Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

▶ CHAPTER 10.7. PHYLOGEOGRAPHIC PATTERNS OF THE SOUTHERN OCEAN CRINOIDS.

Eléaume M., Hemery L.G., Améziane N., Roux M., 2014.

In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. 448-455.

EDITED BY:
Claude DE BROYER & Philippe KOUBBI (chief editors)

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

SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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

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

Edited by:

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

Published by:

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

Publication funded by:

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

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

Publication supported by:

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

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

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

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

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

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

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

Online dynamic version :

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

Recommended citation:

For the volume:

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

For individual chapter:

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

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

10.7. Phylogeographic patterns of the Southern Ocean crinoids (Crinoidea: Echinodermata)

Marc Eléaume, Lenaïg G. Hemery, Nadia Améziane, Michel Roux

Muséum national d'Histoire naturelle, Département Milieux et Peuplements Aquatiques, UMR 7208-BOREA MNHN-CNRS-UPMC-IRD, Paris, France

1. Introduction

Crinoids are well represented in the Southern Ocean. They locally may constitute one of the major mega-epibenthic components and therefore play a crucial role in the functioning of some ecosystems. Because some species are very abundant and well distributed over the whole Southern Ocean (Eléaume 2006; Hemery 2011; Eléaume *et al*. Chapter 5.25, this volume), they have been recognised as model organisms for studying the spatial variance of genetic diversity in the Southern Ocean.

The main hypothesis that explains the patterns of distribution of Antarctic benthic genetic diversity is linked to the cyclical advance of ice sheets on the Antarctic continental shelf. In this hypothesis, the Antarctic shelf ecosystems have undergone cyclical disturbance events during the last 35 My (see review in Turner *et al.* 2009), including as many as 38 sedimentary cycles of ice sheet advance during the last 5 My (Naish *et al.* 2009). It is thought that ice advance has regularly eradicated the benthic shelf fauna. Thatje *et al.* (2005, 2008) suggested that the benthic fauna now flourishing on the shelf arose from refuges either in areas left free of ice on the shelf (e.g. polynyas or areas not impacted by ice advance), on the adjacent slopes and deep-sea floor, or on the shelves of sub-Antarctic islands. Allcock & Strugnell (2012) summarised the expected molecular patterns for each of these hypotheses. As a result, widely distributed populations were fragmented into smaller populations that have diverged, and sometimes developed barriers to reproduction. This may have been followed by range expansion and, in the case of broadcast spawners, rapid recolonisation of habitats left free of ice, and secondary contact of refugial populations. Benthic taxa lacking a dispersal phase are often structured in haplogroups segregated in narrow geographical ranges (Rogers 2007). Clarke & Crame (1992, 2010) proposed that the cyclical nature of the vicariance events that may have resulted in genetic divergence and sometimes in allopatric speciation enhanced the Antarctic "biodiversity pump" that resulted from "*the regular pulses of migration in and out of Antarctica driven by climate variability*" (Clarke & Crame 1992, p. 299). Cycles of ice extension and retreat are often seen as catastrophic disturbance events leading to large-scale environmental instability, leading in turn to large-scale benthic eradication. However, the megabenthic fauna on the Antarctic shelf is thriving and seems to have rapidly recovered from the cyclical disturbance events, the latest being the Last Glacial Maximum (LGM) some 20,000 years ago. Variation of food availability (which may be linked to ice concentration but also to other factors such as current velocity), interspecific competition for space and food, pelagic larval duration or larval mortality, may also have contributed to the observed patterns, and should receive greater attention in the future. Here we explore, using the Cytochrome c Oxydase subunit I (COI) mitochondrial DNA, the spatial variance of the genetic diversity of the most common Southern Ocean crinoid species, which include broadcast spawners as well as brooders, and examine congruence with predictions of the biodiversity pump hypothesis.

2. Datasets used

The datasets analysed here are already available from previous publications and registered in GenBank and BOLD (accession numbers are given in each publication). The sequences used for the phylogenetic reconstruction are available through Hemery *et al*. (2013a) and comprise data from COI, 16S, 18S and 28S genes. DNA extraction, gene amplification techniques and sequences used for the phylogenetic and phylogeographic analyses are described in Wilson *et al*. (2007), Eléaume *et al*. (2011), Hemery (2011), Hemery *et al*. (2012), Hemery *et al*. (2013a) and Hemery *et al*. (2013b).

3. Antarctic crinoids in context

Hemery *et al*. (2013a) published a phylogenetic study based on a high-resolution taxon sampling, which serves as the basis for this study. Here, we use the same DNA markers, the same sampling effort, and the same reconstruction techniques. Hemery *et al*. (2013a) used four mitochondrial and nuclear genes and 105 taxa, which are differently presented here (Fig. 1). The classification and a nomenclature of extant crinoids used here predate the molecular analyses, and are mainly based on Roux *et al*. (2002) for stalked crinoids, and Messing (1997) for comatulids. The position of Antarctic species is highlighted in the tree to clearly demonstrate their phylogenetic context.

Antarctic crinoids are polyphyletic (see blue taxa in Fig. 1). They do not constitute a single clade that could have originated from a single ancestor, but are found scattered in the tree in most of the major clades (e.g. clades A, B1, B2, B3, B4, see Hemery *et al*. 2013a for details). This suggests that crinoids have colonised the Southern Ocean several times at different periods, or that crinoids have colonised the Southern Ocean independently from different ocean basins at roughly the same time. Within the Hyocrinidae, Antarctic and sub-Antarctic taxa are not monophyletic and are found associated with North and South Pacific, and North Atlantic species. Within the Pentametrocrinidae, one *Pentametrocrinus* and one *Thaumatocrinus* species (see Eléaume *et al*. Chapter 5.25, this volume) are known from the Antarctic and sub-Antarctic regions. *Thaumatocrinus* has representatives in the North Atlantic, and *Pentametrocrinus* is found in the Indo-West Pacific and North Atlantic deep basins. In addition, Rouse *et al*. (2013) have demonstrated that the Indo-Pacific stalked crinoid genera *Guillecrinus* and *Vityazicrinus* are closely related to *Pentametrocrinus*. Within Bathycrinidae, a clade composed of Antarctic *Bathycrinus australis* and an Indo-West Pacific *Monachocrinus* sp. (both stalked) is sister to Atelecrinidae, a widespread bathyal family of feather stars. The Antarctic brooding genera *Eumorphometra*, *Eometra* and *Isometra* are related to North-Atlantic and Indo-West Pacific species (clade Antedonidae #1). Heliometrinae, a subfamily of Antedonidae that includes numerous Antarctic species, returns as two separate clades (see Eléaume 2006 for morphological arguments). Heliometrinae #1 is purely Antarctic and may result from in situ diversification events. Heliometrinae #2 comprises one Caribbean species, East Pacific and Arctic taxa, and at least one true Antarctic species, *Anthometrina adriani*.

Antarctic crinoids seem to have originated from ancestors from various ocean basins, including the Southern Ocean. Some taxa seem to have colonised the Southern Ocean repeatedly (e.g. Hyocrinidae, Pentametrocrinidae), other taxa seem to have radiated in situ (e.g. Heliometrinae #1, Notocrinidae, Isometrainae, and the hyocrinid genus *Dumetocrinus*).

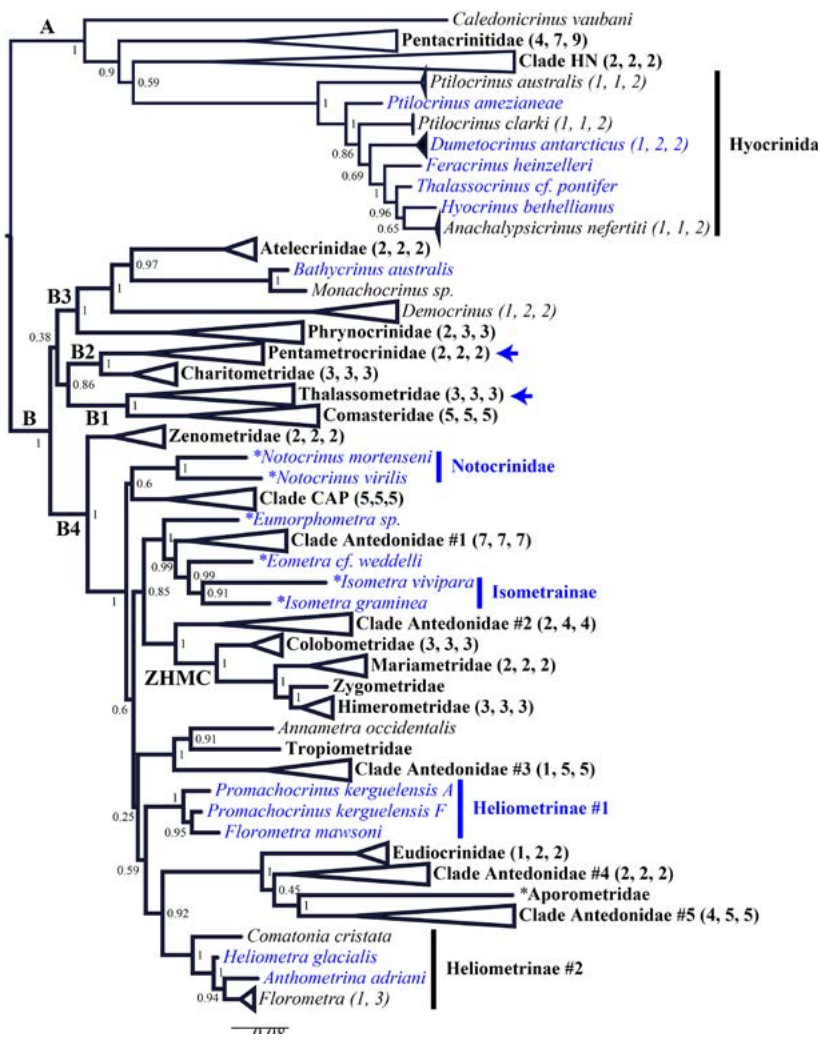


Figure 1 Cladogram of extant crinoids (modified from Hemery *et al.* 2013a) using molecular markers (COI, 16S, 18S and 28S). A total of 105 taxa are included and 3848 base positions were analysed. Maximum Likelihood (ML) and Bayesian Inference (BI) were performed on the four genes combined as an unlinked-partition dataset. For ML analyses, the model GTR+Γ (General Time Reversible) was used for each unlinked-partition, and bootstrapping was carried out with 1000 replicates using the same model. For BI analyses, the model GTR+I+Γ was used for each unlinked-partition. Two iterations of fifty million generations were run with eight chains, sampling every 1000 generations. ML and BI tree topologies were identical. Bayesian posterior probabilities values are given close to nodes; family and subfamily names are in bold; numbers in brackets indicate number of genera, species and specimens, respectively, included in the clade; names of clades discussed in Hemery *et al.* (2013) are given at nodes; Antarctic taxa are highlighted in blue; arrows indicate taxa that contain Southern Ocean species; stars indicate brooding species; HN = Holopus + Neogymnocrinus; CAP = Calometridae + Asterometridae + Ptilometridae; ZHMC = Zygometridae + Himerometridae + Mariametridae + Colobometridae.

