ocean surfaces at such high latitudes, all the more as most of these areas are under-sampled.



Map 1 Distribution (one-degree grid cells) of echinoid species richness (in number of species).

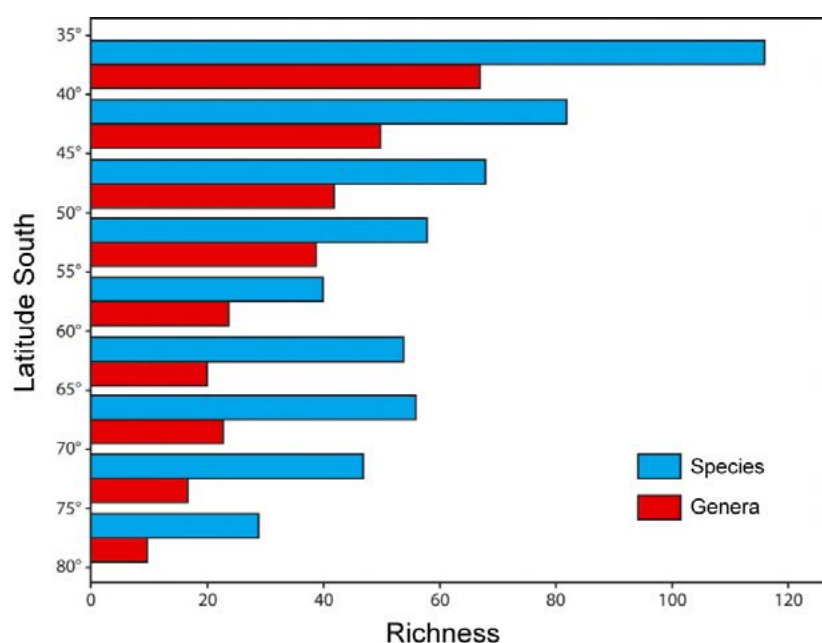


Figure 1 Overall latitudinal gradient of echinoid richness, in number of species (blue) and genera (red).

3.3. Depth gradient (Fig. 2)

Depth gradients in echinoid richness (Fig. 2) show that the highest number of species and genera occurs between 100 m and 1000 m depth. Then richness decreases to a minimum value just below 1500 m. The depth gradient clearly shows that the Antarctic continental shelf, which represents about 11% of continental shelf areas worldwide, encompasses the main part of echinoid richness, with that richness decreasing from the shelf break to the slope and deep-sea basins. Echinoid richness on the Antarctic shelf contrasts markedly with that of deep-sea areas in having a much higher number of species, the Antarctic shelf being inhabited by endemic and diversified echinoid taxa, mainly Ctenodidae and Schizasteridae. A weak increase in richness at approximately 3000 m depth can be explained by the wide ocean surfaces covered by deep-sea basins, in which a higher number of taxa might occur as compared to the relatively smaller surface of slope areas. However, deep-sea echinoids are still insufficiently known and exploration of deepest areas is still too cursory to assert that richness values might also reflect a true deep-sea diversity as suggested for other taxa (Brandt *et al.* 2007, Linse *et al.* 2007). Species and genus richness gradients are quite similar, although variations are less pronounced for genera.

4. Biogeographic patterns

4.1. Species latitudinal range (Fig. 3)

The simple survey of the latitudinal distribution range of the 126 echinoid species ever recorded south of 45°S latitude (Fig. 3) undoubtedly highlights the key role played by the Polar Front in echinoid distribution. Only fourteen species (i.e. 11%) have a wide latitudinal distribution that covers temperate to Antarctic waters. They extend on both sides of the sub-Antarctic area between 45° and 60°S wherein the position of the Polar Front fluctuates. Accordingly, 89% of species display restricted patterns attesting to the structuring of echinoid diversity along latitudinal belts.

Five main patterns can be identified. First, 28 species are distributed south of 60°S latitude and never reach the Polar Front. These can be regarded as “high Antarctic”. A second set encompasses 23 species that never pass the northern limit of the Polar Front (45°S), with most of them extending south of the Polar Front (60°S). These can be defined as “Antarctic and sub-Antarctic”. A third pattern corresponds to 20 species distributed between the northernmost and southernmost limits of the sub-Antarctic area (from 45°S to 60°S) and can be characterised as “true sub-Antarctic”. A fourth pattern is represented by the 14 “widespread” species with extended latitudinal ranges from high Antarctic to cold temperate regions. Finally, a fifth pattern is represented by 41 species that never extend south of 60°S, but extend farther north of 45°S and can be referred to as “cold temperate”.

4.2. Biogeographic zonation

Faunal similarities among bioregions initially defined by Hedgpeth (1969) were studied by Pierrat *et al.* (2013) both at species and genus level using a new non-hierarchical clustering method. Results suggest that echinoid faunas of the Southern Ocean (south of 45°S and less than 1000 m depth) are structured into three main faunal provinces: (1) south of New Zealand, (2) southern South America and sub-Antarctic islands and (3) high Antarctic.

Echinoid biogeographic patterns show a weak faunal similarity between New Zealand southern islands and the Ross Sea, so that New Zealand faunas mostly appear as particularly isolated from sub-Antarctic and Antarctic regions. This suggests that (1) there is no dispersal from sub-Antarctic islands towards New Zealand southern islands through the Antarctic Circumpolar Current (ACC), although the latter flows around the south of the Campbell Plateau, and that (2) the Polar Front may constitute a decisive biogeographical barrier to faunal exchanges between New Zealand southern islands and the Ross Sea (Bargelloni *et al.* 2000).

Bioregions of southern South America and sub-Antarctic islands tend to group into a unique province. Faunal affinities between sub-Antarctic and South American bioregions had already been reported for a wide range of taxonomic groups (Barnes & De Grave 2001, Montiel *et al.* 2005, Linse *et al.* 2006, Rodriguez *et al.* 2007, Griffiths *et al.* 2009) and have been interpreted as the result of larval dispersal through the ACC. This hypothesis is also supported by molecular analyses for echinoids with planktonic larvae (Diaz *et al.* 2011), although long-distance and either passive drafting (Leese *et al.* 2010) or active motion of echinoids without planktonic larvae cannot be excluded.

