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ORIGINAL ARTICLE

# Reproductive strategy as a piece of the biogeographic puzzle: a case study using Antarctic sea stars (Echinodermata, Asteroidea)

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## ABSTRACT

**Aim** To describe and analyse asteroid biogeographic patterns in the Southern Ocean (SO) and test whether reproductive strategy (brooder versus broadcaster) can explain distribution patterns at the scale of the entire class. We hypothesize that brooding and broadcasting species display different biogeographic patterns.

**Location** Southern Ocean, south of 45 °S.

**Methods** Over 14,000 asteroid occurrences are analysed using bootstrapped spanning network (BSN), non-metrical multidimensional scaling (nMDS) and clustering to uncover the spatial structure of faunal similarities among 25 bioregions.

**Results** Main biogeographic patterns are congruent with previous works based on other taxa and highlight the isolation of New Zealand, the high richness in the Scotia Arc area particularly of brooding species, an East/West Antarctic differentiation, and the faunal affinities between South America and sub-Antarctic Islands. Asteroids show lower endemism levels than previously reported with 29% of species occurring in Antarctica only. In particular, asteroids from Tierra del Fuego showed affinities with those of West Antarctica at the species level, suggesting a recent mixing of assemblages. Biogeographic patterns are highly linked to reproductive strategy. Patterns also differ according to the taxonomic level, revealing the underlying role of historical factors.

**Main conclusions** Patterns of sea star biogeography are consistent with results obtained for other marine groups and are strongly linked to reproductive strategy.

**Keywords**

**Antarctica, benthos, biogeographic barrier, Echinodermata, invertebrate, regionalization, reproductive mode, sea stars, Southern Ocean**

## INTRODUCTION

The Southern Ocean *sensu lato* (SO), as defined by oceanographers, includes the marine area south of the Subtropical Front (STF) (Longhurst, 2007; Rintoul, 2007; Post *et al.* 2014). In the framework of large-scale biogeographic studies of marine benthic life, the SO is generally divided into four major geographic entities (i.e. provinces): the Magellanic Plateau, represented by the southern tip of South America (South Chile, South Argentina, Tierra Del Fuego and the Malvinas/Falkland Islands); Southern New Zealand, represented by the Campbell Plateau; the sub-Antarctic area, located between the STF in the north and the Polar Front (PF) in the south, which is mainly composed of abyssal plains and several igneous Islands (e.g. Crozet archipelago, Kerguelen and Heard Islands); and the Antarctic province, defined as the region south of the PF (Griffiths *et al.*, 2009). The Antarctic province is one of the most remote places on Earth, despite representing *c.* 11% of the global continental shelf surface, and surrounded by the SO which surface accounts for *c.* 8% of all the world's oceans (Griffiths, 2010; Ingels *et al.*, 2012). Each of these provinces can then be

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divided into smaller entities, defined as bioregions (cf. Hedgpeth, 1969).

The long-term faunal connections within and among these four provinces cannot be explained by a “one-size-fits-all” biogeographic theory. Indeed, biogeographic patterns appear to be dependent upon the taxon investigated (e.g. Barnes & Griffiths, 2007 for Bryozoa; Griffiths *et al.*, 2009 for Mollusca and Bryozoa; Downey *et al.*, 2012 for Porifera). All large-scale studies on biogeographic patterns of the SO benthic life indicate that oceanographic and historical factors have played a significant role in the current patterns (Linse *et al.*, 2006; Barnes & Griffiths, 2007; Downey *et al.*, 2012; Pierrat *et al.*, 2013). Oceanographic features which are unique to the SO, such as the PF, act as a barrier between polar and sub-Antarctic water masses. Both water masses show contrasting physico-chemical properties, and the PF creates a steep gradient in temperature and salinity (Venables *et al.*, 2012). Geomorphological features, such as a “belt” of abyssal basins surrounding the Antarctic continent, have resulted in the biogeographic isolation of the Antarctic shelf, especially the benthos (see Clarke *et al.*, 2005). The combined impacts of surface currents, the environmental characteristics of the SO and the long-term gradual cooling and past glacial–interglacial cycles occurring during the Plio-Pleistocene have driven biogeographic patterns (González-Wevar *et al.*, 2012; Strugnell *et al.*, 2012). The development of the Antarctic Circumpolar Current (ACC) during the Eocene/Oligocene has and continues to play a major role in the circum-Antarctic structure of environmental and biotic patterns by initiating a fast, clockwise transport of water, dispersing propagules around the entire Antarctic continent (Pearse *et al.*, 2009; Pierrat *et al.*, 2013; David & Saucè, 2015).