4. Phylogeographic patterns and demographic history

Only a subset of the Southern Ocean species collected and presented in the cladogram above were represented by a sufficient number of individuals to be suitable for further phylogeographic analyses. These species, the number of sequences analysed, and their reproductive strategies are as follows: *Anthometrina adriani* (146, broadcast spawner), *Feracrinus heinzelleri* (34, possibly a broadcast spawner), *Florometra mawsoni* (513, broadcast spawner), *Isometra graminea* (47, brooder), *Notocrinus virilis* (175, brooder), *Promachocrinus kerguelensis* (1429, broadcast spawner), and *Ptilocrinus amezianeae* (66, possibly a broadcast spawner). The sampling method was opportunistic and dependent on ship-based and station-based operations in Antarctica. Many areas of interest have not been sampled yet because of ice conditions or remoteness of these areas. Many spatial gaps remain, even though the sampling effort used here is unprecedented and in most cases is likely to encompass the whole distribution range of species under study.

Defining a population is not trivial (Avise 2000). Here we define a population as a group of sequences collected in the same area, typically separated from neighboring population by several hundred nautical miles. Ten different populations have been identified: Amundsen Sea (AS), Burdwood Bank (BB), Bouvet Island (BI), Davis Sea (DS), Dumont d'Urville Sea (DDU), Eastern Weddell Sea (EWS), Kerguelen Plateau (KP), Ross Sea (RS), Admiralty and Scott Island Seamounts (ASIS), Scotia Arc (SA), West Antarctic Peninsula (WAP). In the case of *P. kerguelensis* for which enough specimens are available, the Scotia Arc area has been separated into four distinct populations: South Shetland Islands (SSh), South Orkney Islands (SO), South Sandwich Islands (SSa), and South Georgia (SG). Hemery *et al*. (2012) described the methods used to estimate population diversity and the genealogical relationships among haplotypes. COI sequences were aligned using BioEdit Sequence Alignment Editor v7.0.9.0 (Hall 1999); haplotype networks were constructed using Network software (version 4.5.0.0; http://www.fluxus engineering.com); TCS1.21 (Clément *et al.* 2000) was used to test the connection threshold at which groups of haplotypes disconnect. Population diversity indices (Hd, haplotype diversity; π, nucleotidic diversity; Fu's F^S) were calculated using ARLEQUIN v.3.5.1.2 (Excoffier & Lischer 2010) and are given in Table 1.

Table 1 Diversity indices for seven species largely distributed in the Southern Ocean. An = number of haplotypes; Fu's FS = result of the Fu's FS test; Hd = haplotype diversity; N = number of specimens; π = nucleotidic diversity ; p = significance level of the Fu's FS with * = p<0.05, ** = p<0.01, *** = p<0.005. AS = Amundsen Sea; ASIS = Admiralty and Scott Island Seamounts; BB = Burdwood Bank; BI = Bouvet Island; DDU = Dumont d'Urville Sea; DS = Davis Sea; EWS = Eastern Weddell Sea; HEA = Heard Island; KP = Kerguelen Plateau; RS = Ross Sea, and SA = Scotia Arc, the latter divided for *Promachocrinus kerguelensis* into SSa = South Sandwich Islands, SSh = South Shetland Islands, SO = South Orkney Islands, SG = South Georgia, and WAP = West Antarctic Peninsula.

Species/ phylogroup	Population	N	An	Hd	π	Fu's FS	p
***Promachocrinus kerguelensis* A**	KP	113	16	0.7162	0.0019	-18.519	***
	DS	1	1	—	—	—	
	DDU	32	6	0.6855	0.0043	-1.397	
	RS	86	9	0.6621	0.0048	-3.256	
	SSh	26	2	0.6092	0.0040	1.349	
	SSa	15	3	0.7619	0.0018	-2.841	**
	SG	2	2	—	—	—	
	BI	36	2	0.1619	0.0002	-2.590	***
	EWS1	3	2	—	—	—	
***Promachocrinus kerguelensis* B**	DS	1	1	—	—	—	
	DDU	54	4	0.6988	0.0017	-3.221	*
	RS	40	1	0.5859	0.0015	-0.935	
	SSh	9	0	0.2222	0.0004	-0.263	
	EWS1	2	2	—	—	—	
	EWS2	1	1	—	—	—	
***Promachocrinus kerguelensis* C**	DS	54	2	0.6108	0.0013	-0.987	
	DDU	179	9	0.7423	0.0040	-2.056	
	RS	10	0	0.3778	0.0020	0.683	
	AS	3	1	—	—	—	
	WAP	18	4	0.8301	0.0040	-2.202	
	SSh	13	2	0.6923	0.0016	-2.036	*
	SSa	35	6	0.5664	0.0013	-6.758	***
	SO	34	1	0.4688	0.0010	-0.920	
	EWS2	30	0	0.6644	0.0027	0.430	
	EWS1	71	11	0.8072	0.0059	-3.258	
***Promachocrinus kerguelensis* D**	DS	38	2	0.6088	0.0031	-0.660	
	DDU	82	5	0.6197	0.0044	-1.706	
	RS	53	7	0.8694	0.0074	-0.261	
	AS	13	2	0.7308	0.0029	0.514	
	WAP	10	1	0.5333	0.0047	1.176	
	SSh	18	7	0.8497	0.0083	-1.623	
	EWS1	13	3	0.8590	0.0054	-2.291	
	EWS2	8	0	0.4643	0.0035	1.493	
***Promachocrinus kerguelensis* E1**	DDU	11	0	0.0000	0.0000	—	
	RS	8	0	0.0000	0.0000	—	
	SSh	5	0	0.0000	0.0000	—	
	SO	25	6	0.4300	0.0012	-4.900	***
	SG	6	0	0.0000	0.0000	—	
	EWS1	1	1	—	—	—	
***Promachocrinus kerguelensis* E2**	DS	22	0	0.0000	0.0000	—	
	DDU	51	3	0.1153	0.0002	-4.339	***
	RS	68	1	0.0294	0.0001	-1.894	***
	WAP	2	1	—	—	—	
	EWS1	22	2	0.7056	0.0016	-0.184	
	EWS2	2	2	—	—	—	

Species/ phylogroup	Population	N	An	Hd	π	Fu's FS	p
Promachocrinus kerguelensis F	DS	68	1	0.5083	0.0009	0.580	
	DDU	9	0	0.0000	0.0000	—	
	RS	4	1	—	—	—	
	AS	1	1	—	—	—	
	WAP	9	0	0.0000	0.0000	—	
	SSh	1	1	—	—	—	
	SO	2	1	—	—	—	
	SSa	1	1	—	—	—	
	EWS1	8	1	0.6071	0.0014	-0.224	
Anthometrina adriani	DS	45	7	0.7636	0.002104	-1.606	
	DDU	33	7	0.6818	0.001716	-2.781	*
	RS	50	8	0.6833	0.001627	-3.461	*
	EWS	18	4	0.6078	0.001314	-0.841	
Florometra mawsoni	KP	62	20	0.7039	0.0020	-21.957	***
	DS	90	9	0.2844	0.000705	-8.394	***
	DDU	240	30	0.8009	0.003114	-22.585	***
	RS	27	5	0.4416	0.000879	-2.709	**
	AS	3	1	—	—	—	
	WAP	12	2	0.1667	0.000605	0.432	
	SA	9	3	0.4167	0.0008	-1.081	*
	BB	2	2	—	—	—	
	EWS	68	12	0.6817	0.003611	-2.966	
Notocrinus virilis A	SA	1	1	—	—	—	
	EWS	35	5	0.2185	0.007143	-4.015	***
Notocrinus virilis B	DS	5	1	—	—	—	
	DDU	67	5	0.2687	0.011578	-1.973	
	RS	56	4	0.1052	0.00267	-4.521	***
	SA	6	1	—	—	—	
	EWS	5	1	—	—	—	
Isometra graminea	DDU	31	5	0.5441	0.001282	-1.61702	
	RS	13	2	0.5128	0.000968	1.1512	
	WAP	3	2	0.6667	0.001258	0.20067	
Feracrinus heinzelleri	DS	4	4	1.0000	0.007202	-0.61511	
	RS	28	12	0.8730	0.00674	-1.74279	
	AS	2	2	—	—	—	
Ptilocrinus amezianeae	KP	23	6	0.4585	0.001116	-3.23397	***
	ASIS	40	9	0.5026	0.000932	-7.74253	***
	SA	3	1	—	—	—	

Patterns – Haplotype networks exhibit different topological patterns across all species (Fig. 2). *Promachocrinus kerguelensis* is composed of seven groups of haplotypes (A, B, C, D, E1, E2, F), each displaying a star-like topology, with one central and common (ancestral) haplotype surrounded by a crown of a varying number of derived secondary and less frequent haplotypes or singletons. *Florometra mawsoni*, which displays a star-like topology as well, connects to this network at a larger distance (Fig. 2A). Hemery *et al*. (2012) interpreted this pattern as congruent with the hypothesis of multiple refugia on the high-Antarctic and sub-Antarctic islands shelves during past glaciations, followed by population expansion, rapid recolonisation and secondary contact. Nuclear marker networks (Hemery *et al.* 2012) display two distinct lineages that indicate that the divergence in the mitochondrial genes was not found in the nuclear genes. These results have been interpreted as congruent with a single or two different species in *Promachocrinus*.

