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Distribution patterns in Antarctic and Subantarctic echinoderms

Juan Moles · Blanca Figuerola · Neus Campanyà-Llovet · Toni Monleón-Getino · Sergi Taboada · Conxita Avila

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Abstract Echinoderms are the dominant megafaunal taxa in Antarctic and Subantarctic waters in terms of abundance and diversity, having a predominant role in structuring communities. The current study presents new data on the asteroids, holothuroids, and ophiuroids (three of the five extant classes of echinoderms) collected in seven scientific campaigns (1995–2012) from Bouvet Is., South Shetland Is., and the Eastern Weddell Sea, from a wide bathymetric range (0–1,525 m). Among the 316 echinoderms collected, we extended the bathymetric ranges of 15 species and expanded the geographic distribution of 36 of them. This novel dataset was analyzed together with previous reports in order to establish general patterns of geographic and bathymetric distribution in echinoderms of the Southern Ocean (SO). Nearly 57 % of the assembled-data species resulted endemic of the SO, although further taxonomic efforts in less accessible areas are needed. Interestingly, some islands presented high levels of species richness even comparable to large geographic areas. While generally exhibiting a wide range of eurybathy, there were differences in species composition across depths corresponding to sublittoral, upper and lower bathyal, and abyssal. Bathymetric distribution was analyzed considering biological aspects for each class. As expected, circumpolar trends were found, although hydrographic currents may be the cause of differences in species composition among SO areas. Our analyses suggest zoogeographic links between Antarctica and the adjacent ocean basins, being the Scotia Arc the most remarkable. This study contributes to the knowledge of large-scale diversity and distribution patterns in an Antarctic key group.

Keywords Asteroidea · Holothuroidea · Ophiuroidea · Bathymetric distribution · Geographic distribution · Southern Ocean

Introduction

The separation of Antarctica from South America allowed the formation of the Antarctic Circumpolar Current (ACC) and the establishment of the Polar Front (PF). This thermal and hydrographic barrier hampers marine organisms' dispersion from north to south and vice versa at the Southern Ocean (SO; Barker and Thomas 2004). Simultaneously, the PF promotes the dispersal of marine organisms—larvae or adults—from west to east around Antarctica (Fell 1962; Olbers et al. 2004), and the East Wind Drift along the Antarctic coast deeply affects the distribution of shelf fauna. The combination of geographic isolation and climate change has led to a rich marine Antarctic biota with high number of endemic taxa (Brandt and Gutt 2011). However, numerous species are also shared between the SO and the nearest geographic neighbors mainly due to their connections during the Cenozoic (Clarke et al. 2005).

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J. Moles (✉) · B. Figuerola · S. Taboada · C. Avila
Department of Animal Biology (Invertebrates) and Biodiversity Research Institute (IrBIO), University of Barcelona, Barcelona, Catalonia, Spain
e-mail: moles.sanchez@gmail.com

N. Campanyà-Llovet
Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada

T. Monleón-Getino
Department of Statistics, University of Barcelona, Barcelona, Catalonia, Spain

The Magellanic region, through the Drake Passage and Scotia Arc, especially acts as a potential faunal exchange pathway (Clarke et al. 2005; Brandt et al. 2007a). Despite the present day knowledge, essential baseline data on marine biodiversity and biogeography are still lacking for most regions of the SO (Kaiser et al. 2013). This is urgently required to identify biological responses to predicted environmental changes in Antarctica. Gutt et al. (2004) pointed out the need of comparative studies between Antarctic and South-American fauna to better understand species' dispersion capabilities and the effect of isolation of populations on their distribution.

Diachronic anchor ice greatly influences Antarctic benthic community structure. Short-term seasonal and spatial variations from anchor and sea ice contribute to the patchiness of benthic communities in the Antarctic continental shelf (Raguá-Gil et al. 2004). At the same time, long-term glacial and interglacial cycles allowed allopatric speciation (Thatje et al. 2005), thus promoting diversification and wide bathymetric tolerances for several Antarctic taxa (Brandt et al. 2007a; Rogers 2007). Furthermore, due to a very deep continental shelf and a weakly stratified water column, circumantarctic distributions and broad depth ranges are also widespread characteristic features of marine Antarctic fauna (Brey et al. 1996; Soler i Membrives et al. 2009; Hemery et al. 2012). This suggests that the deep-sea fauna around Antarctica, largely consisting of taxa with high dispersal capabilities, may be related both to adjacent shelf communities and to deep-sea fauna from other oceans, being directly connected below 3,000 m (Brandt et al. 2007a, b; Pawlowski et al. 2007). In fact, differences in the reproductive mode might explain composition variations between sites and depths (Raguá-Gil et al. 2004). Thus, long-range dispersion by pelagic planktotrophic and lecithotrophic larvae facilitates the spreading of many species and increases their colonization capacity of highly disturbed habitats, contrary to brooding organisms that have lower dispersal capabilities (Shilling and Manahan 1994; Poulin et al. 2002).

Recently, total species richness of macrozoobenthic organisms inhabiting the Antarctic continental shelf has been estimated to comprise between 11,000 and 17,000 species, of which over 8,800 are presently known and described (Griffiths 2010; De Broyer et al. 2011). Antarctic benthic fauna is characterized by the lack of durophagous species either as competitors or as predators (Clarke et al. 2004). Thus, echinoderms are the dominant errant megafaunal taxa in the SO in terms of abundance and diversity and have a predominant role in structuring benthic communities (Dayton et al. 1974; Clarke and Johnston 2003; Chiantore et al. 2006). Around 10 % of the known Antarctic macrozoobenthic species are echinoderms, with Asteroidea (208 species; De Broyer et al. 2011), Holothuroidea (187 species; O'Loughlin et al. 2011), and Ophiuroidea (126 species; Stöhr et al. 2012), being the most speciose classes. Although echinoderm species richness is higher in the continental shelf, where dense communities of sessile suspension feeders and its wandering associated fauna dominate, they also show a high diversity along the slope and on the deep-sea plains (Billett et al. 2001; Aronson et al. 2007).

At the beginning of the twentieth century, the South Shetland Is. and the Weddell Sea echinoderm fauna were widely explored (e.g., Ludwig 1903; Vaney 1914; Koehler 1917). More recently, high species richness of asteroids, ophiuroids, and holothuroids has been found on a regular basis in these areas (Gutt 1990a, b; Gutt and Piepenburg 1991; Massin 1992a; Piepenburg et al. 1997; Presler and Figielska 1997; Manjón-Cabeza et al. 2001; Manjón-Cabeza and Ramos 2003). In addition, within the last decades, new collections and re-examinations of previously collected material have contributed to the description of new species (Carriol and Féral 1985; Gutt 1990a, b; Massin 1992a; Stampanato and Jangoux 1993; O'Loughlin 2002, 2009; Massin and Hétérier 2004; O'Loughlin and Ahearn 2008; Janosik and Halanych 2010). Other than the South Shetland Is. and the Weddell Sea, echinoderm fauna from Subantarctic areas such as the remote Bouvet Is. has been also surveyed within the last years (Arntz 2006). Interestingly, it appears to be that the major reason for the impoverished fauna occurring in the vicinities of Bouvet Is. is under-sampling rather than isolation or geological youth (Arntz et al. 2006). This island has been proposed as a missing link in the SO, connecting macrozoobenthic fauna with the adjacent Magellanic South America, the Antarctic Peninsula, and the high Antarctic Weddell Sea (Arntz et al. 2006; Gutt et al. 2006), although little is known about its echinoderm fauna.