Regional-scale processes may also shape biogeographic patterns. For instance, the PF has “marine corridors” connecting distinct regions (Clarke *et al.*, 2005; Barnes & Clarke, 2011). Other oceanographic features, such as regional-scale eddies, island archipelagos, seamounts or refugia during glacial cycles may also have influenced the distribution of benthic species (e.g. Barnes & Kuklinski, 2010). Despite this permeability, benthic fauna living south of the PF are highly adapted to polar environmental conditions (e.g. McClintock, 1994; Peck *et al.*, 2006) and interactions among all the factors mentioned above have resulted in apparently high levels of endemism in many benthic taxa of the SO. The recent Biogeographic Atlas of the Southern Ocean (De Broyer *et al.*, 2014, and chapters herein) estimates 57% endemism for bivalves, 79% for gastropods, 64% for pycnogonids, 87% for isopods, 81% for tanaids, 51% for ascidians and 80% for cumaceans.

Sea stars (Asteroidea, Echinodermata) are common organisms living on the Antarctic seafloor with specimens found in diverse environments (Brandt *et al.*, 2007; Linse *et al.*, 2007a; Mah & Blake, 2012). High latitude asteroids have been studied since the late 19th century in the SO (e.g. Sladen, 1889) with hundreds of species recorded (latest checklist in Moreau *et al.*, 2015) and frequent checklists (e.g. Moles *et al.*, 2015). Moreover, there is a particularly high proportion of brooding sea stars in the SO (Poulin *et al.*, 2002; Pearse *et al.*, 2009). Despite the potential importance of asteroids as ecosystem structuring agents (Mah & Blake, 2012; Lawrence, 2013), very few studies have assessed the overall distribution pattern of SO asteroid diversity (Danis *et al.*, 2014; Moles *et al.*, 2015) and the relative importance of each driving factor involved in the observed patterns has not yet been addressed.

In a recent update of the Register of Antarctic Marine species (RAMS), Moreau *et al.* (2015) reported a total of 295 species, representing more than 15% of the nearly 1,900 extant species of asteroids (Mah & Blake, 2012). Initiatives such as RAMS and the World Register of Marine Species (WoRMS Editorial Board, 2015) enable the use of global data systems [e.g. Ocean Biogeographic Information System (OBIS – http://www.iobis.org/), Global Biodiversity Information Facility (GBIF – http://www.gbif.org/)] to compile hundreds of thousands georeferenced data entries (Costello *et al.*, 2013; Jossart *et al.*, 2015). Such extensive datasets can be used to address key biological questions, such as the origin and the structure of asteroid biogeographic patterns in the SO.

The objectives of this work were to describe and analyse asteroid biogeographic patterns in the Southern Ocean (SO) and test whether reproductive strategy (brooder versus broadcaster) can explain distribution patterns. Specifically, we hypothesize that the contrasting ability of asteroids to disperse (short range for brooders and long range for broadcasters) will generate contrasting biogeographic patterns.