Anthometrina adriani displays a very different, much simpler, pattern with two major haplotypes surrounded by a crown of derived less frequent haplotypes and singletons (Fig. 2B). *Anthometrina adriani* is only found on the high-Antarctic shelf (Eléaume *et al*. Chapter 5.25, this volume). This less complex phylogeographic pattern is in agreement with the interpretation that this species is well mixed today or survived the LGM in fewer refugia on the High Antarctic shelf.

Isometra graminea, *Notocrinus virilis*, and *Ptilocrinus amezianeae* exhibit clear geographical structure. *Isometra graminea* is divided in three distant haplogroups (Fig. 2D), one restricted to the Ross Sea, a second to the Dumont d'Urville Sea, and the third to the West Antarctic Peninsula (Marguerite Bay). *Notocrinus virilis* also is divided into five distant haplogroups (Fig. 2C): two very distinct from each other restricted to the Eastern Weddell Sea, another two very distinct restricted to the Scotia Arc, and one restricted to a larger area comprising the Ross, Dumont d'Urville and Davis seas. The haplogroups containing more than one haplotype consist of one or two central haplotypes surrounded by a small number of singletons. *Ptilocrinus amezianeae* displays a dumbbell-shape topology with two haplogroups separated by nine unsampled haplotypes. One haplogroup is restricted to the Kerguelen Plateau and the second to the Admiralty and Scott Island Seamounts and Scotia Arc (Fig. 2E). Populations in the first two areas display a star-like topology, with one central and common (ancestral) haplotype surrounded by a crown of derived singletons. The recent discovery of *P. amezianeae* on the Kerguelen Plateau and Scotia Arc, in addition to the population known from the Admiralty and Scott Island Seamounts (Bowden *et al.* 2011; Eléaume *et al.* 2011), seems to suggest that this species may be well-distributed in the Southern Ocean and that the gap observed between the two haplogroups may be due to a sampling bias.

A fourth type of haplotype network pattern is the bush-like topology displayed by *Feracrinus heinzelleri* (Fig. 2F) which is a deep-sea, more-or-less eurybathic species. The genetic pattern observed could be a signature of a slope-dwelling species that may have found refuge during glacial periods in the deep basins around the continental shelf.

Demography – Based on the number of samples available, a total of seven species and up to ten populations within a species were analysed (Table 1). Most of the populations display medium to high haplotype diversity and medium to high nucleotidic diversity, indicating an overall rather high within- and among-sequences diversity. Within *P. kerguelensis*, phylogroups A, C and D are composed of generally highly diverse populations showing signatures of a bottleneck (or genetic sweep) followed by population expansion. A reduced gene flow between several populations also characterises these phylogroups. Other phylogroups are less diverse and show no sign of expansion, and some level of connectivity between populations is suspected (Fig. 7 in Hemery *et al*. 2012). Within each phylogroup, the populations seem to have either been variously impacted or reacted differently to past glaciations. The DS, RS, SA, and WAP populations of *F. mawsoni*, and DDU and RS populations of *N. virilis*, display a low haplotype diversity and low nucleotidic diversity suggesting a recent bottleneck or genetic sweep. In addition, significant negative Fu's Fs results support the idea that *Anthometrina adriani* DDU and RS populations, and *Florometra mawsoni* DDU, DS, KP, RS and SA populations have undergone a recent expansion, purifying selection or selective sweep. If the recent expansion hypothesis is confirmed, these results would suggest that DS, RS and WAP populations may be recovering from benthic eradication due to one of many glaciation events, as previously observed for *P. kerguelensis* (Hemery *et al*. 2012). Other populations seem to have recovered from more diverse and less impacted populations. *Anthometrina adriani* DS and EWS populations appear stable with a smaller number of singleton haplotypes, suggesting that these populations have been less impacted by, for example, past glaciation

events. *Feracrinus heinzelleri* displays stable population structure and no sign of population decrease or expansion, a result congruent with populations not impacted by drastic events, and capable of surviving glaciation periods on the slopes or deeper environnements.

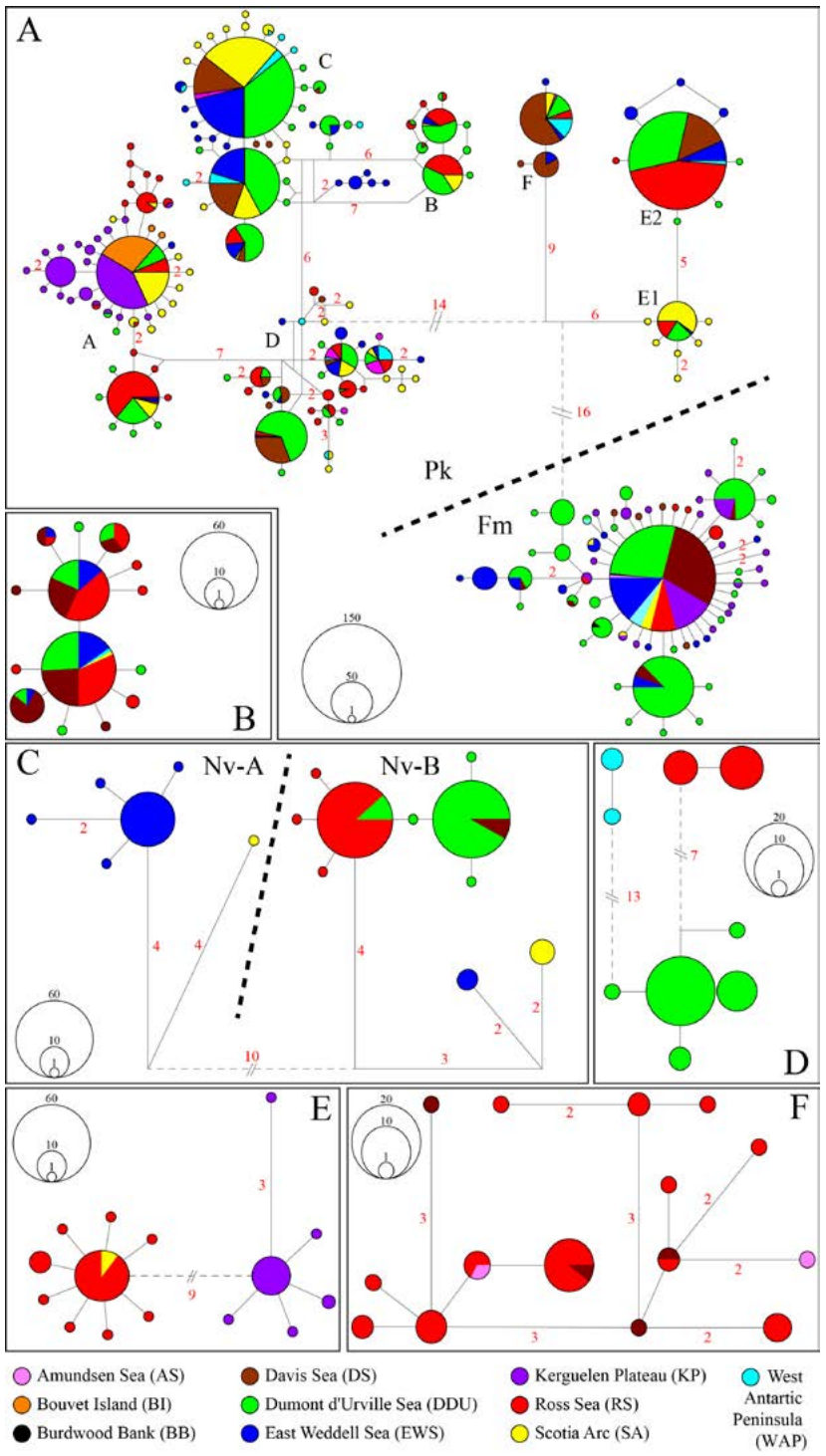


Figure 2 Haplotype networks for seven of the most common species of crinoids in the Southern Ocean. Haplotypes are derived from COI sequences. The genealogical relationships among haplotypes were estimated using the median-joining algorithm, allowing for the definition of clades (based on divergence up to 0.5%), and using statistical parsimony. A - *Promachocrinus kerguelensis* and *Florometra mawsoni* networks are shown as connected because *F. mawsoni* has been shown to be closely related to *P. kerguelensis* and may be considered another lineage within the *P. kerguelensis* complex. All lineages are represented and indicated with an uppercase letter from A to F. B – *Anthometrina adriani* network showing two major haplotypes surrounded by secondary less frequent haplotypes. C - *Notocrinus virilis* network showing the relationship between haplogroups A and B. Haplogroup A displays one major haplotype in the Eastern Weddell Sea and 3 secondary ones found in the Eastern Weddell Sea and in the Scotia Arc. Haplogroup B is more diverse and distributed in both East and West Antarctica. These patterns are not typical of brooders and suggest some dispersal capabilities for this species. D – *Isometra graminea* network showing strict geographical segregation of all three haplogroups. This pattern is typical of a non-dispersive species, i.e., a brooder. E – *Ptilocrinus amezianeae* network showing two major haplotypes apparently geographically segregated but with gene exchange between the Scotia Arc and the Admiralty and Scott Island Seamounts some 5000 km away. F – *Feracrinus heinzelleri* network showing no particular spatial patterning. Pk = Promachocrinus kerguelensis; Fm = *Florometra mawsoni*; Nv-A = *Notocrinus virilis* haplogroup A; Nv-A = *N. virilis* haplogroup B. All circles reprsent a unique COI sequence (haplotype), and their diameter is proportionnal to the number of specimens sharing this haplotype. Numbers in red indicate the number of unsampled haplotypes between two closely related haplotypes.