Bearing in mind the ecological importance of echinoderms as one of the major groups structuring the Antarctic and Subantarctic benthos, our aim was twofold: first, to enhance the present knowledge of Antarctic echinoderms species and their geographic and bathymetric distribution by identifying species from widely studied (Eastern Weddell Sea and South Shetland Is.) and poorly explored (Bouvet Is.) areas; second, to determine the bathymetric and geographic distributions of Antarctic echinoderms in the SO combining our data with all bibliographic resources available so far. Species composition of the areas studied was compared to the adjacent ocean basins and discussed. Asteroids, ophiuroids, and holothuroids were selected as target classes within echinoderms to address both objectives.

Materials and methods

Collection and identification of newly collected samples

The study area comprised Bouvet Is., the South Shetland Is., and the Eastern Weddell Sea. Samples from Bouvet Is. and the Weddell Sea were collected during the Antarctic cruises ANT XV/3 (February 1998) and ANT XXI/2 (November 2003–January 2004) on board the R/V *Polarstern* (AWI, Bremerhaven, Germany) at 33 stations. Samples from the South Shetland Is. (mostly from the vicinities of Deception and Livingston Is.) were collected at eight stations on board the BIO-*Hespérides* in January 1995 and January 2006 during the BENTART and ECOQUIM-2 cruises, respectively. During the ACTIQUIM campaigns at Deception and Livingston Is. (2007–2008, 2008–2009, and 2010–2011), 18 stations were surveyed by SCUBA diving. Collection ranged from 0 to 1,525 m depth using Agassiz trawl, bottom trawl, epibenthic sledge, giant box corer, and Rauschert dredge in Bouvet Is. and the Weddell Sea, and Agassiz trawl and rock dredge in the South Shetland Is. (Table 1). In all cases, sampling was qualitative.

After photographing the living animals, they were preserved in 70 % ethanol for further taxonomic identification to the lowest possible taxonomical level (Table 2). Key references and synopses used for the identification within the different classes of echinoderms were: Ludwig (1903), Koehler (1917), Clark (1962, 1963), Clark and Downey (1992), Stampanato and Jangoux (1993), and Presler and Figielska (1997) for asteroids; Koehler (1917), Mortensen (1936), Fell (1961), and Madsen (1967) for ophiuroids; Théel (1886), Vaney (1914), Carriol and Féral (1985), Gutt (1990a, b), Massin (1992a, b, 2010), Massin and Hétérier (2004), O'Loughlin (2002, 2009), O'Loughlin and Ahearn (2005, 2008), Cross et al. (2009), O'Loughlin et al. (2009, 2011), O'Loughlin and VandenSpiegel (2010), O'Loughlin and Whitfield (2010), and O'Loughlin personal notes (unpublished data) for holothuroids. Crinoids and echinoids were not studied here due to the low number of samples collected during our surveys.

Assembled data

Our data (Table 2) were analyzed together with the Antarctic and Subantarctic echinoderm species list gathered from the available literature, the 'Scientific Committee on Antarctic Research Marine Biodiversity Information Network', and the SCAR's Marine Biodiversity Information database (SCAR-MarBIN; http://www.scarmarbin.be/; De Broyer et al. 2012). Metadata were checked against the major world databases, World Ophiuroidea (Stöhr and O'Hara 2012), World Asteroidea (Mah 2009), and complemented with the Antarctic Marine Invertebrates of the NMNH/Smithsonian Institution Databases (Lemaitre et al. 2009). Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) and Ocean Biogeographic Information Systems (OBIS; http://iobis.org/) databases were used together with information within keys to compile all metadata (Online Resources 1–3). Due to the heterogeneous nature of the compiled data and the assignment of the occurrences of the species to geographic areas (see below), sampling effort could not be calculated in this study.

Study area

Bathymetric and geographic metadata from other cruises reported in the literature and online databases together with our own new data were pooled and analyzed in order to evaluate the relationships between taxa in 20 areas of the SO (Fig. 1). Following several authors (Clarke and Johnston 2003; Barboza et al. 2011; O'Loughlin et al. 2011), Antarctica was divided into eight geographic areas: Antarctic Peninsula, Amundsen Sea, Bellingshausen Sea, Dumont D'Urville Sea (including Ballenny Is.), Enderby Plain, Prydz Bay, Ross Sea, and Weddell Sea. Also, eight island groups were considered: Bouvet Is., Heard and McDonald Is., Kerguelen Is., South Georgia Is., South Sandwich Is., South Shetland Is., South Orkney Is., and the Subantarctic Marion, Prince Edward, and Crozet Is. (these last three considered as a single group). Due to proximity to the study area, Australia, New Zealand (including Macquarie Is.), South Africa, and South America shared species distribution were also included in the analysis for comparison purposes.

Data analysis

Due to unequal sampling efforts (in both terms of regions surveyed and bathymetry) and use of heterogeneous gear to obtain all metadata included in the analysis, binary data (presence/absence) were chosen to construct the echinoderm data matrix. Echinoderm presence/absence was preferred rather than abundance because our study treated a large-scale area; therefore, habitat patchiness and/or heterogeneity would bias our results. We performed cluster and MDS analyses to examine the faunal patterns among the different areas and across depths. The widely used Bray-Curtis index was used to build the similarity matrix, being this index equivalent to the Sörensen index for presence/absence matrices (Clarke et al. 2006). Hierarchical clustering was obtained using the group linkage clustering technique to evaluate the similarities in species composition between regions. Depths were divided into 500-m categories, except for the bathymetric range of 0–100 m as