## MATERIALS AND METHODS

### Area of interest

The geographic area investigated in this study focuses on the SO, at latitudes higher than 45 °S (Fig. 1). The SO was then subdivided into the following 25 bioregions based on several recent biogeographic studies (Linse *et al.*, 2006; Clarke *et al.*, 2007; Spalding *et al.*, 2007; Pierrat *et al.*, 2013; De Broyer & Jażdżewska, 2014) and to take into account all occurrences data available for the SO asteroids (see Fig. 1): Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS).

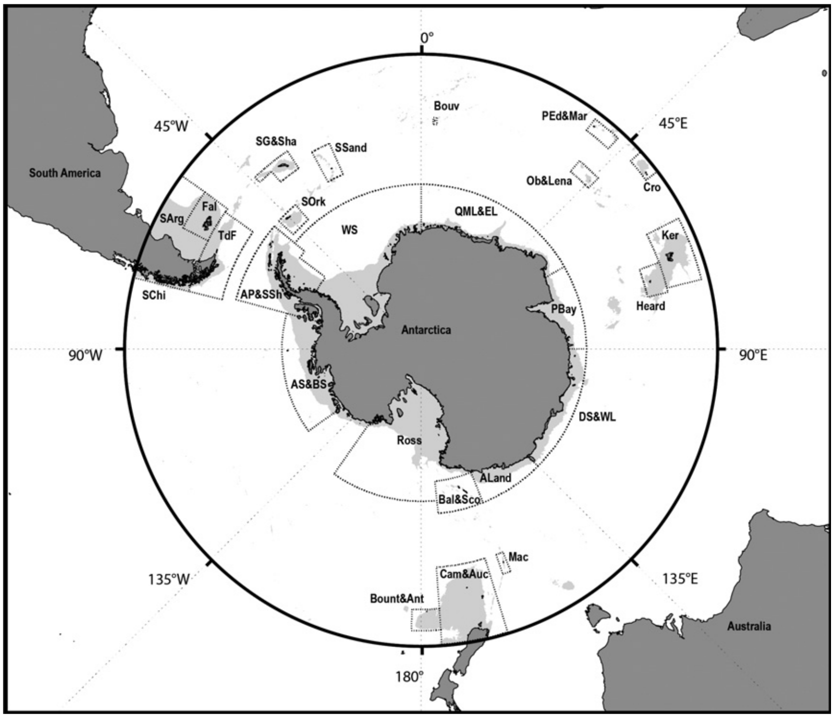


**Figure 1** Map of the Southern Ocean. Area of study (below 45 °S) showing the bioregions: Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS). Depth of study, between 0 and 1500 m is shown in light grey. Projection: South Pole stereographic.

## Data analyses

Cleaned data (See Appendix S1 in Supporting Information for data sources and quality control) were compiled into a matrix providing information for each species on the bioregion and depth of occurrence. The dataset was used in its entirety for richness analyses. For biogeographic analyses, occurrences from depths lower than 1,500 m (abyssal domain and beyond) were excluded to only focus on shelf areas and on the upper slope. This depth range also includes shallow canyons and troughs. The main changes in faunal communities of the SO occur at around 1,500 m depth, deeper than elsewhere in the world's oceans (Brandt *et al.*, 2014). Bathymetric data were compiled using the GEBCO (2014) grid (www.gebco.net). Analyses were performed at the genus and species levels. At the species level, brooding and broadcasting species were also investigated separately to test our working hypothesis (see Appendix 1 for sources regarding the reproductive strategy). Species accumulation curves were calculated to test the consistency of richness estimation using PRIMER 6 (Clarke & Gorley, 2006) with a focus on the first 250 stations (Fig. 2a).

Three complementary approaches were used to quantitatively investigate faunal similarities between the 25 bioregions. Two multivariate analyses, non-metrical multidimensional scaling (nMDS) and clustering, were carried out using PRIMER 6 (Clarke & Gorley, 2006) and the Bray–Curtis coefficient (Bray & Curtis, 1957). A similarity percentage (SP) is given by the cluster analyses to measure similarities among bioregions or groups of bioregions. We also used the bootstrap spanning network (BSN) procedure to visualize non-metric inter-assemblages similarity structure as a connected network. BSN allows the simultaneous identification of partially or totally nested patterns as well as gradational linear or reticulated biogeographic structures (see detailed description in Brayard *et al.*, 2007, 2009). These three methods can be used to identify transitional areas between bioregions and groups of bioregions in term of faunal similarities.