5. Geographic distributions of haplogroups

The following maps show the distribution and haplotype composition of populations of *Promachocrinus kerguelensis* phylogroups A to F (Maps 1 to 7), *Florometra mawsoni* (Map 8), *Anthometrina adriani* (Map 9), *Isometra graminea* (Map 10), *Notocrinus virilis* haplogroups A and B (Maps 11, 12), *Ptilocrinus amezianeae* (Map 13) and *Feracrinus heinzelleri* (Map 14). On each map, each color represents a different haplotype and the pie size is proportionnal to the total number of specimens analysed per population.

6. Conclusion

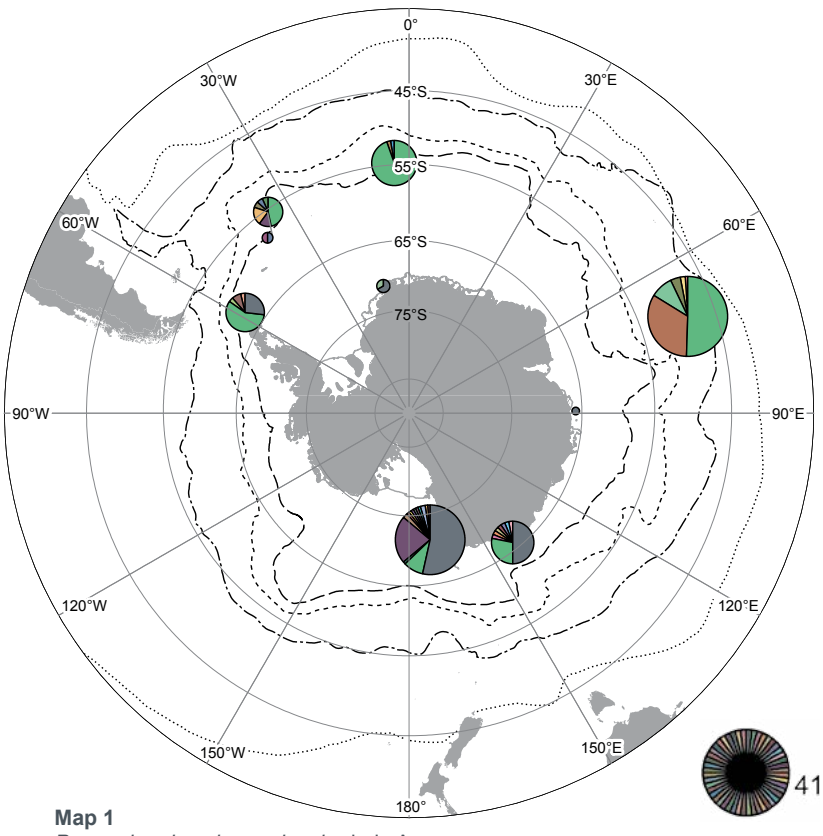
Sample bias is only to be expected in the Southern Ocean, because of the logistic challenges that remoteness, ice and cold confer. However, we have tried to cover, as best as possible, the distributional range and habitat of selected crinoid species. Still, deep-sea habitats are obviously undersampled, as well as a large area between the Eastern Weddell Sea and the Davis Sea, between the Ross Sea and the West Antarctic Peninsula, and the southern part of the Atlantic sector (i.e., Burdwood Bank, Bouvet Island). Unsampled haplotypes (see Fig. 2) from these regions, if added to our dataset, might change some of the conclusions drawn here.

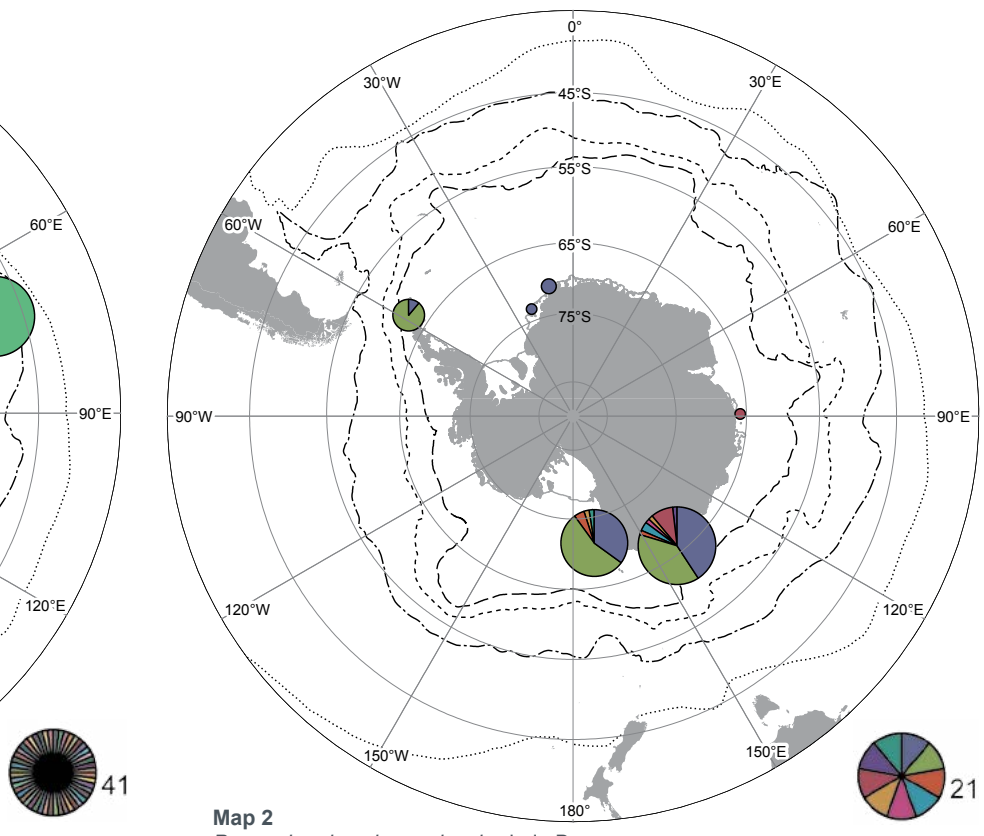
Brooders and broadcast spawners showed strongly contrasting population structures. As expected, brooders showed high levels of geographic structure, whereas broadcast spawners did not. This is probably due to their contrasting life history traits. Planktonic larvae are usually produced in larger numbers and are able to cover longer distances. Among the brooders, *I. graminea* haplogroups have never been found sympatrically on the Antarctic shelf. This species seems to lack the ability to disperse and rapidly colonise new habitats. By contrast, *Notocrinus virilis*, another brooder, seems to be capable of larval dispersion (S. Schiaparelli, pers. com.). Among boadcast spawners, all phylogroups are found sympatrically except within *P. kerguelensis* at Bouvet Island and on the Kerguelen Plateau, where only the clade A is present.

Demographic approaches indicate that populations display contrasting histories, depending on the species or phylogroup. Population expansion after a bottleneck or genetic sweep can be detected, but not in all populations under study. Population expansion after a bottleneck is an expected signature after a drastic demographic event such as a large-scale benthic eradication resulting from grounded ice expansion during a glacial period. The “biodiversity pump” scenario, which states that population fragmentation and isolation in refugia during glacial periods may have induced allopatric speciation in Antarctic taxa, is therefore congruent with these results.

Acknowledgements

We would like to thank the many people who were involved in the collection of specimens: S. Arnaud-Haond (IFREMER), P. Bouchet and S. Samadi (MNHN), P. Chevaldonné (IMBE), M. Frederiks (RBCM), T. Fujita (NSMT), E. Lodde (ZSM), S. Keable (AM), G. Woerheide (LMU), T. O’Hara (Museum Victoria), C. Messing (NOVA Southeastern University), T. Hibberd, A. Constable and M. Riddle (AAD), D. Bowden, S. Mills and K. Schnabel (NIWA), J. Bohn and E. Lodde (ZSM), K. Linse and H. Griffiths (BAS), S. Schiaparelli (University of Genoa). Other people from different institutions need to be thanked for their help and time: D. Pawson (NMNH, Smithsonian Institution), A. Mironov (ZMMSU), C. Massin and Y. Samyn (RBINS). This work was jointly funded by the ANTFLOCKS project (ANR USAR no 07-BLAN-0213-01) and four Actions Transversales du MNHN: Biodiversité actuelle et fossile; crises, stress, restaurations et panchronisme: le message systématique’, ‘Taxonomie moléculaire: DNA Barcode et gestion durable des collections’, ‘Formes possibles, formes réalisées’, and ‘Biominéralisation’. Part of the molecular work was also supported by collaboration between the Census of Antarctic Marine Life, the Marine Barcode of Life (MarBOL) project and the Canadian Centre for DNA Barcoding (CCDB). Laboratory analyses on sequences generated at the CCDB were funded by the Government of Canada through Genome Canada and the Ontario Genomics Institute (2008-OGI-ICI-03). This work was supported by the Consortium National de Recherche en Génomique, and the Service de Systématique Moléculaire (SSM) at the MNHN. It is part of the agreement number 2005/67 between the Génoscope and the MNHN on the project ‘Macrophylogeny of life’ directed by G. Lecointre. Taxonomic expertise was facilitated by three Synthesys grants awarded to M. Eléaume: DE-TAF-324, SE-TAF-1003 and GB-TAF-1093. Special thanks are due to Huw Griffiths for his help in drawing the maps. We also wish to thank Christoph Held (AWI) and Charles Messing (NSU) for their thorough reviews that helped impove this manuscript. This is CAML contribution # 146.