Table 1 Data related to the stations surveyed in the present study

SN	Area	Location	Station code	Date	Latitude	Longitude	Depth (m)	Gear
1	Bouvet region	Bouvet Is.	PS65/020-1	24/11/2003	54°36,95′S	3°17,58′E	553	AT
2	Bouvet region	Bouvet Is.	PS65/029-1	25/11/2003	54°31,59′S	3°13,05′E	377	AT
3	Bouvet region	Bouvet Is.	PS65/019-1	24/11/2003	54°30′S	3°13,99′E	260	AT
4	Bouvet region	Bouvet Is.	PS65/028-1	25/11/2003	54°22′S	3°16,99′E	134	AT
5	South Shetlands	Deception Is.	AGT-9	07/01/2006	60°36,36′S	63°02,29′W	100	RoD
6	South Shetlands	Deception Is.	AGT-12	08/01/2006	63°01,91′S	60°32,64′W	216	RoD
7	South Shetlands	Deception Is.	3, Whalers Bay	11/01/2010	62°59,37′S	60°33,42′W	0–15	SD
8	South Shetlands	Deception Is.	10, Murature	15/01/2010	62°47′S	60°41′21″W	0–15	SD
9	South Shetlands	Deception Is.	11, Whalers Bay	16/01/2010	62°59,37′S	60°33,42′W	0–15	SD
10	South Shetlands	Deception Is.	13, Baily Head	19/01/2010	62°57,79′S	60°30,65′W	0–15	SD
11	South Shetlands	Deception Is.	14, Fildes Point	23/01/2010	62°59′29″S	60°33′43″W	0–15	SD
12	South Shetlands	Deception Is.	21, Pete's Pillar	18/01/2012	62°59′32″S	60°33′W	15	SD
13	South Shetlands	Deception Is.	36, Fildes Point	29/01/2012	62°59′29″S	60°33′43″W	20	SD
14	South Shetlands	Deception Is.	50, Neptune's Bellows	14/02/2012	62°59′32″S	60°33′58″W	15	SD
15	South Shetlands	Deception Is.	52, Fildes Point	17/02/2012	62°59′29″S	60°33′43″W	20	SD
16	South Shetlands	Deception Is.	7, Whalers Bay	11/12/2008	62°59,37′S	60°33,42′W	0–16	SD
17	South Shetlands	Deception Is.	10, Whalers Bay	16/12/2008	62°59,37′S	60°33,42′W	4	SD
18	South Shetlands	Deception Is.	15, Whalers Bay	20/12/2008	62°59,37′S	60°33,42′W	16	SD
19	South Shetlands	Deception Is.	17, Whalers Bay	24/12/2008	62°59,37′S	60°33,42′W	17	SD
20	South Shetlands	Deception Is.	26, Fildes Point	30/12/2008	62°59′29″S	60°33′43″W	0–15	SD
21	South Shetlands	Deception Is.	27, Fildes Point	31/12/2008	62°59′29″S	60°33′43″W	0–15	SD
22	South Shetlands	King George Is.	KG1	01/01/1995	n.a.	n.a.	15	SD
23	South Shetlands	Livingston Is.	ANT95-A30	01/01/1995	n.a.	n.a.	15	SD
24	South Shetlands	Livingston Is.	AGT-3	05/01/2006	62°43,57′S	60°27,49′W	50	AT
25	South Shetlands	Livingston Is.	AGT-5	05/01/2006	62°40,56′S	60°42,41′W	25	AT
26	South Shetlands	Livingston Is.	AGT-6	06/01/2006	62°43,12′S	60°43,68′W	78	RoD
27	South Shetlands	Livingston Is.	AGT-7	06/01/2006	62°41,58′S	60°44,83′W	37	RoD
28	South Shetlands	Livingston Is.	2, Hannah Point	06/02/2012	62°39′25,7″S	60°36′54,0″W	15	SD
29	South Shetlands	Livingston Is.	4, Raquelia Rocks	07/02/2012	62°38′59,7″S	60°22′54,0″W	15	SD
30	South Shetlands	Livingston Is.	12	12/02/2012	62°39′52,1″S	60°35′35,8″W	15	SD
31	Bouvet region	Spiess Seamount	PS65/344-1	11/01/2004	54°43,99′S	0°7,99′W	576	AT
32	Weddell Sea	Austasen	PS65/090-1	09/12/2003	70°55,92′S	10°32,37′W	288	AT
33	Weddell Sea	Austasen	PS65/109-1	10/12/2003	70°47,88′S	11°24,13′W	1,525	AT
34	Weddell Sea	Austasen	PS65/121-1	11/12/2003	70°50,08′S	10°34,76′W	274	AT
35	Weddell Sea	Austasen	PS65/132-1	12/12/2003	70°56,42′S	10°31,61′W	284	BT
36	Weddell Sea	Austasen	PS65/148-1	13/12/2003	70°56,67′S	10°32,05′W	302	BT
37	Weddell Sea	Austasen	PS65/173-1	16/12/2003	70°56,82′S	10°31,76′W	296	AT
38	Weddell Sea	Austasen	PS65/259-1	24/12/2003	70°57,00′S	10°33,02′W	333	BT
39	Weddell Sea	Austasen	PS65/276-1	28/12/2003	71°06,44′S	11°27,76′W	277	AT
40	Weddell Sea	Austasen	PS65/336-1	05/01/2004	72°49,99′S	10°28′W	281	AT
41	Weddell Sea	Austasen	PS65/039-1	05/12/2003	71°6′S	11°31,99′W	175	AT
42	Weddell Sea	Austasen	PS65/145-1	13/12/2003	70°57,01′S	10°48,64′W	406	ES
43	Weddell Sea	Austasen	PS65/166-1	15/12/2003	70°55,99′S	10°31,99′W	338	BT
44	Weddell Sea	Austasen	PS65/175-1	16/12/2003	70°55,99′S	10°31′W	337	BT
45	Weddell Sea	Austasen	PS65/237-1	22/12/2003	70°50,50′S	10°35,54′W	264	BT
46	Weddell Sea	Austasen	PS65/245-1	22/12/2003	70°55,99′S	10°31,99′W	337	BT
47	Weddell Sea	Austasen	PS65/253-1	23/12/2004	71°04,30′S	11°33,92′W	309	BT
48	Weddell Sea	Austasen	PS65/265-1	27/12/2003	70°52,75′S	10°51,24′W	295	BT

Table 1 continued

SN	Area	Location	Station code	Date	Latitude	Longitude	Depth (m)	Gear
49	Weddell Sea	Austasen	PS65/279-1	29/12/2003	71°07′S	11°28,99′W	120	AT
50	Weddell Sea	Kapp Norvegia	PS65/233-1	21/12/2003	71°18,99′S	13°56,56′W	848	AT
51	Weddell Sea	Kapp Norvegia	PS65/232-1	21/12/2003	71°18′0″S	13°55′W	910	ES
52	Weddell Sea	Vestkapp	PS65/297-1	01/01/2004	72°48,50′S	19°31,60′W	668	RD
53	Weddell Sea	Vestkapp	PS65/308-1	02/01/2004	72°50,18′S	19°35,94′W	622	RD
54	Weddell Sea	Vestkapp	PS65/292-1	31/12/2003	72°51,43′S	19°38,62′W	598	BT
55	Weddell Sea	North Halley	PS48/150 + 154	11/02/1998	74°0,66′S	27°0,21′W	567–789	BT
56	Weddell Sea	North Halley	PS48/150 + 155	11/02/1998	74°0,66′S	27°0,21′W	567–789	BT
57	Weddell Sea	North Halley	PS48/150 + 156	11/02/1998	74°0,66′S	27°0,21′W	567–789	BT
58	Weddell Sea	North Halley	PS48/150 + 157	11/02/1998	74°0,66′S	27°0,21′W	567–789	BT
59	Weddell Sea	North Halley	PS48/150 + 158	11/02/1998	74°0,66′S	27°0,21′W	567–789	BT

SN station number

AT Agassiz trawl, *BT* bottom trawl, *ES* epibenthic sledge, *RD* Rauschert dredge, *RoD* rock dredge, *SD* SCUBA diving

n.a. not available

it was statistically different to the closer ranges, and included into the MDS plot; less surveyed depths (>6,000 m) were not included in the MDS analysis presented here since their composition was remarkably different from the rest of bathymetric categories.

Results

New data

A total of 316 specimens were identified in this study, including asteroids, ophiuroids, and holothuroids (Table 2). Out of these, 32 asteroids (107 specimens) from four orders were identified to species level. The most represented asteroid families in number of species were Asteriidae and Odontasteridae (five species each), followed by Pterasteridae (four), Ganeriidae, Goniasteridae, and Solasteridae (three species each), Astropectinidae, Echinasteridae, Poranidae, and Stichasteridae (two species each), and finally Asterinidae (one). Thirteen ophiuroid species (53 specimens) from the two existing orders (Euryalida and Ophiurida) were identified. The greatest number of ophiuroid species was found within the Ophiuridae family (six species), and two different species were identified from each Gorgonocephalidae, Amphiuridae, and Ophiacanthidae families; Ophiodermatidae had only one species. Out of the 156 holothuroid specimens collected, 34 species from the six existing orders were found. The most speciose families were the dendrochirotid Cucumariidae (14) and Psolidae (nine) followed by the families Chiridotidae, Elpidiidae, and Synallactidae (three species each), while Ypsilothuriidae and Molpadiidae had only one species each.