The grouping of Hedgpeth's Antarctic bioregions into one single circum-Antarctic province contrasts with previously adopted biogeographical schemes (Ekman 1953, Hedgpeth 1969) but agrees with most recent works (Barnes & De Grave 2001, Rodriguez *et al.* 2007, Griffiths *et al.* 2009, 2010). Finally, in echinoids, the Scotia Arc seems to constitute a preferred exchange way between sub-Antarctic and Antarctic provinces across the Drake Passage, as in other taxa (Bargelloni *et al.* 2000, Page & Linse 2002, Göbbeler & Klusmann-Kolb 2010, Diaz *et al.* 2011).

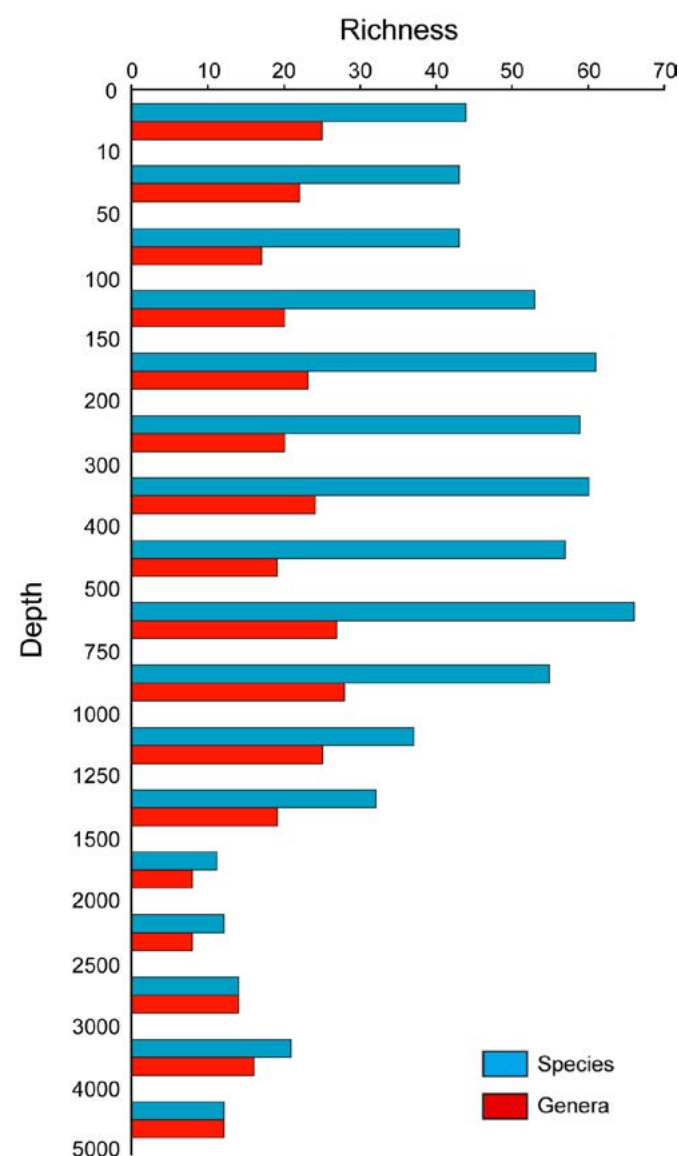


Figure 2 Overall depth gradient of echinoid richness, in number of species (blue) and genera (red).

4.3. Case-studies

The three chosen *Ctenodidae* species mainly differ in the extent of their respective latitudinal ranges (Fig. 3). *C. gigantea* has been mostly sampled in the Weddell Sea, the Antarctic Peninsula, the Ross Sea and Adélie Land (Map 2a). It is distributed from 77.15°S to 60.6°S, and is clearly a high Antarctic species with a mean latitude value of 70°S. Depth range varies from the shore to 2315 m, the species being mostly present between 200 and 500 m. According to the species distribution model (SDM) performed, the high Antarctic continental shelf corresponds to the species' most suitable habitat, with depth and sea surface temperature being the strongest contributing factors governing species distribution (Map 2b). *C. perrieri* has been sampled all around Antarctica up to Tierra del Fuego (but only a single specimen has been collected there) (Map 3a). It is both an Antarctic and sub-Antarctic species distributed from 77.5°S to 55.56°S latitude (Fig. 3), between 30 and 2468 m depth, but is mostly common between 150 and 750 m depth. According to the SDM (Map 3b), the high Antarctic shelf constitutes the species' most suitable area, whereas the sub-Antarctic area is just suitable. Depth is the only limiting factor of species distribution. *C. nutrix* has mostly been collected in the east Weddell Sea and on the Kerguelen Plateau (Map 4a). It is Antarctic and sub-Antarctic with a mean latitudinal range of 60°S, although it is recorded from 76.13°S to 47.5°S latitude (Fig. 3). It is present on the shelf between the shore and 650 m depth. According to the SDM (Map 4b), the sub-Antarctic area is