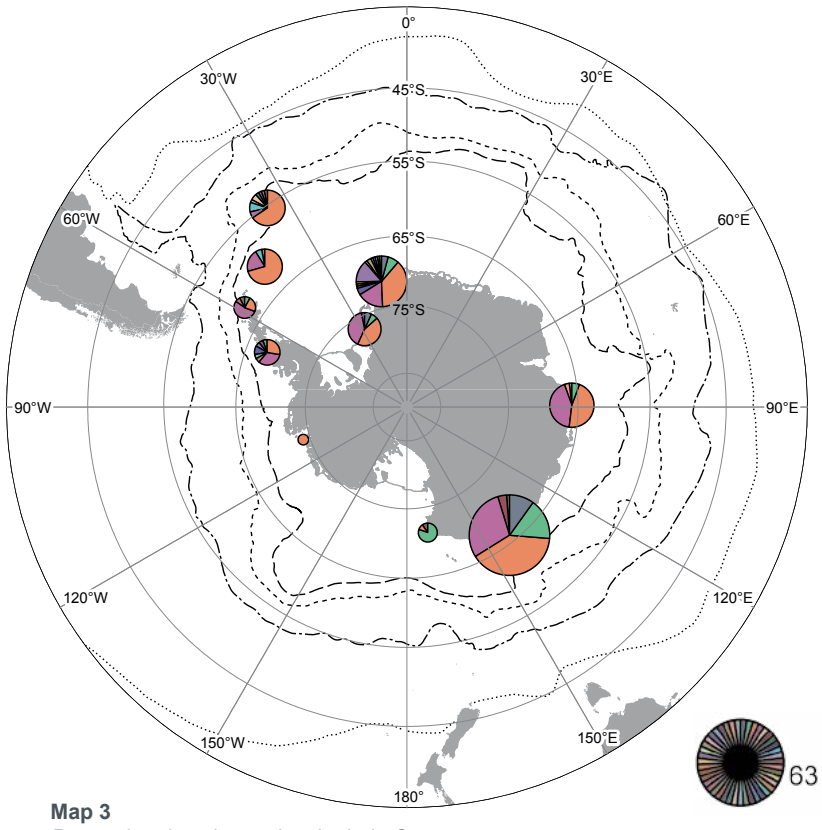


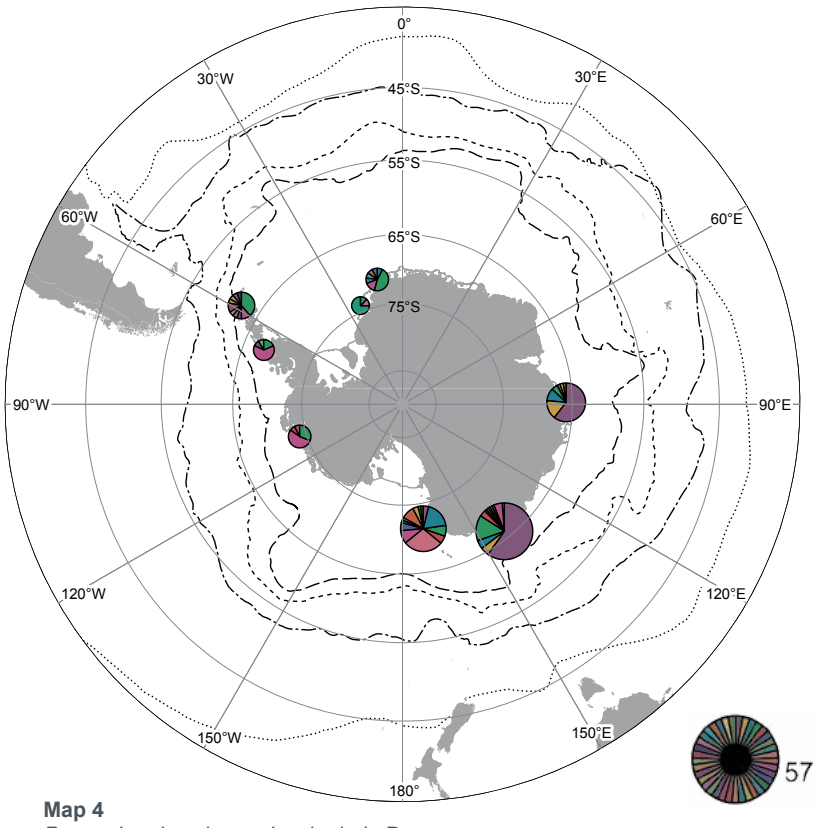
Map 1
Promachocrinus kerguelensis clade A

H007	H030	H065	H105	H136	H144
H015	H058	H066	H107	H137	H145
H016	H059	H067	H109	H138	H146
H017	H060	H068	H110	H139	H147
H026	H061	H071	H111	H140	H148
H027	H062	H072	H115	H141	H149
H028	H063	H086	H134	H142	H150
H029	H064	H104	H135	H143	H151

Map 2
Promachocrinus kerguelensis clade B

H001	H025
H005	H032
H013	H050
H014	H055
H021	





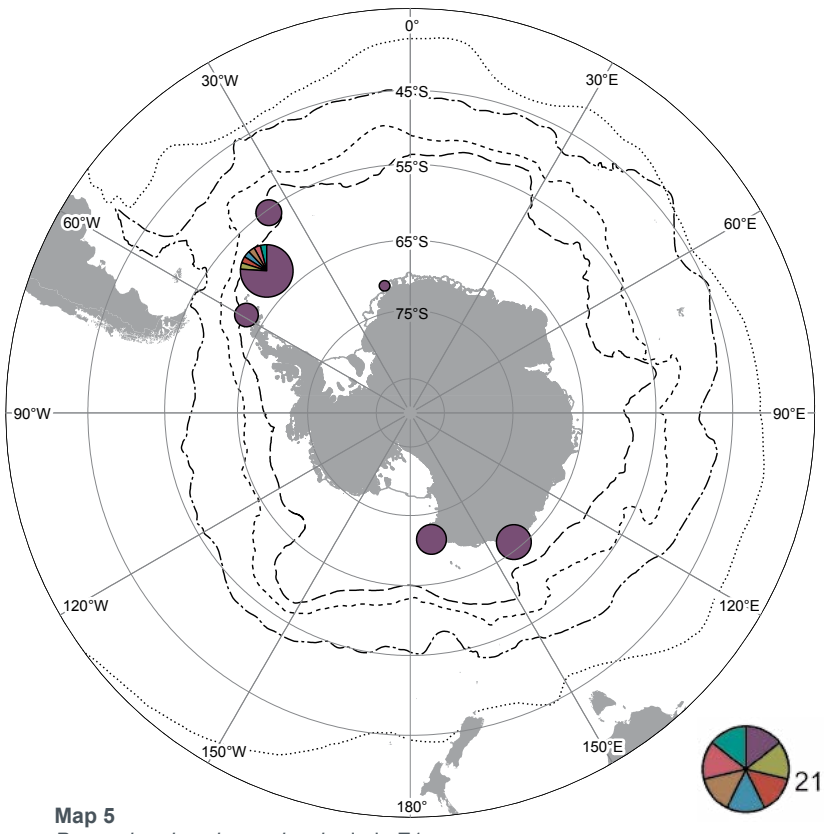
Map 3
Promachocrinus kerguelensis clade C

H004	H034	H049	H083	H106	H123
H008	H035	H075	H084	H108	H125
H009	H037	H076	H085	H114	H126
H010	H039	H077	H087	H116	H127
H011	H040	H078	H088	H117	H128
H024	H042	H079	H091	H118	H133
H033	H047	H082	H095	H119	H152
					H155

Map 4
Promachocrinus kerguelensis clade D

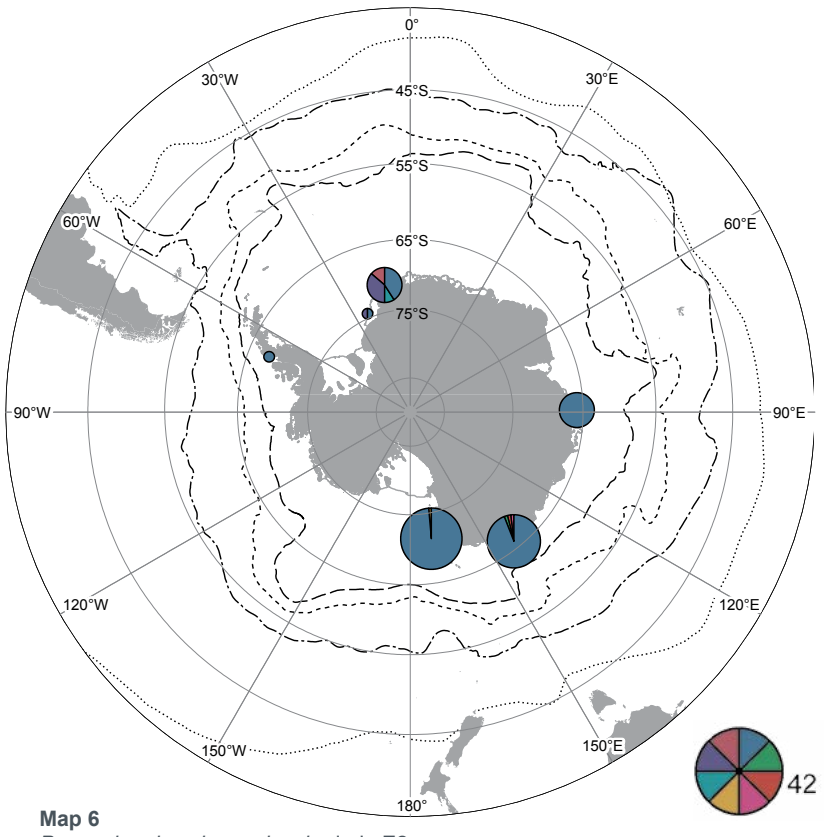
H002	H036	H051	H070	H090	H112
H018	H041	H052	H073	H099	H124
H019	H043	H053	H074	H100	H129
H022	H045	H054	H080	H101	H130
H023	H046	H056	H081	H102	H132
H031	H048	H069	H089	H103	H156
					H157

Phylogeography Crinoida Maps 1-4 Map 1 *Promachocrinus kerguelensis* clade A is well represented on the Kerguelen Plateau, East Antarctic Ross Sea and Dumont d'Urville Sea shelves, tip of the Peninsula and in the sub-Antarctic Islands but the number of haplotypes is higher on the east Antarctic Ross Sea and Dumont d'Urville Sea shelves. In contrast, this clade is rare on the shelves extending from the Weddell Sea to the Davis Sea. The haplotype composition of each population may be indicative of a past refuge on the Kerguelen Plateau, and subsequent recolonisation from different source haplotype in the East and West Antarctic. Map 2 *Promachocrinus kerguelensis* clade B is well represented on the East Antarctic Ross Sea and Dumont d'Urville Sea shelves. It is rare from other part of the Antarctic shelf, and absent from all sub-Antarctic islands. Map 3 *Promachocrinus kerguelensis* clade C is well represented on the high-Antarctic shelves. It displays a higher number of haplotypes in the West Antarctic: Weddell Sea, Peninsula, South Orkney and South Shetland Islands. It is less diverse on the East Antarctic Ross Sea, Davis Sea and Dumont d'Urville Sea shelves and completely absent from other sub-Antarctic localities. Map 4 *Promachocrinus kerguelensis* clade D is well represented on the East Antarctic Dumont d'Urville Sea and Ross Sea shelves. It is completely absent from the sub-Antarctic Islands. Proportion of haplotypes in the East Antarctic Davis Sea and Dumont d'Urville Sea differs from elsewhere on the Antarctic shelf.