Our data extended the bathymetric ranges of 15 species (10 Holothuroidea and 4 Asteroidea) and enlarged the geographic distribution of 36 species (19 Holothuroidea, 13 Asteroidea, and 4 Ophiuroidea; see Table 2). Our data expanded the bathymetric range of *Diplasterias kerguelenensis* to superficial waters (0 m), and four species of holothuroids down to 1,525 m (*Paradota weddellensis*, *Peniagone vignioni*, *Protelpidia murrayi*, *Rhipidothuria racovitzai*). Remarkably, although some species were found for the first time in Bouvet Is. (*Cucamba psolidiformis*, *Cucumaria attenuata*, *Ophiacantha antarctica*, *Ophioplinthus gelida*, *Ophiura rouchi*, *Psolidium incubans*, *R. racovitzai*), the Weddell Sea (*Acodontaster elongatus*, *Perknaster fuscus*, *Psolidium whittakeri*, *Psolus paradubiosus*, *Pteraster rugatus*, *Pteraster stellifer*), and the South Shetland Is. (*Cladodactyla crocea*, *Crucella scotiae*, *D. kerguelenensis*, *Echinocucumis hispida*, *Psolus charcoti*), they were previously recorded from the vicinities of these regions or they were considered as circumantarctic. The asteroid *Solaster longoi* and the holothuroid *Trachythyone cynthiae*, previously known only from Marion Is. group and Pridz Bay, respectively, have been reported for the first time in the Weddell Sea.

Assembled data

Species richness

To date, a total of 555 species of echinoderms (excluding echinoids and crinoids) have been recorded from Antarctic waters including our data and previous literature: 229 asteroids, 129 ophiuroids, and 197 holothuroids. The total number of species was slightly higher than those reported by recent studies (De Broyer et al. 2011; O'Loughlin et al. 2011;

Table 2 Depth and collection site of the identified species of this study collected in Bouvet Is., South Shetland Is., and the Weddell Sea

	Depth (m)	Collection site	SN
Asteroidea			
Acodontaster elongatus granuliferus (Koehler, 1912)	567–789	Weddell Sea[a]	55, 56
Acodontaster hodgsoni (Bell, 1908)	294–337	Weddell Sea	46, 48
Adelasterias papillosa (Koehler, 1906)	14–342	Deception Is.[a]	16
Bathybiaster loripes loripes Sladen, 1889	1,525	Weddell Seaa	33
Chitonaster johannae Koehler, 1908	567–789	Weddell Sea	56
Cryptasterias turqueti (Koehler, 1906)	0–15[a] (Prev. 25–498)	Deception Is.[a]	14, 20
Cuenotaster involutus (Koehler, 1912)	332	Weddell Sea	38
Diplasterias kerguelenensis (Koehler, 1917)	0–16[a] (Prev. 601–3,950)	Deception Is.[a]	7, 16, 21
Diplopteraster sp.	308	Weddell Sea	47
Granaster nutrix (Studer, 1885)	20	Deception Is.[a]	13
Henricia smilax (Koehler, 1920)	567–848	Weddell Sea	50, 55
Kampylaster incurvatus Koehler, 1920	848	Weddell Sea	50
Lysasterias hemiora Fisher, 1940	295–308	Weddell Sea	47, 48
Neosmilaster sp.	0–17	Deception Is.[a]	8, 18, 19, 20
Notioceramus anomalus Fisher, 1940	597–848	Weddell Sea	50, 54
Odontaster meridionalis (E.A. Smith, 1876)	0–264	Deception Is., Weddell Sea	19, 21, 45
Odontaster penicillatus (Philippi, 1870)	567–789	Weddell Sea	55
Odontaster validus Koehler, 1906	0–100	Deception Is., Weddell Sea	5–21, 41
Paralophaster antarcticus (Koehler, 1912)	567–789	Weddell Sea	59
Paralophaster lorioli (Koehler, 1907)	1,525	Weddell Sea	33
Pergamaster incertus (Bell, 1908)	567–789	Weddell Sea	55
Perknaster densus Sladen, 1889	405	Weddell Sea	42
Perknaster fuscus Sladen, 1889	337	Weddell Sea[a]	46
Porania (*Porania*) *antarctica* Smith, 1876	376–789	Bouvet Is., Weddell Sea	2, 58
Psilaster charcoti (Koehler, 1906)	332	Weddell Sea	38
Pteraster rugatus Sladen, 1882	338	Weddell Sea[a]	43
Pteraster stellifer hunteri (Koehler, 1920)	567–790[a] (not recorded Prev.)	Weddell Sea[a]	56
Pteraster stellifer stellifer Sladen, 1882	405	Weddell Sea[a]	42
Rhopiella hirsuta (Koehler, 1920)	332–789	Weddell Sea	38, 57
Smilasterias triremis Sladen, 1889	0–15[a] (Prev. 94–2,710)	Deception Is.[a]	9, 11
Solaster longoi Stampanato and Jangoux, 1993	333	Weddell Sea[a]	38
Spoladaster sp.	295	Weddell Sea	48
Ophiuroidea			
Amphioplus acutus Mortensen, 1936	78	Livingston Is.	26
Amphiura joubini Koehler, 1912	337	Weddell Sea	44
Astrochlamys bruneus Koehler, 1911	337–338	Weddell Sea	43, 44
Astrotoma agassizii Lyman, 1875	277–338	Weddell Sea	39, 43, 44
Ophiacantha antarctica Koehler, 1900	260–622	Bouvet Is.[a], Weddell Sea	3, 53
Ophiacantha vivipara Ljungman, 1870	622	Weddell Sea	53
Ophiolimna antarctica (Lyman, 1879)	277–337	Weddell Sea	39, 44
Ophionotus victoriae Bell, 1902	0–260	Bouvet Is., Deception Is.	3, 4, 16
Ophioplinthus brevirima (Mortensen, 1936)	120–337	Weddell Sea	39, 41, 46, 49

Table 2 continued

	Depth (m)	Collection site	SN
Ophioplinthus gelida (Koehler, 1901)	78–910	Weddell Sea, Bouvet Is.[a], Deception Is.[a], Livingston Is.	3, 5, 6, 26, 39, 40, 44, 48, 51, 52
Ophiosteira echinulata Koehler, 1922	277	Weddell Sea	39
Ophiosteira rotundata Koehler, 1922	277–337	Weddell Sea	39, 44
Ophiura rouchi (Koehler, 1912)	260–377	Bouvet Is.[a]	2, 3
Holothuroidea			
Bathyplotes bongraini Vaney, 1914	377	Bouvet Is.	2
Cladodactyla crocea var. *croceoides* (Vaney, 1908)	37–50[a] (Prev. 64–462)	Livingston Is.[a]	24, 27
Crucella scotiae (Vaney, 1906)	25–281	Deception Is.[a], Livingston Is.[a], Weddell Sea	5, 24, 25, 34, 40
Cucamba psolidiformis (Vaney, 1908)	50–78	Livingston Is.[a]	24, 26
Cucumaria attenuata Vaney, 1906	134–281	Bouvet Is.[a], Weddell Sea	4, 39, 40
Echinocucumis hispida (Barrett, 1857)	15[a] (Prev. 121–3,850)	Livingston Is.[a]	23
Echinopsolus acanthocola Gutt, 1990	284–333	Weddell Sea	32, 35, 38
Heterocucumis denticulata (Ekman, 1927)	175	Weddell Sea	41
Heterocucumis steineni (Ludwig, 1898)	0–302	Deception Is.[a], King George Is., Weddell Sea	13, 15, 20, 22, 32, 35, 36
Microchoerus splendidus Gutt, 1990	288	Weddell Sea	32
Molpadia musculus Risso, 1826	78	Livingston Is.	26
Paradota weddellensis Gutt, 1990	274–1,525[a] (Prev. 59–1,191)	Weddell Sea	33, 36, 44
Peniagone vignoni Hérouard, 1901	1,525[a] (Prev. 300–787)	Weddell Sea	33
Protelpidia murrayi (Théel, 1879)	1,525[a] (Prev. 0–807)	Weddell Sea	33
Pseudostichopus peripatus (Sluiter, 1901)	78[a] (Prev. 134–5,453)	Livingston Is.	26
Pseudostichopus spiculiferus (O'Loughlin, 2002)	338–1,525	Weddell Sea	33, 43
Psolicrux coatsi (Vaney, 1908)	50–288	Livingston Is., Weddell Sea	24, 32
Psolidiella mollis (Ludwig and Heding, 1935)	78–134	Bouvet Is., Livingston Is.	4, 26
Psolidium incubans Ekman, 1925	134[a] (Prev. 12–38)	Bouvet Is.[a]	4
Psolidium poriferum (Studer, 1876)	575	Spiess Seamount[a]	31
Psolidium whittakeri O'Loughlin and Ahearn, 2008	175–553[a] (Prev. 200–1,435)	Bouvet Is., Weddell Sea[a]	1, 41
Psolus antarcticus (Philippi, 1857)	575	Spiess Seamount	31
Psolus charcoti Vaney, 1906	50–296	Livingston Is.[a], Weddell Sea	24, 26, 35, 37, 40, 41
Psolus granulosus Vaney, 1906	15–50[a] (Prev. 5)	Deception Is.[a], Livingston Is.[a]	12, 14, 24
Psolus koehleri Vaney, 1914	288–333	Weddell Sea	32, 38
Psolus paradubiosus Carriol and Féral, 1985	284–553	Bouvet Is., Weddell Sea[a]	1, 35, 37, 44
Rhipidothuria racovitzai Hérouard, 1901	553–1,525[a] (Prev. 200–800)	Bouvet Is.[a], Weddell Sea	1, 33
Sigmodota contorta (Ludwig, 1875)	284	Weddell Sea	35
Sigmodota magnibacula (Massin and Hétérier, 2004)	134	Bouvet Is.[a]	4
Staurocucumis liouvillei (Vaney, 1914)	134–337	Bouvet Is., Weddell Sea	4, 35, 36, 38, 44
Staurocucumis turqueti (Vaney, 1906)	50–338	Weddell Sea	36, 43
Trachythyone bouvetensis (Ludwig and Heding, 1935)	50–175	Deception Is.[a], Livingston Is.[a], Weddell Sea	5, 24, 41