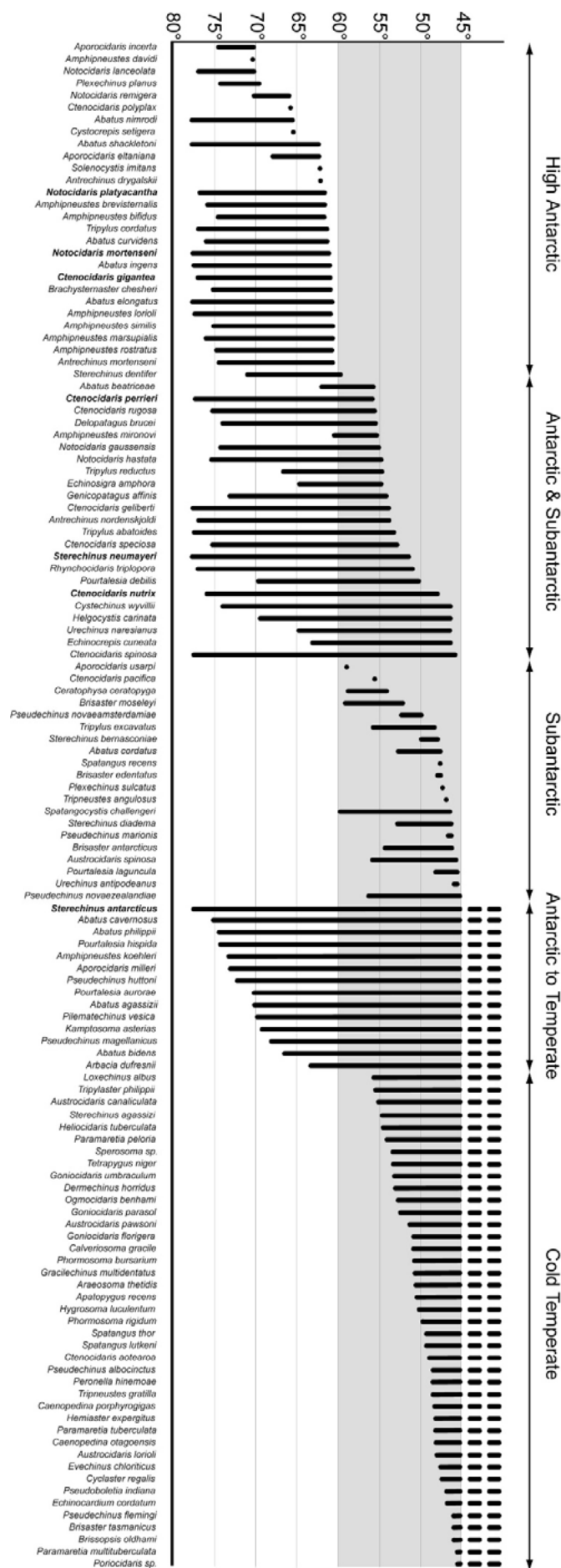


Figure 3 Latitudinal distribution range of the 126 echinoid species recorded south of 45°S latitude. Species rank ordered from left to right by decreasing both northernmost and southernmost latitudes. Dotted lines indicate distribution ranges that extend northward beyond 45°S latitude. Shaded grey corresponds to the sub-Antarctic area as delimited southward by the Polar Front and northward by the Sub-Tropical Front. The seven species selected for biogeographical maps and SDM are in bold.

the species' most suitable area, with high Antarctic and temperate regions being just suitable to the species distribution. Depth seems to be the only limiting factor.

Regarding the genus *Notocidaris*, *N. mortenseni* is recorded all around Antarctica on the continental shelf (Map 5a). It is a high Antarctic species (Fig. 3), distributed from 77.8° to 60.8°S between 100 and 1432 m depth, though mainly present between 200 and 750 m depth. According to the SDM (Map 5b), the species' most suitable area is Antarctic and sub-Antarctic, and mainly determined by depth. *N. platyacantha* is only known in high Antarctic regions (Fig. 3) to the East, between the Ross Sea and Enderby Land (Map 6a). It has been sampled from 77° to 61.42°S between 184 to 1233 m depth with a main occurrence between 200 and 750 m depth. According to the SDM (Map 6b), the species' most suitable area is restricted to the inner shelf area all around Antarctica (not just to the East) and limited by sea surface temperature and depth.

S. antarcticus is a very widespread species, recorded from 77.7° to 45.48°S (Fig. 3) from high Antarctica to cold temperate areas of southern South America (Map 7a). It has been sampled from the shore to 2043 m depth, but mainly occurs between 150 and 750 m depth. According to the SDM (Map 7b), the species' most suitable area goes from Antarctica to southern South America and is just limited by depth. *S. neumayeri* is geographically and bathymetrically more restricted, being known from 77.75° to 51.29°S latitude in Antarctic and sub-Antarctic regions (Fig. 3, Map 8a) between 3 and 916 m depth, but mainly between the shore and 500 m depth. According to the SDM (Map 8b), only Antarctic and sub-Antarctic areas are highly suitable to the species, which is limited by depth and sea ice cover.

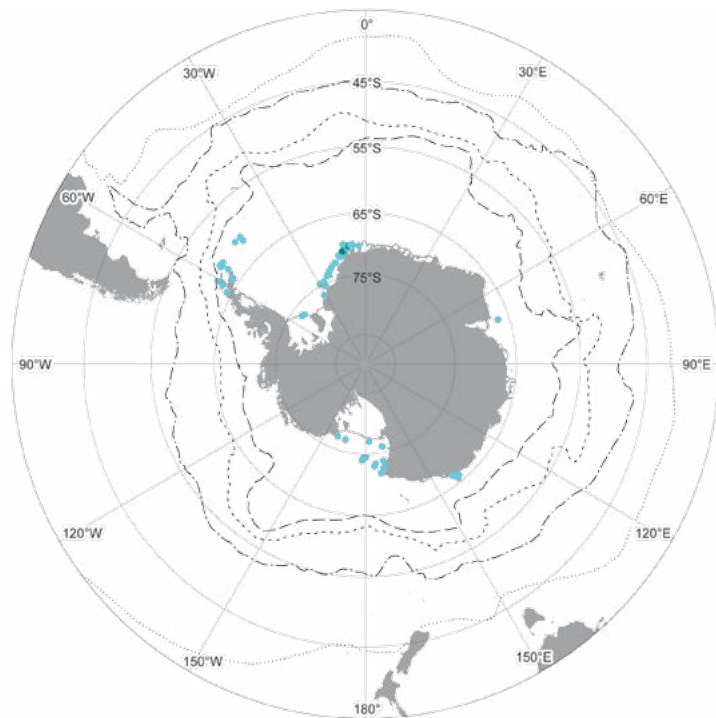
From comparison of these phylogenetically, ecologically, and biogeographically disparate species, it turns out that depth is the physical parameter that most contributes to species distribution models. Hence, sub-Antarctic species seem to have the most extended distribution areas that are chiefly controlled by depth (*C. nutrix* and *S. antarcticus*). Among the four species endemic to the Southern Ocean, *C. gigantea*, *C. perrieri*, *N. mortenseni*, and *N. platyacantha*, temperature tolerance seems to be the main factor that varies among species. As expected, the species that are spatially the least restricted, *N. mortenseni* and *C. perrieri*, are only limited by depth and either observed or predicted in sub-Antarctic regions, whereas sea surface temperature also controls the distribution of high Antarctic species. The two *Notocidaris* species illustrate the good match between the known ecology of species and modeled distributions. That is, *N. mortenseni* is more widely distributed than *N. platyacantha* and the SDM also modeled the species distribution in sub-Antarctic areas. This is consistent with species ecology, *N. mortenseni* being suspected to be a broadcaster (Gutt *et al.* 2011) and also known as a generalist carnivore (C. De Ridder pers. comm). Moreover, recent studies (Saucède 2008, Hardy *et al.* 2011) highlighted the species dispersal and colonization capabilities. Finally, sea ice cover only contributes to the distribution of the Antarctic and sub-Antarctic shallow-water species, *S. neumayeri*. This physical factor does not seem to be decisive for the distribution of the strictly high Antarctic species *C. gigantea*, *N. mortenseni*, and *N. platyacantha*, perhaps because they inhabit deeper waters of the Antarctic shelf.