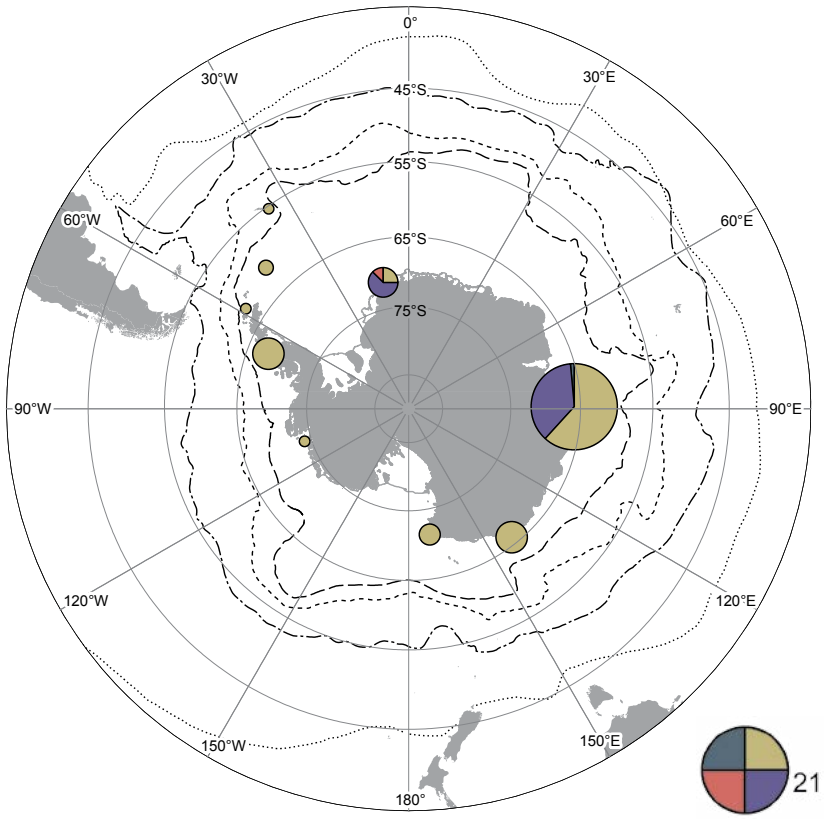
Map 5
Promachocrinus kerguelensis clade E1

H003 H096
H092 H097
H093 H098
H094



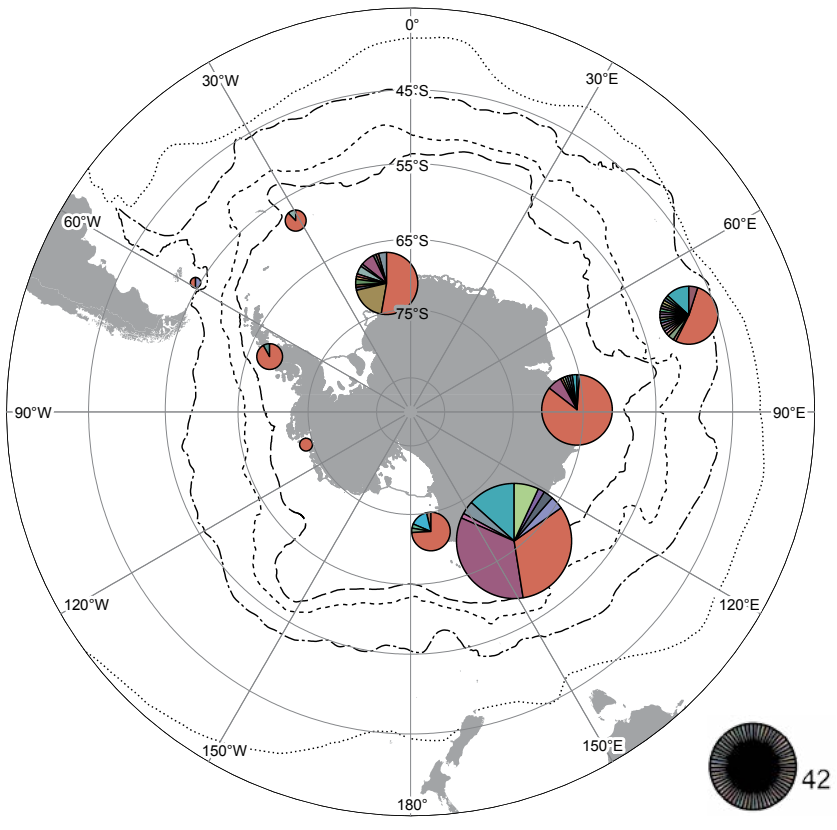
Map 6
Promachocrinus kerguelensis clade E2

H006 H057
H020 H113
H038 H120
H044 H121



Map 7
Promachocrinus kerguelensis clade F

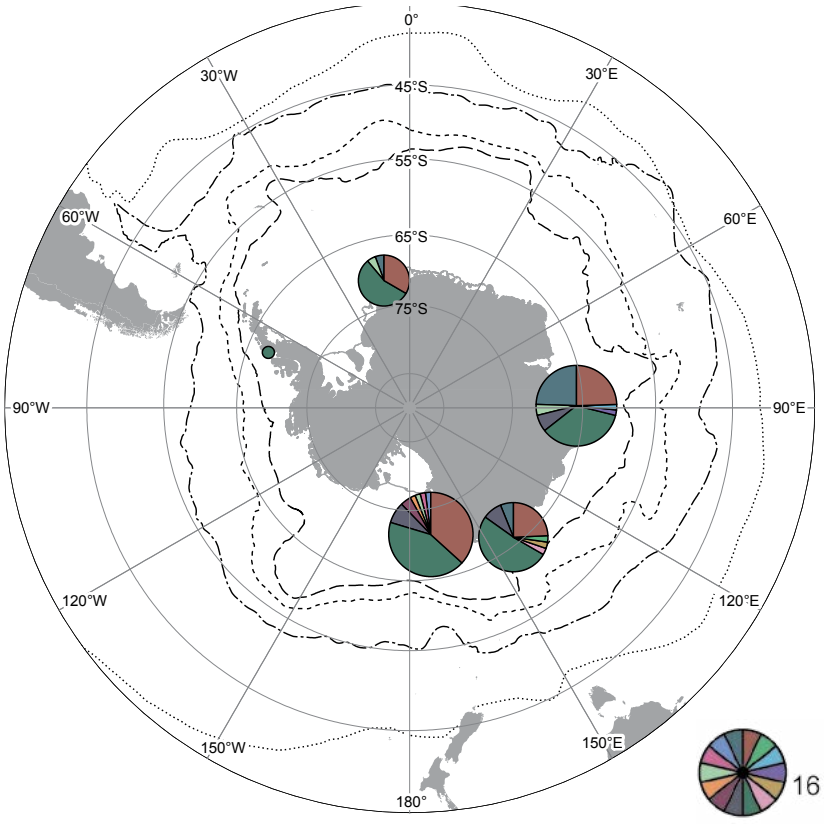
H012
H122
H131
H154



Map 8
Florometra mawsoni

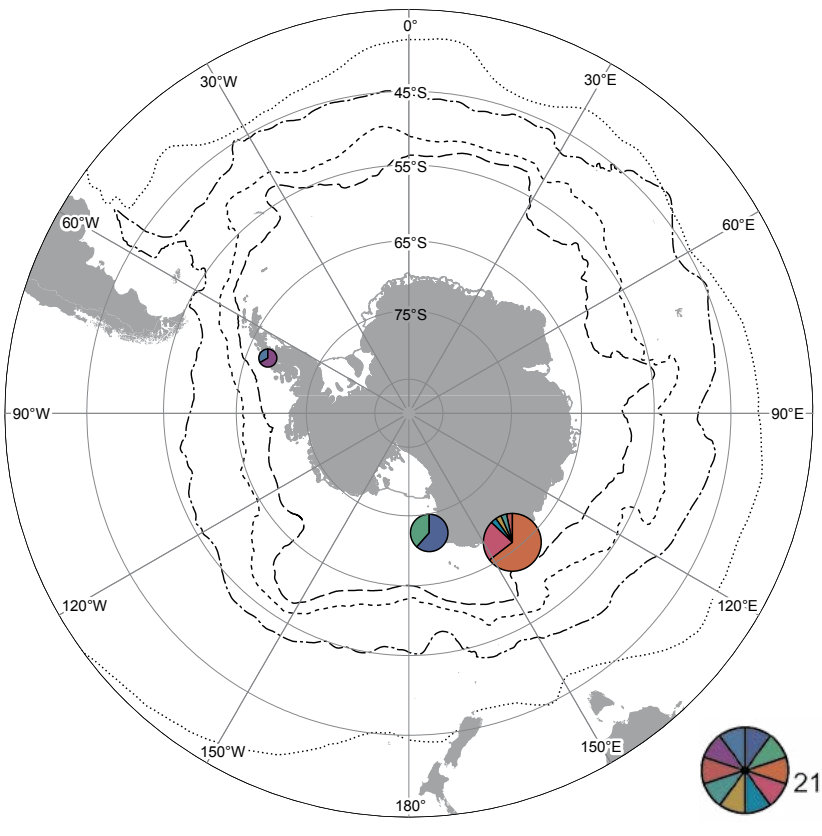
H1 H18 H26 H34 H42 H50 H59
H10 H19 H27 H35 H43 H51 H6
H11 H2 H28 H36 H44 H52 H60
H12 H20 H29 H37 H45 H53 H61
H13 H21 H3 H38 H46 H54 H62
H14 H22 H30 H39 H47 H55 H63
H15 H23 H31 H4 H48 H56 H7
H16 H24 H32 H40 H49 H57 H8
H17 H25 H33 H41 H5 H58 H9