Table 2 continued

	Depth (m)	Collection site	SN
Trachythyone cynthiae O'Loughlin, 2009	333	Weddell Sea[a]	38
Trachythyone maxima Massin, 1992	337	Weddell Sea	44

SN Station Number. See correspondence in Table 1

Prev. Previous reports

[a] New record for this depth or area

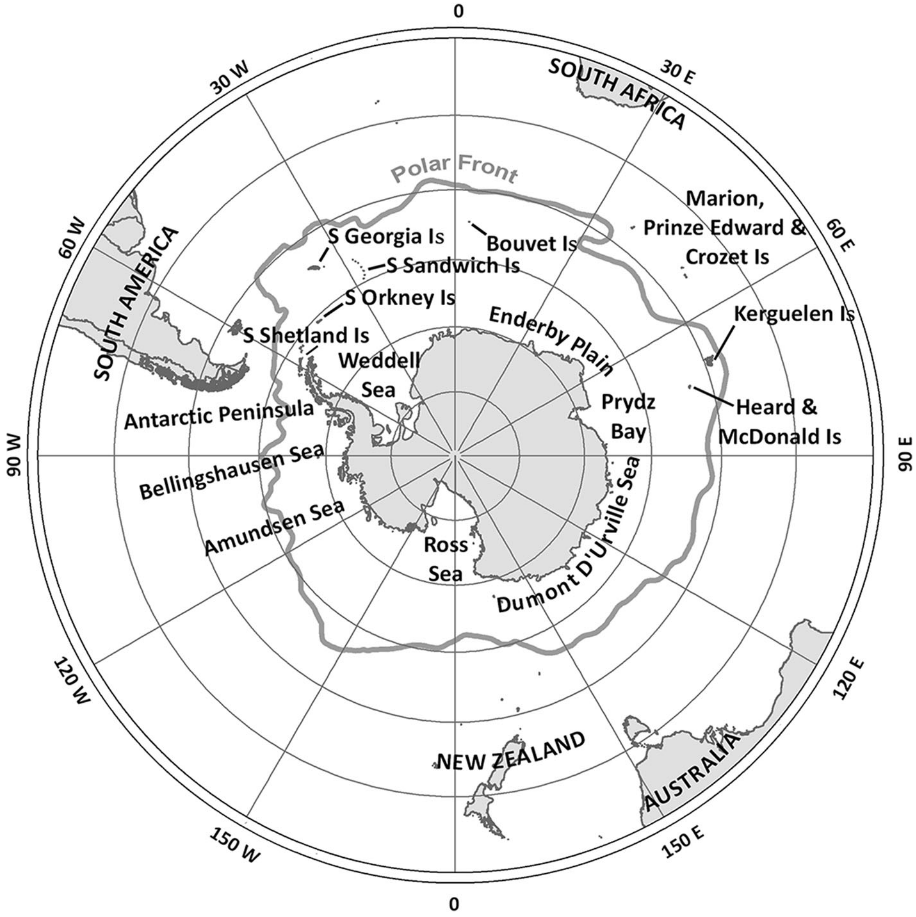


Fig. 1 Map of the Southern Ocean and adjacent waters showing Antarctic regions used in the analysis of species distribution (assembled data)

Stöhr et al. 2012) as we have also included here works with some species only identified to genus level. The regions with the highest species richness were as follows: South Shetland Is. (229), Antarctic Peninsula (211), Weddell Sea (201), South Orkney (184), South Georgia (182), and South Sandwich (180) islands (the last three being part of the Scotia Arc), and Ross Sea (176). Dumont D'Urville Sea (151) and Enderby Plain (134) had intermediate species richness, while Prydz Bay (112), Marion, Prince Edward and Crozet Is. (99), Bellingshausen Sea (96), Kerguelen Is. (80), Amundsen Sea (69), Heard Is. (66), and Bouvet Is. (52) presented the lowest species richness values (Fig. 2). Asteroids dominated at all regions except for the Amundsen Sea and the Scotia Arc, which are dominated by holothuroids and ophiuroids.

Endemic and shared species

Remarkable differences were found between classes and areas studied when considering endemic species in Antarctic regions (Fig. 3). More than half of the species of each class appeared to be endemic to the SO: 63 % (125 species) in holothuroids, 59 % (76 species) in ophiuroids, and ca. 50 % (113 species) in asteroids. The highest endemism rates were present in the Weddell Sea and the Marion Is. group for asteroids, the Antarctic Peninsula and the Dumont D'Urville Sea for ophiuroids, and the Scotia Arc and the Marion Is. group for holothuroids (Fig. 3). Among the shared species with other non-Antarctic geographic regions, 38 % appeared under 2,500 m. Antarctic

Fig. 2 Number of species per each class and per each geographic region (assembled data), ordered clockwise for big geographic areas and island groups, respectively