5. Biogeographic processes

The existence of a unique Antarctic shelf province and continuous circum distribution of most Antarctic echinoid species can be interpreted as an outcome of the long influence of Antarctic surface currents, which might have limited both faunal ingressions from the north and promoted the dispersal of Antarctic species over the Antarctic continental shelf (Barnes & De Grave 2001, Griffiths *et al.* 2009, Pearse *et al.* 2009). In contrast, some studies have suggested that Antarctica could be split into an East and West Province in which different oceanographic conditions have prevailed in the past (Ekman 1953, Hedgpeth 1969, Clarke 1996, Linse *et al.* 2006). East Antarctica has been characterised by a relatively stable ice-sheet over time, whereas west Antarctica is considered to have been much more impacted by the alternation of glacial and interglacial pulses in the past (Clarke 1996). The occurrence of *N. platyacantha* in East Antarctica while present-day conditions are suitable to its presence all around the continent could be a legacy of the contrasting climatic history of Antarctica, favored by the species' limited dispersal capability.

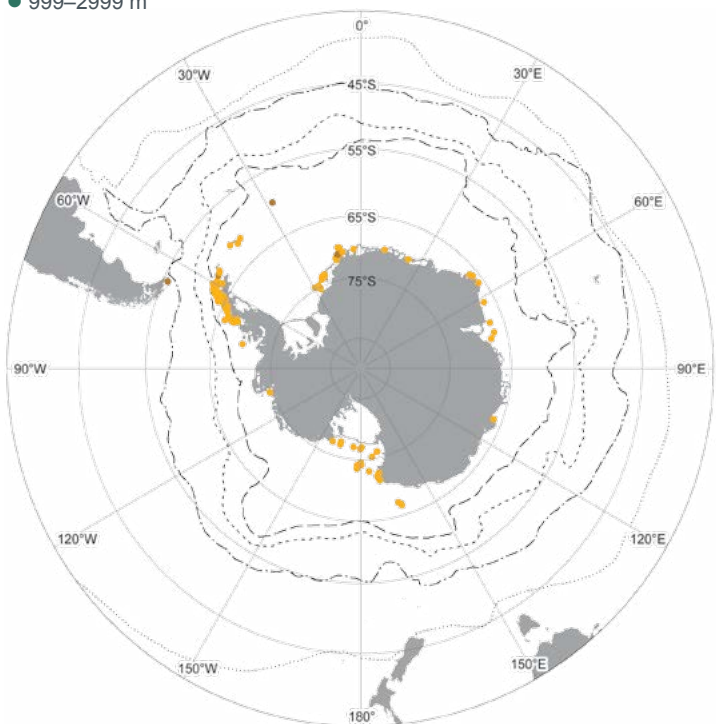
The historical legacy of Antarctica is also highlighted in a recent study on echinoid biogeography Pierrat *et al.* (2013), in which robust faunal affinities are shown between the Amundsen and Bellingshausen Seas and the Weddell Sea, although the two regions are now separated by the landmass and ice sheets of the Antarctic Peninsula. These trans-Peninsula affinities cannot be interpreted except by a long-term though recently vanished faunal connection between the two sides of the Antarctic Peninsula. This could be explained by the setting-up of trans-Antarctic sea-ways and surface currents between the two areas during the Pleistocene as a result of the west Antarctic ice sheet collapse (Pollard & De Conto 2009).

The legacy of the climatic history of Antarctica in biogeography has been also invoked to account for the affinities noticed between benthic species of the Antarctic shelf and deep-sea faunas that border this shelf. Two main scenarios were proposed to account for the putative evolutionary connection between the two faunas, based upon geological evidence that during glacial maxima, Antarctic ice-sheets were much more extended than they are today and used to cover most of the Antarctic shelf. According to the first scenario, shelf taxa were hypothesised to have moved down to deep waters to find refuges (submergence hypothesis) (Held 2000, Pawlowski *et al.* 2007, Strugnelli *et al.* 2008), while the second scenario postulates that deep-sea taxa colonised the continental shelf, promoted by the greater similarity between deep water and shallow water habitats at that time (emergence hypothesis) (Dayton & Oliver 1977, Berkman *et al.* 2004). Alternatively, Brandt *et al.* (2007) suggested that both hypotheses could account for faunal affinities between shelf and deep-sea faunas. There is no evidence to support either the emergence or the submergence hypothesis in echinoids. In contrast, Diaz *et al.* (2011) argued that phylogenetic relationships among *Stereochinus* species could be best explained by another history. Based on phylogenetic relationships and estimated divergence times between *Stereochinus* species, the authors showed that the Antarctic deep-sea echinoid *S. dentifer* is more closely related to the Antarctic and sub-Antarctic species *S. antarcticus* than to the shallow Antarctic species *S. neumayeri*. Thus for this genus neither the submergence