Phylogeography Crinoida Maps 5-8 Map 5 *Promachocrinus kerguelensis* clade E1 is rare overall with very low haplotype diversity. It is better represented with a higher diversity on the West Antarctic South Orkney shelf, and seems absent from the sub-Antarctic islands. Map 6 *Promachocrinus kerguelensis* clade E2, like E1, is also very rare with low haplotype diversity. It is only found on the high-Antarctic shelf and is absent from all sub-Antarctic islands. Map 7 *Promachocrinus kerguelensis* clade F is also rather rare and shows very reduced haplotype diversity. It is found on the high-Antarctic shelf and from the West Antarctic South Orkney and South Sandwich Islands. It is absent from other sub-Antarctic islands. Map 8 *Florometra mawsoni* is closely related to *P. kerguelensis*. It is well represented on the East Antarctic shelf. It is found in lower abundance in the Peninsula, Scotia Arc, and Burdwood Bank. It seems to be absent from other sub-Antarctic localities except the Kerguelen Plateau. The Kerguelen, Dumont d'Urville Sea and Weddell Sea populations are composed of high numbers of different haplotypes and show high levels of diversity. As in the case of *P. kerguelensis* clade A, *F. mawsoni* may have found refuge on the Kerguelen Plateau during past glaciation, and recolonised high-Antarctic areas from there.



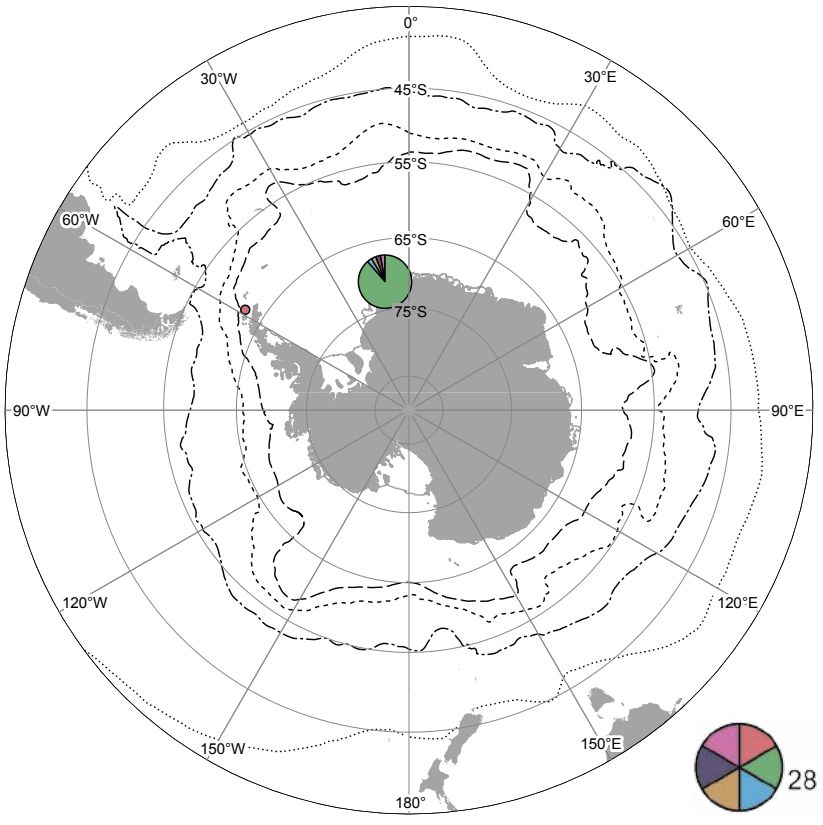
Map 9
Anthometrina adriani

Hap_1 Hap_13 Hap_4 Hap_8
Hap_10 Hap_14 Hap_5 Hap_9
Hap_11 Hap_2 Hap_6
Hap_12 Hap_3 Hap_7



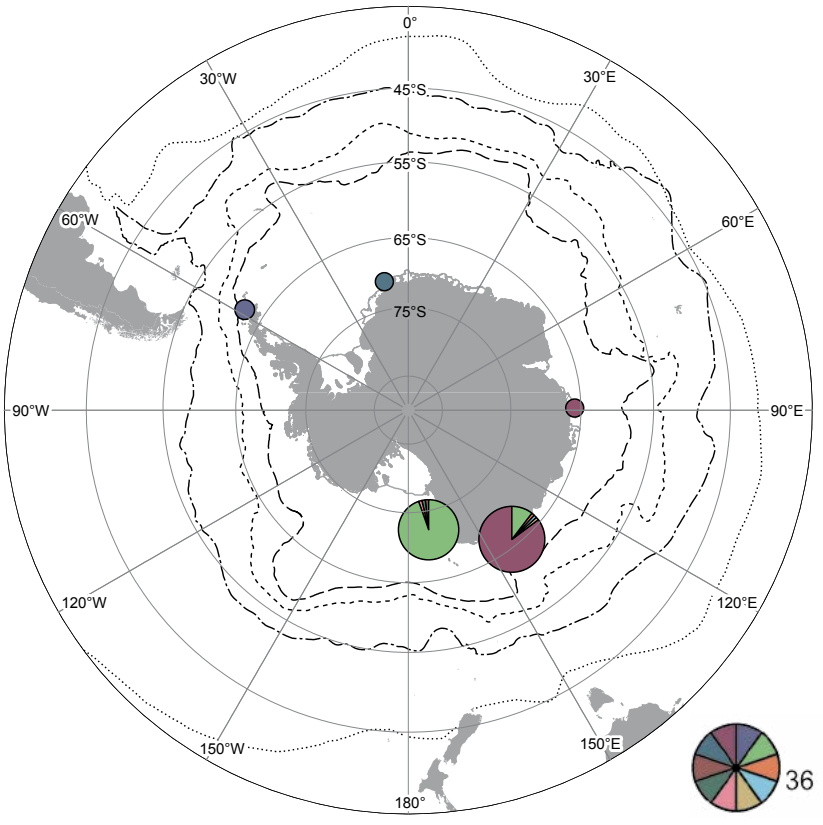
Map 10
Isometra graminea

Hap_1 Hap_5 Hap_8
Hap_2 Hap_6 Hap_9
Hap_3 Hap_6
Hap_4_ Hap_7



Map 11
Notocrinus virilis haplogroup A

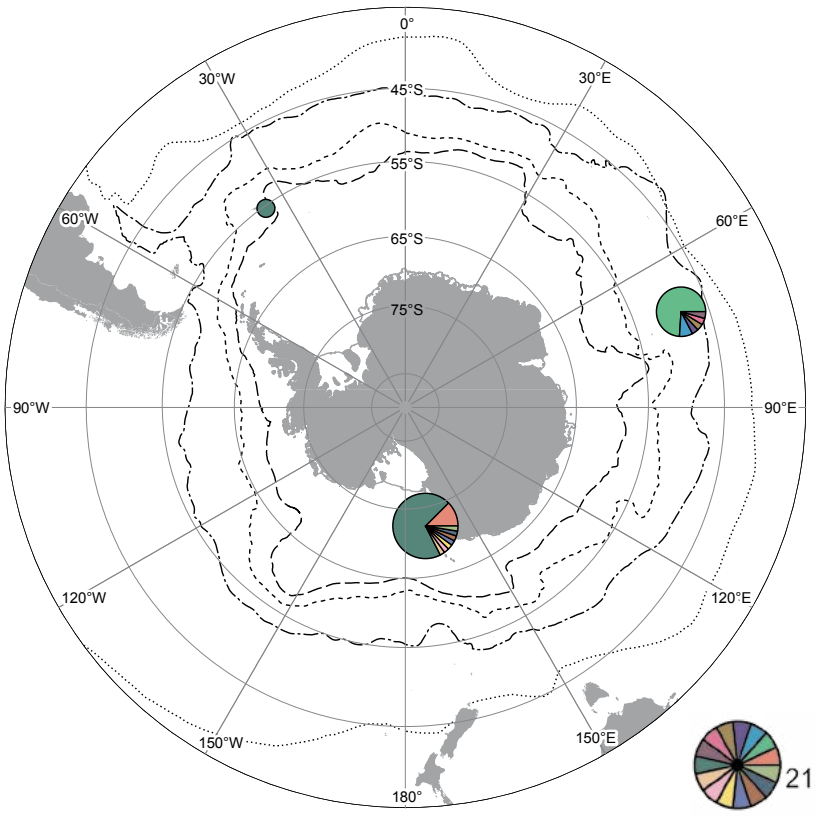
Hap_2_ Hap_6_
Hap_4_ Hap_7_
Hap_5_ Hap_8_