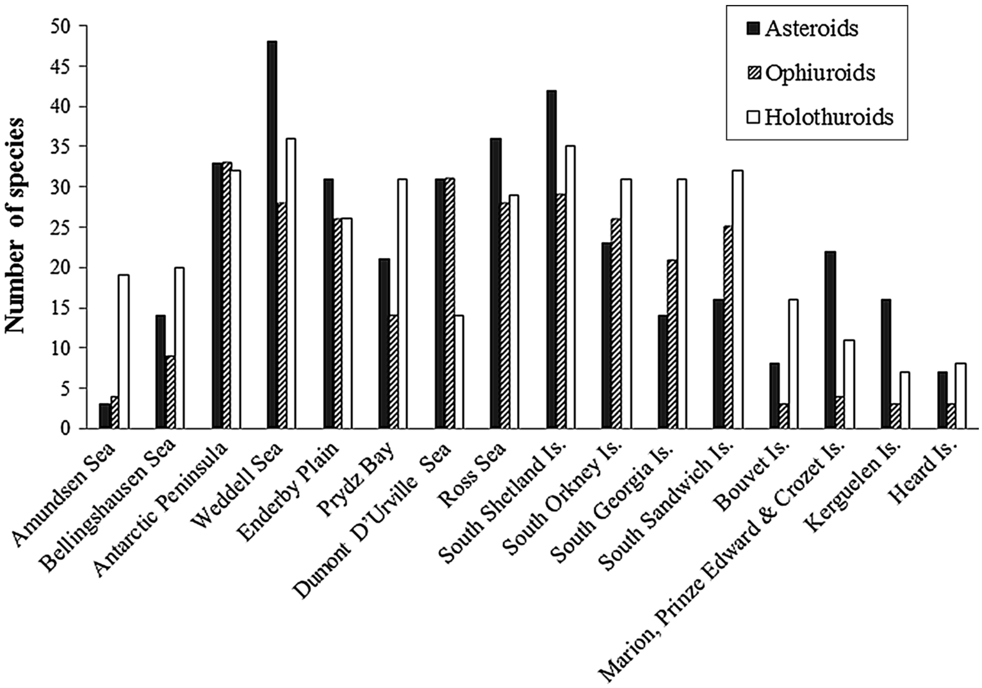
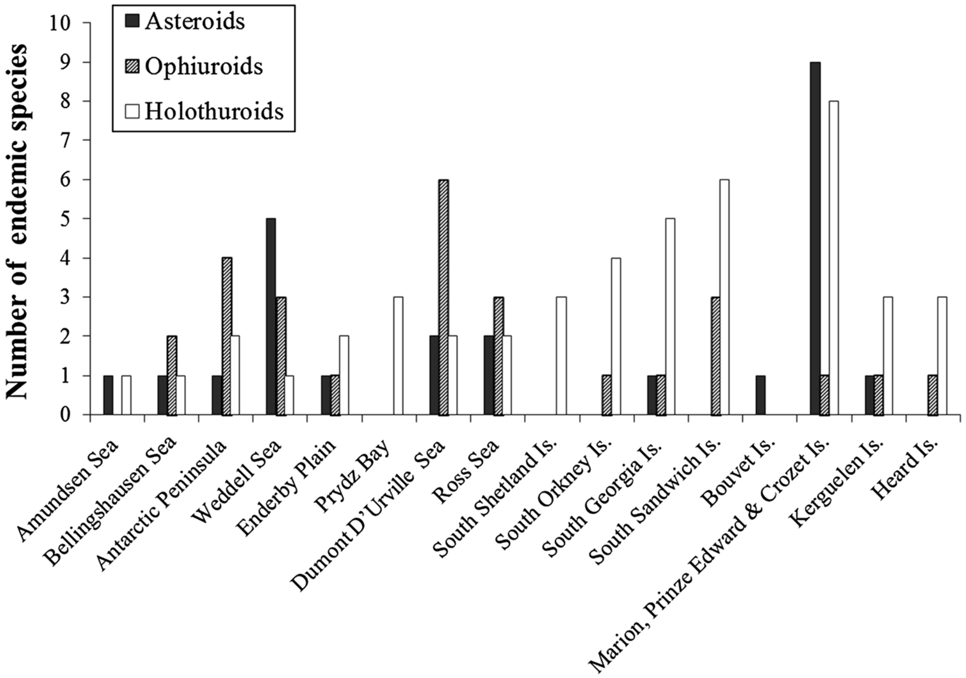


Fig. 3 Number of endemic species per each class and geographic region (assembled data), ordered clockwise for big geographic areas and island groups, respectively



fauna was more related to South America (36 % species similarity) in species composition than to New Zealand (13 %), Australia (9 %), or South Africa (7 %; see Online Resource 4).

Bathymetric ranges and distribution

As a general trend, species composition gradually changed across depths and was separated accordingly to the sublittoral, upper and lower bathyal, and upper and lower abyssal (Fig. 4a; Vinogradova 1997; Zezina 1997). However, asteroids appeared to be distributed in wider depth bands, since the distance between depth ranges in the MDS was less pronounced (Fig. 4b). Thus, asteroids, which have an 80 % of similarity, had four clusters of species restricted to the sublittoral and upper bathyal (0–1,000 m), lower bathyal (1,000–3,500 m), upper abyssal (3,500–5,500 m), and lower abyssal (>5,500 m). With a 60 % of similarity between ophiuroid samples, four different ophiuroid groups could be distinguished: sublittoral and upper bathyal (0–1,000 m), lower bathyal (1,000–2,500 m), upper abyssal (2,500–4,500 m), and lower abyssal (>4,500 m; Fig. 4c). Holothuroids had a distinct shallow-water fauna (0–100 m) with only species of the order Dendrochirotida (*Neopsolidium convergens*, *Pseudocnus intermedia*, *Psolus granulosus,* and *Squamocnus* spp.). Sea cucumber assemblages seemed to segregate in sublittoral and upper bathyal (100–1,000 m), lower bathyal (2,000–3,500 m), upper abyssal (3,500–5,000 m), and lower abyssal (>5,000 m; Fig. 4d). High species richness found between 100 and 500 m was the general tendency for the three echinoderm classes—with more than 65 % of species reported within this depth range—progressively decreasing with depth, although holothuroids had a less pronounced decrease in species composition until 3,000 m (Online Resource 5). Abyssal depths had less species richness for asteroids (20 %) and ophiuroids (10 %), which had only two and one species at these depths, respectively. Conversely, holothuroids had more than 30 % of species richness (eight species) restricted to abyssal depths.

Geographic relationships

Cluster analyses suggested several regional groups with similar faunal composition (Fig. 5). The dendrogram obtained after pooling data of all classes established four distinct geographic zones with a similarity greater than 40 % in the echinoderm fauna (Fig. 5a): cluster 1, formed by the Scotia Arc Is., the Antarctic Peninsula, the Ross and Weddell seas, and the East Antarctic areas (Dumont D'Urville Sea, Enderby Plain, and Prydz Bay); cluster 2, formed by the remote Bouvet Is. alone, and related to cluster 1; cluster 3, formed by the Amundsen and Bellingshausen seas; and cluster 4, formed by the Subantarctic Heard Is., Kerguelen Is., and the Marion, Prince Edward, and Crozet Is. group. Bathymetric distributions of the species of each cluster are specified in Online Resources 1–3 (for Asteroidea, Ophiuroidea, and Holothuroidea, respectively). There were mild differences in the cluster analysis when treating echinoderm classes separately. The clusters observed for asteroids and ophiuroids were quite similar to those obtained for the whole echinoderm dataset, except for the case of Amundsen and Bellingshausen seas, which did not fall within the same cluster (Fig. 5b, c). As for holothuroids, areas from cluster 1 and cluster 3 were grouped together, while the East Antarctica areas were more related to areas from cluster 2; in addition, Marion, Prince Edward, and Crozet Is. were not grouped together with Heard Is. and Kerguelen Is. (Fig. 5d).