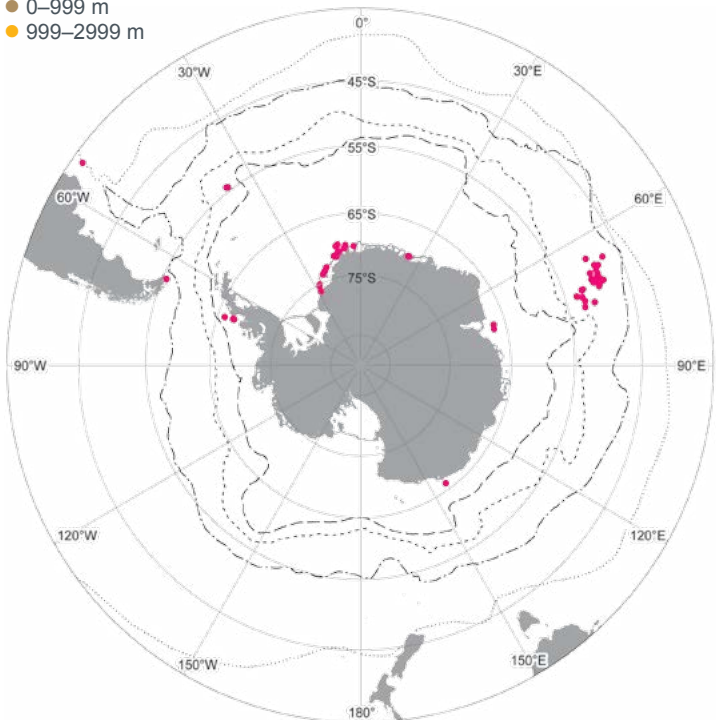
Map 2a *Ctenocidaris gigantea*

● 0–999 m
● 999–2999 m



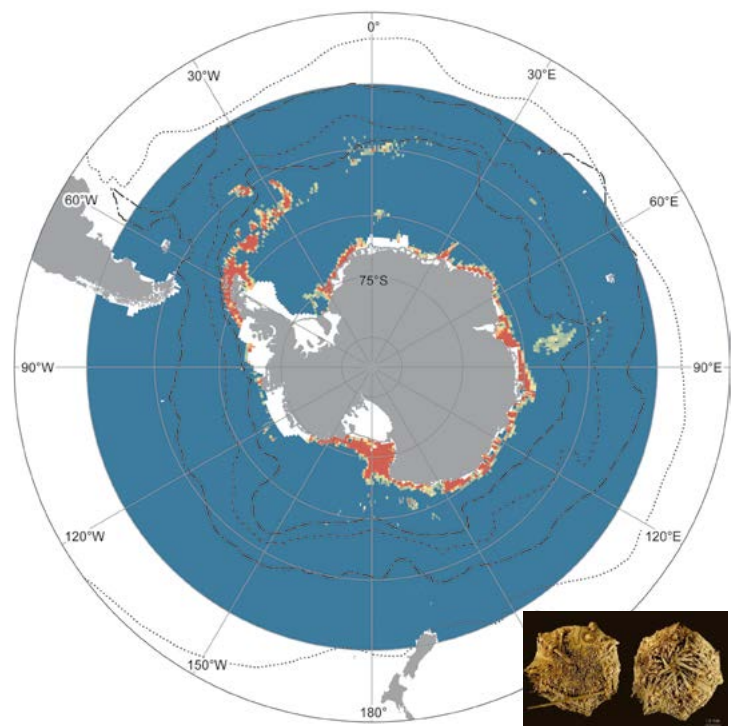
Map 3a *Ctenocidaris perrieri*

● 0–999 m
● 999–2999 m



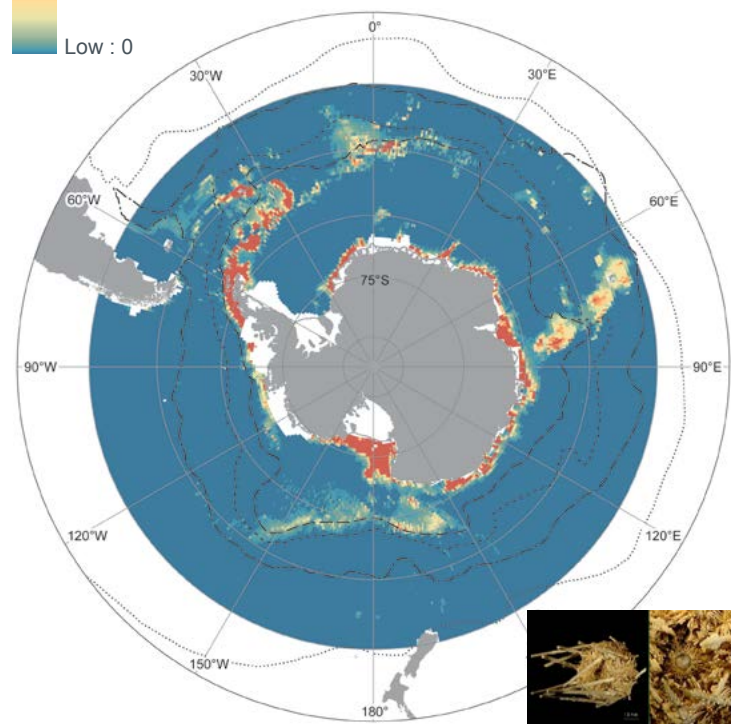
Map 4a *Ctenocidaris nutrix*

● 0–999 m



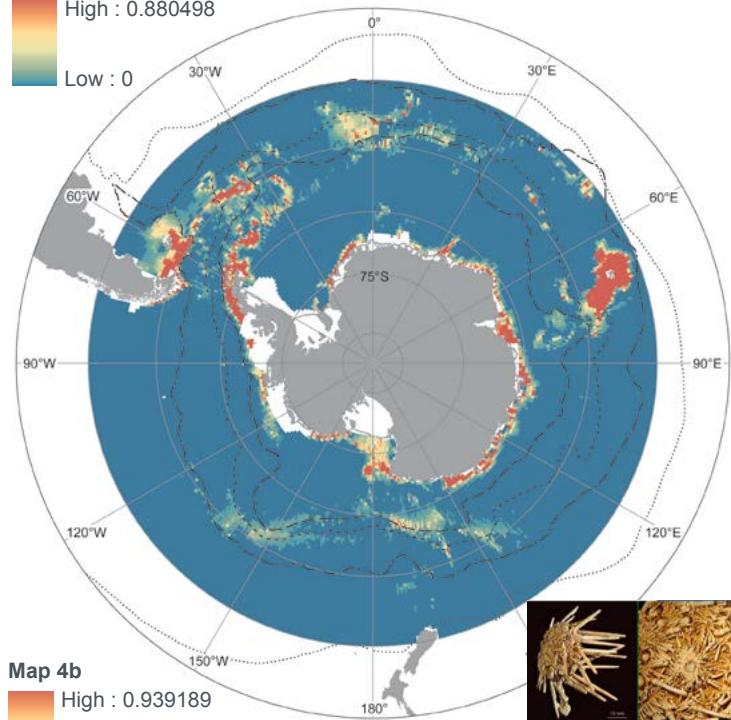
Map 2b

High : 0.916766
Low : 0



Map 3b

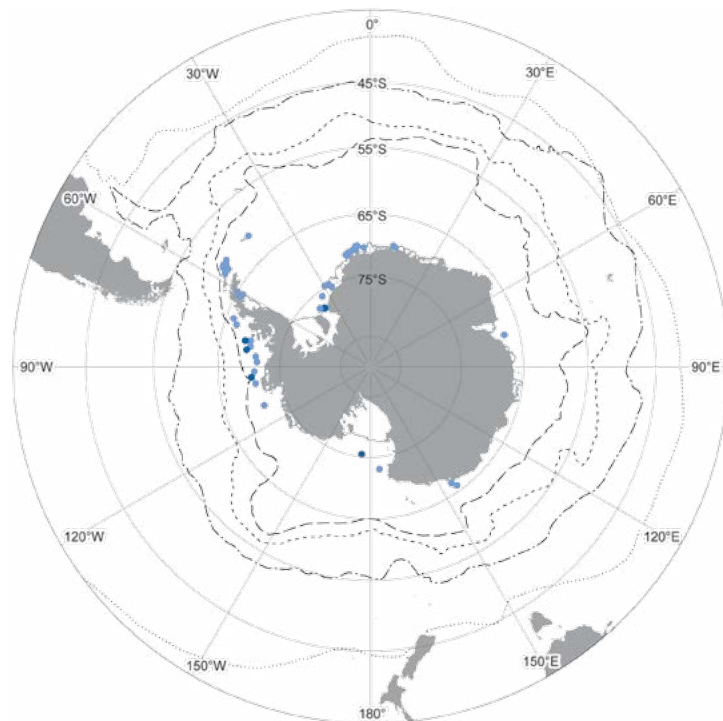
High : 0.880498
Low : 0



Map 4b

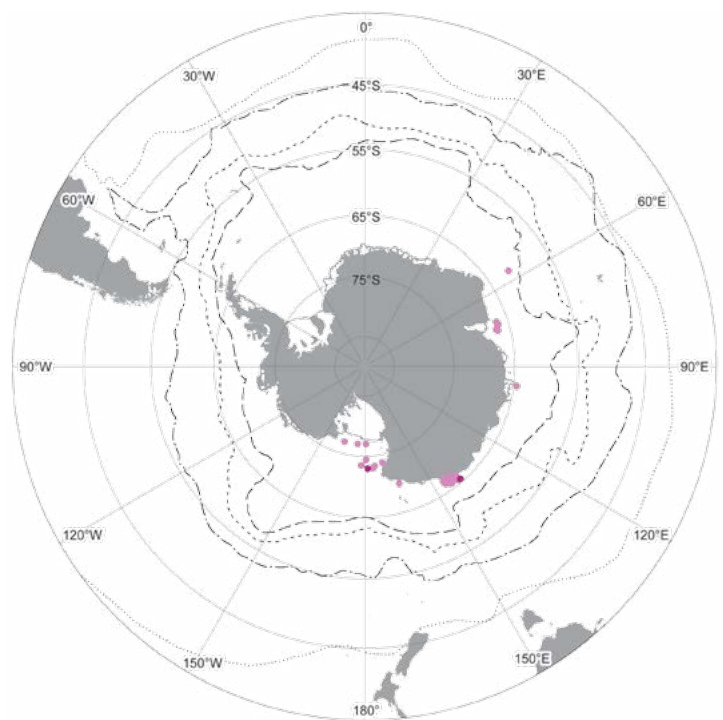
High : 0.939189
Low : 0

Echinoidea Maps 2–4 *Ctenocidaris* spp Species occurrence records (Maps 2a, 3a, 4a) and SDMs (Maps 2b, 3b, 4b) for the three species *Ctenocidaris gigantea*, *Ctenocidaris perrieri* and *Ctenocidaris nutrix* respectively. SDMs were generated using Maxent and including ten environmental parameters (Table 1). The “suitable area” (yellow pixels) encompasses all pixels for which probability is over the minimal probability value assigned to a true occurrence (100% of occurrence data are included in this area). The “highly suitable area” (red pixels) corresponds to a threshold that excludes the 5% of true occurrences that show the lowest probability values (95% of true occurrences are still included in this second area). Hatched areas correspond to areas where data are missing for at least one environmental parameters.