Map 12
Notocrinus virilis haplogroup B

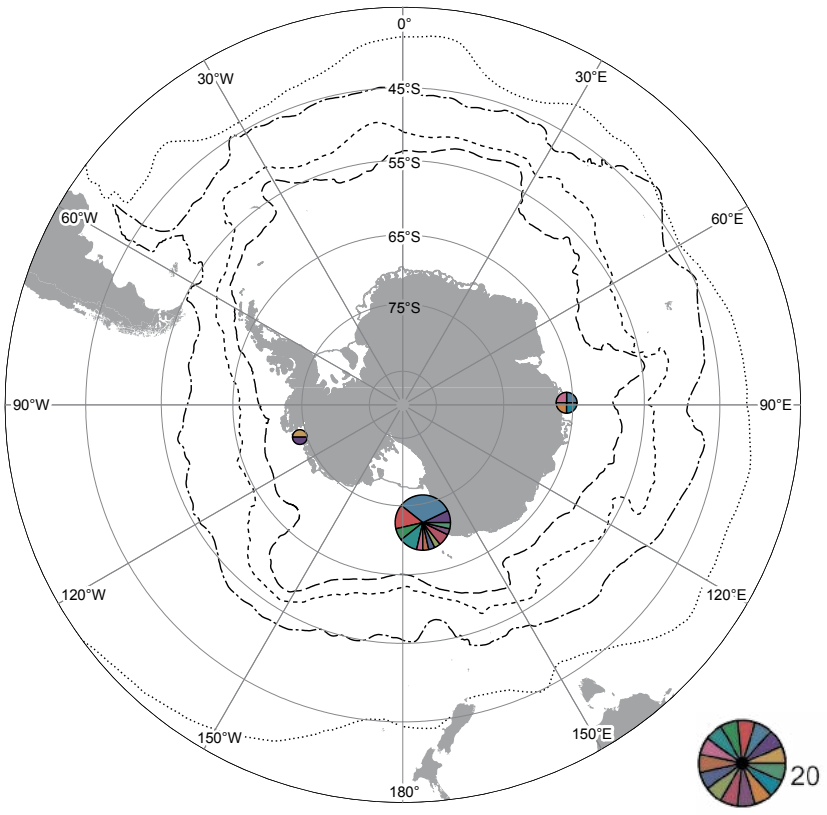
Hap_1_ Hap_14_
Hap_10_ Hap_15_
Hap_11_ Hap_16_
Hap_12_ Hap_3_
Hap_13_ Hap_9_

Phylogeography Crinoida Maps 9-12 Map 9 *Anthometrina adriani* is confined to the high-Antarctic shelf and is absent from the South Shetland Islands and the Scotia Arc as well as from the sub-Antarctic islands. The number of haplotypes is higher on the East Antarctic shelf. The number of specimens analysed is much smaller in the Antarctic Peninsula area. This is probably not a sampling bias; *A. adriani* populations from the Peninsula consist of fewer individuals (M. Eléaume, personal observations). Map 10 *Isometra graminea* is restricted to the high-Antarctic. The higher diversity detected on the East Antarctic Dumont d'Urville Sea shelf is probably linked to the greater number of specimens collected there. Each locality displays a set of endemic haplotypes, suggesting absence of gene flow in the past. However, the current situation remains unknown. It is possible that each of these populations represent a separate species. Map 11 *Notocrinus virilis* haplogroup A is restricted to the West Antarctic Weddell Sea and Scotia Arc. It shows a high level of geographic segregation with two populations displaying no haplotype in common. It is possible that the Weddell Sea and the South Shetland Islands populations may represent two distinct species. Map 12 *Notocrinus virilis* haplogroup B shows a high level of geographic segregation. The West and East Antarctic populations have no haplotypes in common. The East Antarctic populations display a reduced number of haplotypes in common, suggesting some degree of connectivity in the past. The current situation is unknown. It is, however, possible that the West and East Antarctic populations may represent two or three separate species. Colors and pies as in Map 1.



Map 13
Ptilocrinus amezianeae

Hap_1 Hap_13 Hap_3 Hap_7
Hap_10 Hap_14 Hap_4 Hap_8
Hap_11 Hap_15 Hap_5 Hap_9
Hap_12 Hap_2 Hap_6



Map 14
Feracrinus heinzelleri

Hap_1 Hap_5 Hap_9 Hap_13
Hap_2 Hap_6 Hap_10 Hap_14
Hap_3 Hap_7 Hap_11 Hap_15
Hap_4 Hap_8 Hap_12

Phylogeography Crinoida Maps 13-14 Map 13 The Kerguelen and Admiralty and Scott Island Seamounts *Ptilocrinus amezianeae* populations display no haplotype in common. The Ross Sea and South Sandwich populations have one haplotype in common, suggesting some degree of gene flow in the past. This pattern is suggestive of two disconnected populations that may have diverged into separate species. However, a detailed morphological analysis (Eléaume *et al.* 2011), and the fact that only a portion of the potential habitat of this species has been explored (sample bias), argue in favor of a single, undersampled species possibly a ring species. Map 14 *Feracrinus heinzelleri* shows a greater number of haplotypes in the Ross Sea population. This is probably due to the much greater number of specimens analysed in this population. New samples from the Kerguelen Plateau indicate that this species is also well represented there.

References

Allcock, A.L., Strugnell, J.M., 2012. Southern Ocean diversity: new paradigms from molecular ecology. *Trends in Ecology and Evolution*, **27**: 520–528.

Avise, J.C., 2000. *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, MA: 1-447.

Bowden, D.A., Schiaparelli, S., Clark, M.R., Rickard, G.J., 2010. A lost world? Archaic crinoid-dominated assemblages on an Antarctic seamount. *Deep-Sea Research II*, **58**(1–2): 119–127.

Clarke, A., Crame, J.A.,1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **338**: 299-309.

Clarke, A., Crame, J.A., 2010. Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **365**: 3655-3666.

Clément, M., Posada, D., Crandall, K.A., 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology,* **9**: 1657-1659.

Eléaume, M., 2006. Approche morphométrique de la variabilité phénotypique : conséquences systématiques et évolutives. Application aux crinoïdes actuels (Crinoidea: Echinodermata). PhD dissertation, *Muséum national d'Histoire naturelle*, Paris: 402 pp.

Eléaume, M., Hemery, L.G., Bowden, D.A., Roux, M. (2011) A large new species of the genus *Ptilocrinus* (Echinodermata, Crinoidea, Hyocrinidae) from Antarctic seamounts. *Polar Biology,* **34**: 1385-1397.

Eléaume, M., Hemery, L.G., Roux M., Améziane N., 2014. Chapter 5.25. Southern Ocean crinoids. In: De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., Udekem d'Acoz, C. d' *et al*. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge.

Excoffier, L., Lischer, H.E.L., 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, **10**: 564-567.

Hall, T.A., 1999. BioEdit: a user□friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series,* **41**: 95-98.

Hemery, L.G., 2011. Diversité moléculaire, phylogéographie et phylogénie des Crinoïdes (Echinodermes) dans un environnement extrême : l'océan Austral. PhD dissertation, *Muséum national d'Histoire naturelle*, Paris: 381 pp.

Hemery, L.G., Eléaume, M., Roussel, V., Améziane, N., Gallut, C., Steinke, D., Cruaud, C., Couloux, A., Wilson, N.G., 2012. Comprehensive sampling reveals circumpolarity and sympatry in seven mitochondrial lineages of the Southern Ocean crinoid species *Promachocrinus kerguelensis* (Echinodermata). *Molecular Ecology*, **21**: 2502-2518.

Hemery, L.G., Roux, M., Améziane, N., Eléaume, M., 2013a. High-resolution crinoid phyletic interrelationships: a preliminary study. *Cahiers de Biologie Marine,* **54**(4): 511-523.

Hemery, L.G., Améziane, N., Eléaume, M., 2013b. Circumpolar dataset of sequenced specimens of *Promachocrinus kerguelensis* (Echinodermata, Crinoidea). *Zookeys*, **315**: 55-64.

Kumar, S., Dudley, J., Nei, M., Tamura, K., 2008. MEGA: A biologist centric software for evolutionary analysis of DNA and protein sequences. *Briefings in Bioinformatics,* **9**: 299-306.

Messing, C.G., 1997. Living comatulids. *In:* Waters JA, Maples CG (eds.), *Geobiology of Echinoderms*. Paleontological Society Papers **3**: 3-30.

Naish, T., Powell, R., Levy, R., Wilson, G., Scherer, R., Talarico, F., Krissek, L., Niessen, F., Pompilio, M., Wilson, T., Carter, L., DeConto, R., Huybers, P., McKay, R., Pollard, D., Ross, J., Winter, D., Barrett, P., Browne, G., Cody, R., Cowan, E., Crampton, J., Dunbar, G., Dunbar, N., Florindo, F., Gebhardt, C., Graham, I., Hannah, M., Hansaraj, D., Harwood, D., Helling, D., Henrys, S., Hinnov, L., Kuhn, G., Kyle, P., Läufer, A., Maffioli, P., Magens, D., Mandernack, K., McIntosh, W., Millan, C., Morin, R., Ohneiser, C., Paulsen, T., Persico, D., Raine, I., Reed, J., Riesselman, C., Sagnotti, L., Schmitt, D., Sjunneskog, C., Strong, P., Taviani, M., Vogel, S., Wilch, T., Williams, T., 2009, Obliquity-paced Pliocene West Antarctic ice sheet oscillations, *Nature* **458**: 322–328.

Rogers, A.D., 2007. Evolution and biodiversity of Antarctic organisms: a molecular perspective. *Philosophical Transactions of the Royal Society B,* **362**: 2191-2214.

Rouse G.W., Jermiin L., Oji T., Young C.M., Lanterbecq D., Eeckhaut I., Browning T., Cisternas P., Stuckey M., Helgen L., Wilson N.G., Messing, C.G., 2013. Fixed, free and fixed: Phylogeny and Permian-Triassic origin of extant crinoid echinoderms. *Molecular Phylogenetics and Evolution*, **66**: 161-181.

Roux, M., Messing, C.G., Améziane, N., 2002. Artificial keys to the genera of living stalked crinoids (Echinodermata). *Bulletin of Marine Science,* **70**: 799-830.

Thatje, S., Hillenbrand, C.D., Larter, R., 2005. On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution*, **20**(10): 534-540.

Thatje, S., Hillenbrand, C.D., Mackensen, A. & Larter, R., 2008. Life hung by a thread: Endurance of Antarctic fauna in glacial periods. *Ecology*, **89**: 682-692.

Turner J, Bindschadler, R., Convey, P., Di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D.A., Mayewski, P.A., Summerhayes, C.P., 2009. *Antarctic Climate Change and the Environment*. Cambridge: Scientific Committee for Antarctic Research: 1-526.

Wilson, N.G., Hunter, R.L., Lockhart, S.J., Halanych, K.M., 2007. Multiple lineages and absence of panmixia in the "circumpolar" crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. *Marine Biology,* **152**: 895-904.

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

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

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

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

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

The Census of Antarctic Marine Life (CAML)

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

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

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

The Editorial Team

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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