Discussion

Our work has contributed to expand the knowledge on echinoderm bathymetric and geographic distribution in the

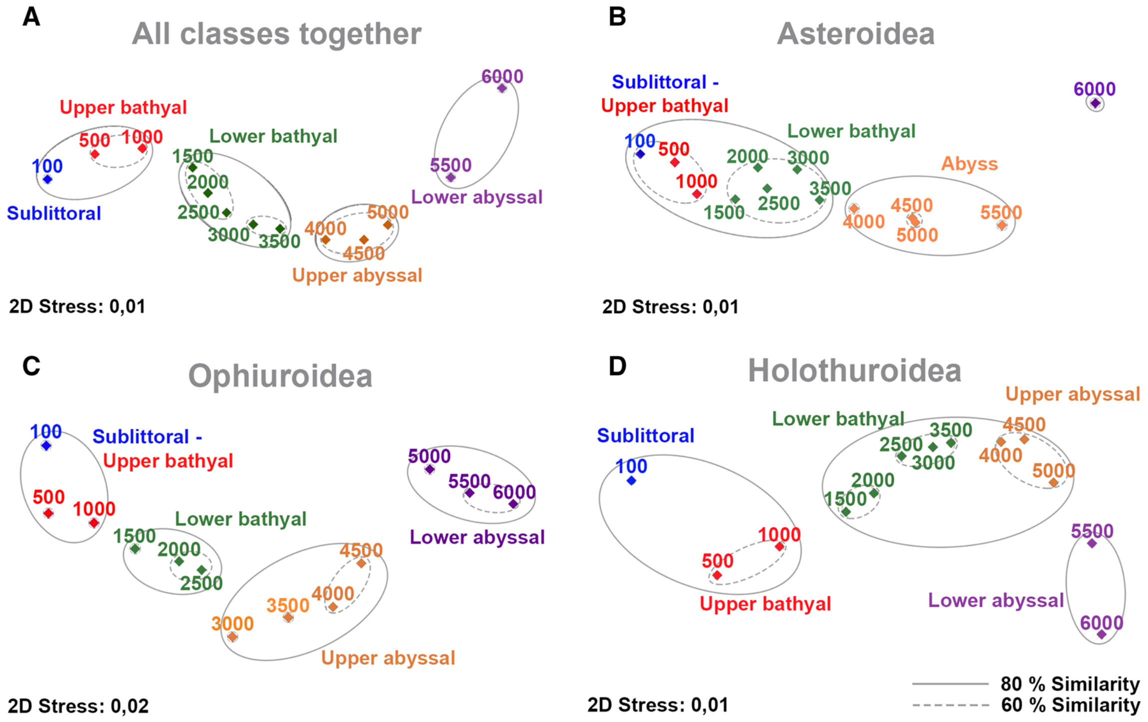


Fig. 4 MDS plots using Bray-Curtis distance of the species (assembled data) in relation to depth for (**a**) the three classes grouped together, **b** Asteroidea, **c** Ophiuroidea, and **d** Holothuroidea

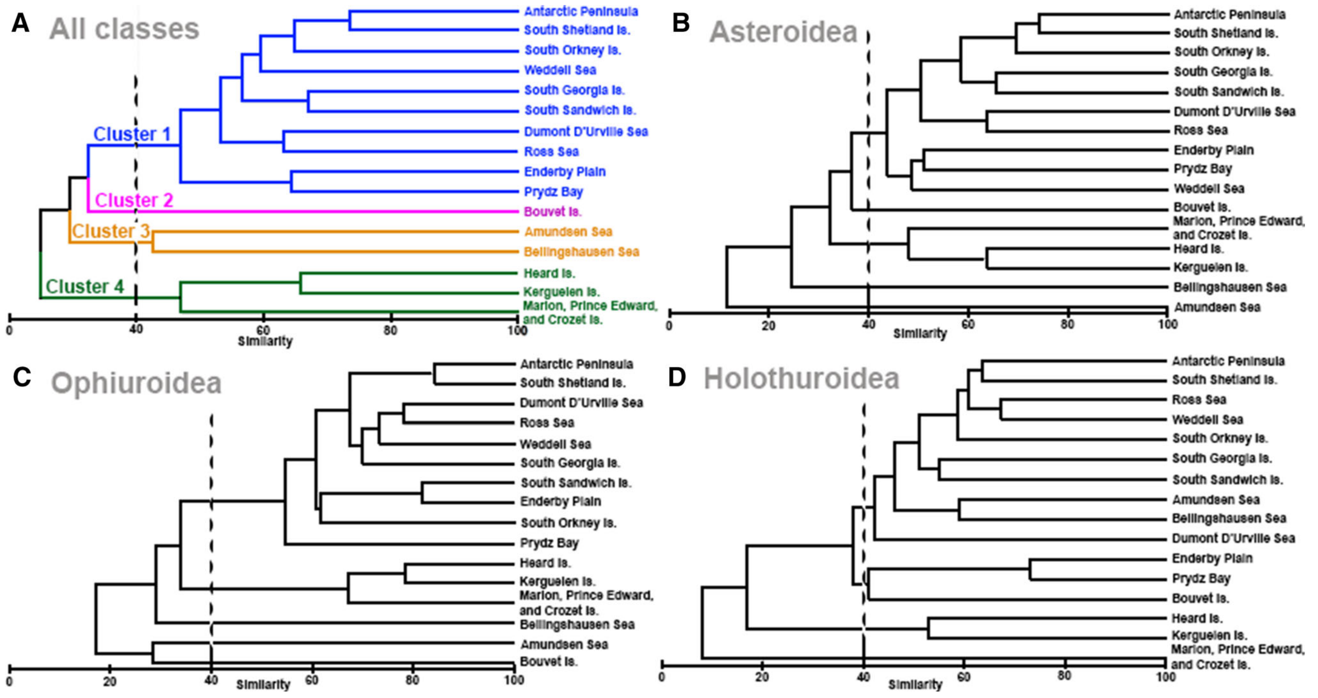


Fig. 5 Hierarchical clustering (group average) of the echinoderm fauna analyzed from the Southern Ocean using the Bray-Curtis distance (assembled data). **a** The three classes grouped together, indicating the four clusters in different colors, **b** Asteroidea, **c** Ophiuroidea, and **d** Holothuroidea. In all cases, 40 % of similarity was chosen as a threshold to group regions. (Color figure online)

SO. Within the 79 species identified in our survey pertaining to the classes Asteroidea, Ophiuroidea, and Holothuroidea, the families Asteriidae, Odontasteridae, Ophiuridae, Cucumariidae, and Psolidae were the most speciose in Bouvet Is., the Eastern Weddell Sea, and the South Shetland Is. at shelf depths (0–800 m). Our data show that, even though these areas have been widely sampled through the last decades (Gutt 1990a, b; Gutt and Piepenburg 1991; Massin 1992a; Piepenburg et al. 1997; Presler and Figielska 1997; Manjón-Cabeza et al. 2001; Manjón-Cabeza and Ramos 2003; Arntz 2006; Arntz et al. 2006; Gutt et al. 2006), new species records are still being found. This is especially true for Bouvet Is. with seven echinoderm species recorded for the first time in this study. More importantly, the echinoderm diversity described so far in the SO is surely underrepresented since several newly recorded taxa still are currently undescribed (Kaiser et al. 2013). In addition, cryptic speciation may also cause underestimations of echinoderm diversity in the SO. As an example, two new sea star species of the well-known genus *Odontaster* have recently been described combining molecular and morphological analyses (Janosik and Halanych 2010). Interestingly, these new species occurred along the Antarctic Peninsula, perhaps one of the best-studied regions in the SO (Griffiths 2010). Indeed, integrative taxonomic approaches revealed that some species defined by morphological characters are in fact complexes of cryptic species (Rogers 2007; O'Loughlin et al. 2011). Thus, future work on the re-evaluation of identified sibling species will probably enrich the number of taxa in the SO.