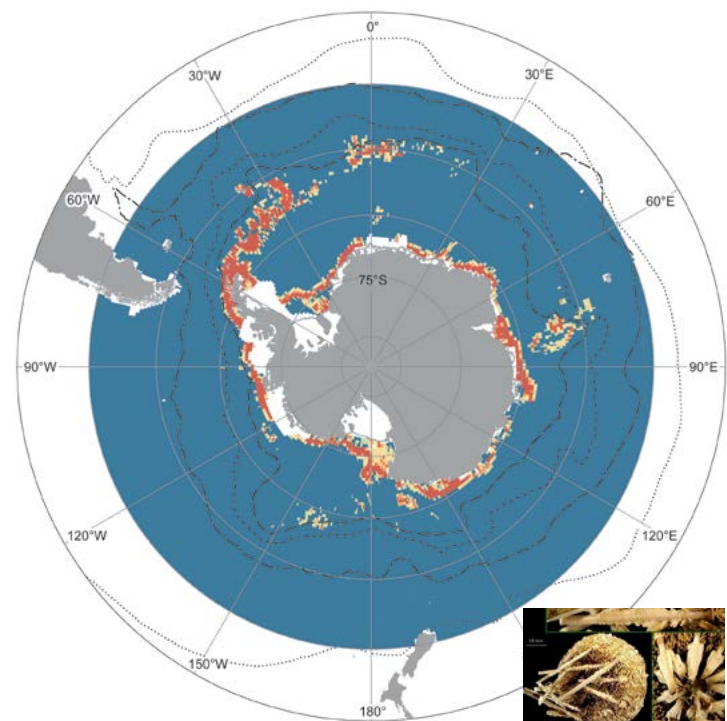
Map 5a *Notocidaris mortenseni*

● 0–999 m
● 999–2999 m



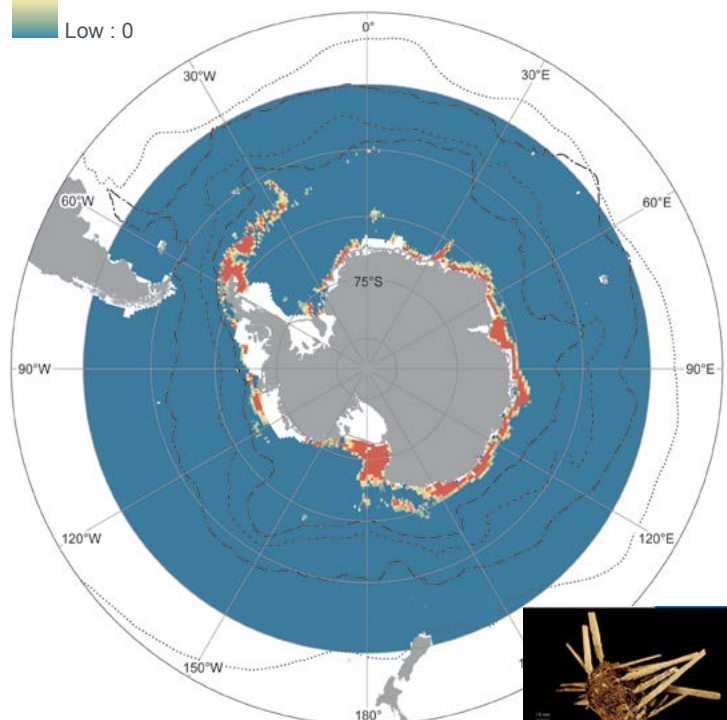
Map 6a *Notocidaris platyacantha*

● 0–999 m
● 999–2999 m



Map 5b

High : 0.962984
Low : 0



Map 6b

High : 0.922403
Low : 0

Echinoidea Maps 5–6 *Notocidaris* spp Species occurrence records (Maps 5a, 6a) and SDMs (Maps 5b, 6b) for the two species *Notocidaris mortenseni* and *Notocidaris platyacantha* respectively. SDMs were generated using Maxent and including ten environmental parameters (Table 1). The “suitable area” (yellow pixels) encompasses all pixels for which probability is over the minimal probability value assigned to a true occurrence (100% of occurrence data are included in this area). The “highly suitable area” (red pixels) corresponds to a threshold that excludes the 5% of true occurrences that show the lowest probability values (95% of true occurrences are still included in this second area). Hatched areas correspond to areas where data are missing for at least one environmental parameters.

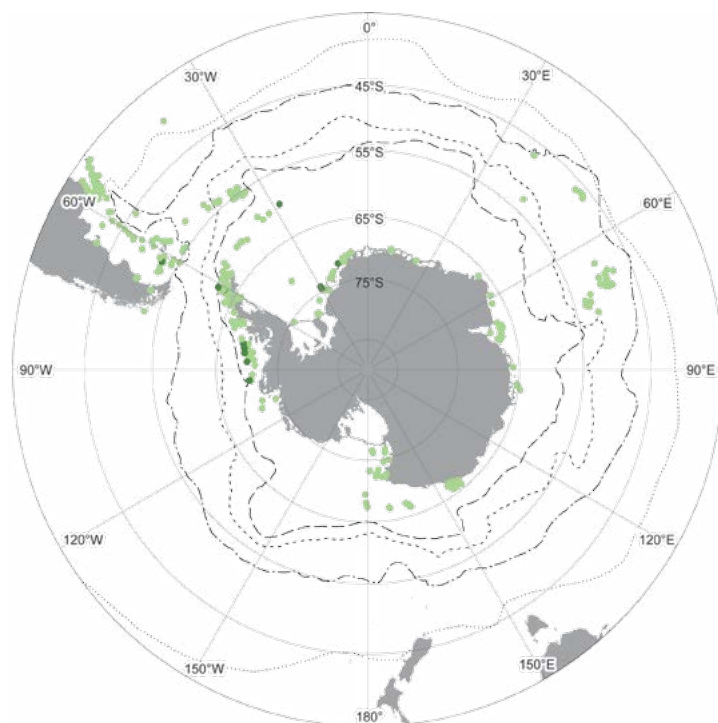
nor emergence scenario would explain the relationships between shallow and deep-sea species. The authors suggested firstly an initial separation between Antarctic and sub-Antarctic shallow species by Upper Miocene or Early Pliocene due to an intensifying ACC as an oceanographic barrier to gene flow between the two areas (Crame 1999, Thornhill *et al.* 2008). Then, the colonization of the deep ocean would have occurred from the sub-Antarctic zone much later, probably promoted by the geomorphology of the Scotia Arc (Thompson 2004), therefore leading to the close relationship between deep-sea and shallow sub-Antarctic species.

Regarding deeper time, some elements can be examined with the latitudinal gradient in echinoid richness (Fig. 1). Species richness increases south of the Polar Front, making the Southern Ocean an enriched area for echinoids. Moreover, the high ratio of echinoid species over genera (Figs. 1 & 2) supports an evolutionary scenario of regional diversification of echinoids over the Antarctic continental shelf, which can be considered as a species flock generator (Eastman & McCune 2000) for certain taxa. This is in part the case in echinoids for the speciose Ctenocidarinae and Schizasteridae (Poulin & Féral 1996), which represent about 65% of Antarctic species and are highly endemic to the Antarctic continental shelf (81% and 67% of species respectively) (David *et al.* 2005 a, Pearse *et al.* 2009). Fossil representatives of the genera from the two families are known in west Antarctica as early as

the Upper Eocene (Hotchkiss & Fell 1972, Hotchkiss 1982, McKinney *et al.* 1988). Despite the fragmented nature of the Antarctic fossil record, it can be assumed that the origination and diversification of those two clades took place during the Cenozoic (Pearse *et al.* 2009) and contributed to the global increase in marine diversity at that time (Crame 2004). In Antarctic echinoids as in other marine taxa, biogeographic structuring has been shaped by the long history of the Gondwanan break up and subsequent tectonic drift of continental shelf margins (South Africa, South America, Antarctica, Australia, and New Zealand) that were once grouped together. This has been accompanied by the onset of the southern Pacific and circumpolar Antarctic surface currents during the Cenozoic, which 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, Pearse *et al.* 2009).