Antarctic and Subantarctic regions presented general trends in species composition when treating metadata of all compiled species records. Species richness among classes was relatively high and similar between the well-studied areas, such as Scotia Sea Is., Weddell and Ross seas, Antarctic Peninsula, and adjacent islands, as seen in Griffiths (2010). In turn, when considering less-sampled areas, such as Amundsen and Bellingshausen seas, Bouvet Is. or the Kerguelen group, their number of species decreased, possibly due to their geographic isolation. Notice that asteroids were the most diverse class in the Marion group, with values similar to those of larger geographic areas (Fig. 2). Arntz (2006) suggested that Subantarctic islands may have served as refugia for benthic shallow-water organisms during Cenozoic glacial maxima. The current island patchiness and/or habitat heterogeneity may have allowed higher numbers of species with different ecological niches, leading to high degrees of endemism, something that has already been observed for holothuroids (Gutt 2007). In fact, asteroids and holothuroids showed the highest endemism values in the Marion Is. area (Fig. 3) possibly due to marked isolation of this Subantarctic area. Other regions with a high degree of endemism for holothuroids were Amundsen and Bellingshausen seas, while ophiuroids exhibited higher endemism in the East Antarctica and the Antarctic Peninsula, probably due to recent increase in sampling effort in these areas (Manjón-Cabeza and Ramos 2003; O'Loughlin et al. 2009). To achieve a better understanding on the echinoderm biodiversity in these areas, different sampling methods and greater collecting efforts are specially needed.

In agreement with other studies dealing with various invertebrate taxa, Antarctic echinoderms also exhibited a high range of eurybathy (Brey et al. 1996; Soler i Membrives et al. 2009; Figuerola et al. 2012). This seems to be explained by both the palaeoclimatic history of Antarctica and the current iceberg scour activity (Clarke et al. 2004; Thatje et al. 2005; Smale et al. 2008). It is hypothesized that Cenozoic glacial–interglacial cycles may have driven an environmental force toward the evolutionary trend of eurybathy in many Antarctic benthic invertebrates. During the extension of continental ice sheet, shelf fauna may have gone extinct or forced to go into deeper water refugia. Conversely, during the shelf ice retreats at the subsequent interglacial, the defaunated shelf could have been re-colonized by fauna from the slope (Clarke et al. 2004), deep sea, or shelters on the continental shelf (Thatje et al. 2005). In addition, eurybathic tendencies of the current benthic shelf fauna (to depths of 500 m) are reinforced by the erosive action of recurrent iceberg scouring (Smale et al. 2008). Our analysis showed that echinoderms were gradually distributed across depths. Bathymetric distribution in Ophiuroidea fitted with the depth limits suggested by Clarke and Johnston (2003), and also for other studies using other taxa (Piepenburg et al. 1997; Aldea et al. 2008; Figuerola et al. 2012). Thus, ophiuroid communities were distinguished in sublittoral and upper bathyal (0–1,000 m), lower bathyal (1,000–2,500 m), upper abyssal (2,500–4,500 m), and lower abyssal (>4,500 m). Asteroid communities from sublittoral and bathyal depths were similar in species composition, thus reinforcing the proposed tendency of eurybathy. This result might be influenced by the generalist and opportunistic feeding strategies observed for several species of this class (McClintock 1994). We distinguished a stenobathic shallow-water fauna for Holothuroidea, mainly characterized by the occurrence of suspension-feeding Dendrochirotida species. Generally, all classes decreased in species richness with depth probably due to a reduction in organic matter input, the main factor controlling Antarctic benthos (Arntz et al. 1994). However, holothuroid's species richness decreased moderately when compared to asteroids and ophiuroids. The diversity of feeding strategies in this class (i.e., suspension-feeding dendrochirotids from shallow waters, deposit-feeding deep-sea elasipodid holothuroids) may use different food qualities of the suspended matter equally along water depth (Gutt and Piepenburg 1991; McClintock 1994). This might reflect the mild reduction in species richness across depths.

The cluster analysis suggested four groups or clusters of similar echinoderm faunal composition. Cluster 1, comprising Antarctic Peninsula, South Shetland Is., South Orkney Is., Weddell Sea, South Georgia Is., and South Sandwich Is., has been identified in previous studies on Echinodermata and other phyla, and the relationship between these areas might be influenced by the Weddell Gyre (Arntz et al. 2005; Barnes et al. 2009; Barboza et al. 2011; Figuerola et al. 2012). This clockwise current connects the Weddell Sea with the Scotia Arc through the Antarctic Peninsula (Orsi et al. 1993), allowing dispersion of echinoderm's planktonic larvae or even epiplanktonic adults (Olbers et al. 2004). The rest of the areas in cluster 1 are located in the Eastern Antarctica (Dumont D'Urville Sea, Ross Sea, Enderby Plain, and Prydz Bay) and may be connected to the above-mentioned Weddell Gyre areas through the East Wind Drift (Brey et al. 1996; Olbers et al. 2004). Cluster 2 was only composed by Bouvet Is., a remote area probably also influenced by the Weddell Gyre, as previously reported for different taxa (Barnes 2005; Arntz et al. 2006; Gutt et al. 2006).

Amundsen and Bellingshausen seas comprised cluster 3 and were the areas with less species richness relative to their extension, which may in part be due to the comparatively less sampling effort conducted in these areas (Griffiths 2010). In fact, due to the relative ancient formation of both seas, a higher number of species, when compared to close seas, would have been expected (Thomson 2004). Nevertheless, Saiz et al. (2008) described low species richness in the Bellingshausen Sea and suggested that this impoverished fauna was related to low-food supply, a situation exacerbated by the influence of periodic physical disturbances (such as iceberg scour).

Finally, cluster 4 was composed by Heard and McDonald Is., Kerguelen Is., and the Marion, Prince Edward, and Crozet group, a series of Subantarctic islands located in the Southern Indian Ocean at the edge of the PF. Their species composition similarity might be explained by the effects of the ACC, which promotes the dispersal of marine organisms from west to east in a clockwise pattern, as it has already been suggested for echinoderms (Fell 1962) and other taxa (Barnes 2002; Raguá-Gil et al. 2004). The geographic proximity of Heard and Kerguelen Is. might also have an effect in their similar echinoderm fauna. In fact, they lay on the so-called Kerguelen Plateau (1,000–2,500 m deep), which has recently been proposed as a glacial refugium for echinoderm species (Hemery et al. 2012).

Comparing SO echinoderms with the adjacent ocean basins, South America was the basin that shared more species with all the areas considered in this study. In particular, the Scotia Sea shared the highest number of species, since its intermediate location represents a physical link between both the SO and South America (Barnes 2005; Kim and Thurber 2007). Their biogeographic similarities might be explained by geological history (both areas were connected during the Cenozoic) or by a two-way migration of both shallow-water and the deep ocean fauna. Turbulent flow structures, called eddies, have been also hypothesized as a mechanism for transport of bathyal organisms (to 1,000 m) from north to south of the ACC and vice versa (Clarke et al. 2005). Moreover, there is a global thermohaline circulation of Antarctic Bottom Water, which connects the abyssal Weddell Sea with the southwest Atlantic basin, allowing the dispersal of deep-sea organisms (Pawlowski et al. 2007). Other than South America, areas such as New Zealand, Australia, and South Africa harbor echinoderm species in common to the SO; this may also be explained by global patterns of deep-sea water circulation.

We firmly believe that our data input analyzed together with bibliographic datasets in this biogeographic study will serve to understand the dynamics of a key group structuring the Antarctic benthic fauna. However, the amount of new data reflects the need of more taxonomic and biogeographic studies in Antarctic and Subantarctic areas. Different sampling methods and an increase of survey efforts are specially needed in the less surveyed areas with supposedly low species richness (e.g., Amundsen Sea, Bellingshausen Sea, Bouvet Is.), while in higher-sampled areas major taxonomic effort is also necessary.

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