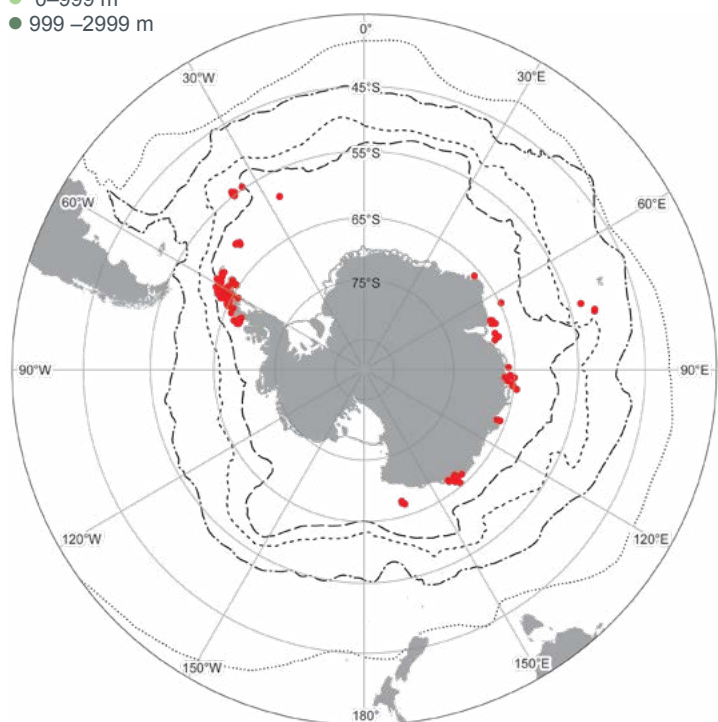
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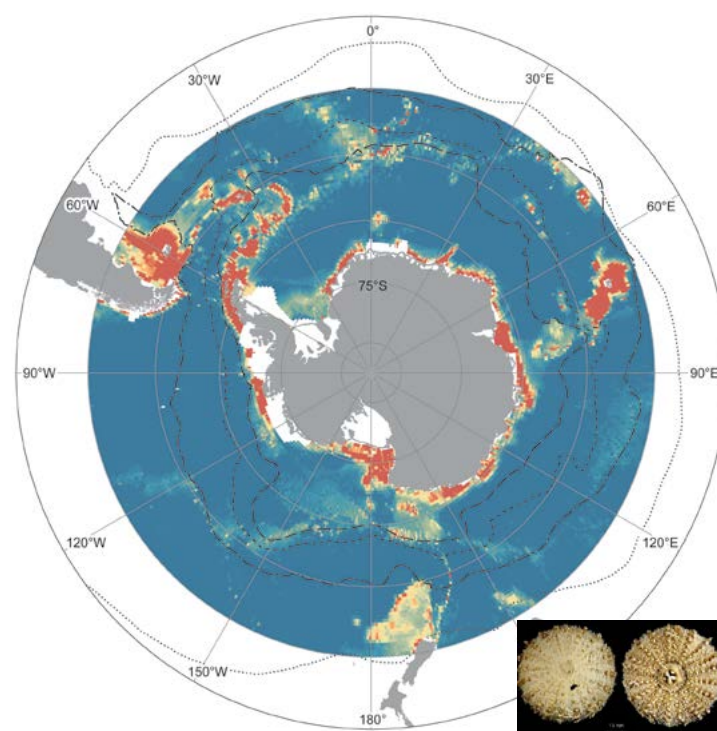
Map 7a *Stereochinus antarcticus*

● 0–999 m
● 999–2999 m



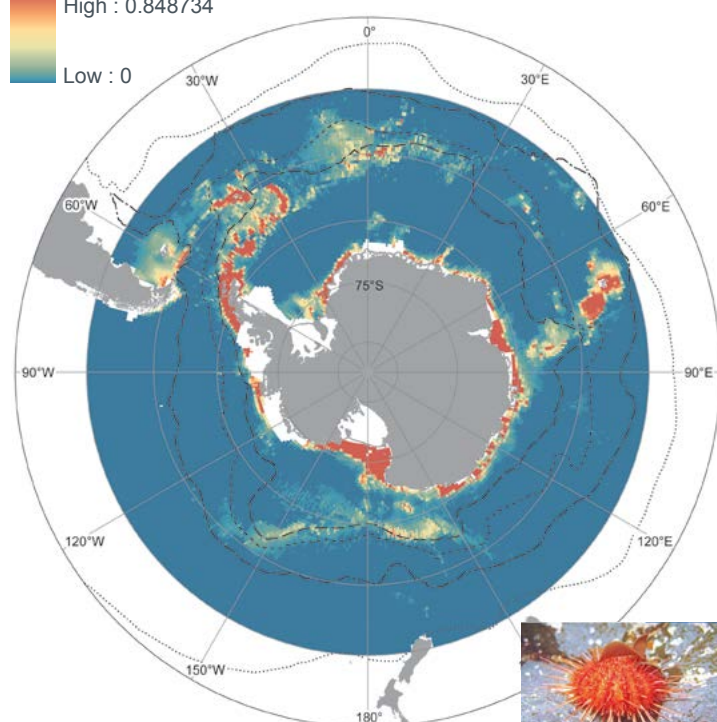
Map 8a *Stereochinus neumayeri*

● 0–999 m



Map 7b

High : 0.848734
Low : 0



Map 8b

High : 0.914047
Low : 0

Echinoidea Maps 7–8. *Stereochinus* spp Species occurrence records (Maps 7a, 8a) and SDMs (Maps 7b, 8b) for the two species *Stereochinus antarcticus* and *Stereochinus neumayeri* respectively. SDMs were generated using Maxent and including ten environmental parameters (Table 1). The “suitable area” (yellow pixels) encompasses all pixels for which probability is over the minimal probability value assigned to a true occurrence (100% of occurrence data are included in this area). The “highly suitable area” (red pixels) corresponds to a threshold that excludes the 5% of true occurrences that show the lowest probability values (95% of true occurrences are still included in this second area). Hatched areas correspond to areas where data are missing for at least one environmental parameters.

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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.

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



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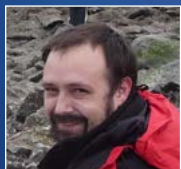
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Yan ROPERT COUDERT spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (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.