A dissimilarity matrix was calculated using the Bray–Curtis coefficient (Bray & Curtis, 1957). Following the BSN procedure (see Brayard *et al.*, 2007), similarity relationships were displayed as a connected network directly superimposed on geographic maps. Nodes of the network represent studied bioregions and the robustness of each BSN link between nodes was evaluated by bootstrap replications (10,000 replicates were computed here). A bootstrap support values (BSV: i.e. a confidence interval) is obtained for each link between bioregions (see Brayard *et al.*, 2007, 2009 for details). When superimposed on geographic maps, the BSN provides an intuitive visualization, as well as a quantitative appraisal of faunal exchange pathways and biogeographic structures. BSNs were created with the software BSN 1.0 (Brayard *et al.*, 2007) and visualizations were created in PAJEK 1.07 (Batagelj & Mrvar, 2005). In order to quantitatively compare BSN among different taxonomic levels and reproductive strategies, we built a triangular matrix by multiplying the BSV between bioregions for each of our four studied situations (genus level, species level, brooding and broadcasting species). When two or more pathways were possible in the BSN, we kept the smallest value in order to reflect the highest similarity relationship. The bioregions Bount&Ant, Cam&Auc, ASBS and Mac were removed from correlation analyses because they were rarely connected to

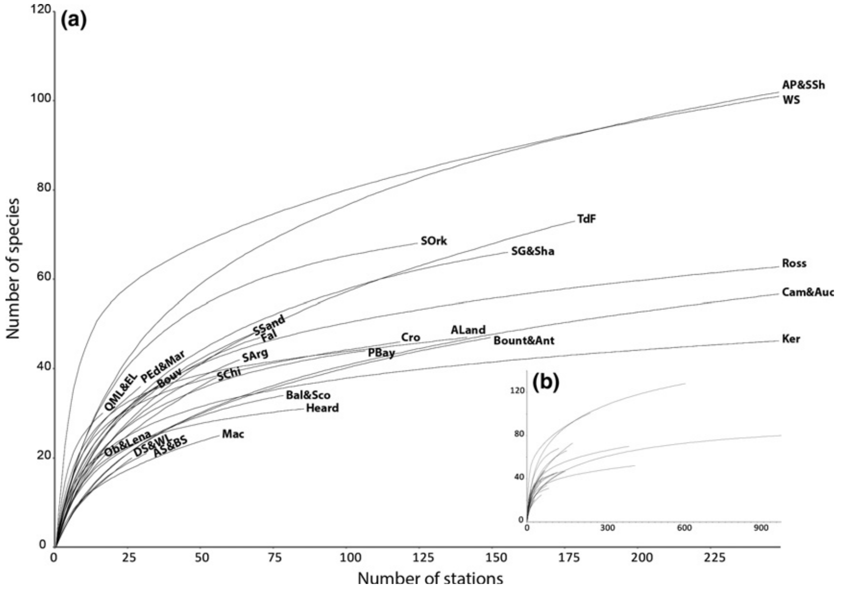


**Figure 2** Accumulation curves at the species level of Asteroidea for each investigated bioregions: Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS). (a) Close-up of the first 250 stations. (b) Complete dataset.

other bioregions in the BSN analyses. A Mantel test using the Spearman coefficient was used to measure correlations between the BSN structures. Finally, endemism levels of asteroid species were analysed by comparing the SO area dataset and the OBIS/GBIF occurrences for the rest of the world. Endemism within each bioregion was also quantified.

## RESULTS

### Sampling effort, richness patterns and endemism

There are clear differences in sampling effort intensity among the bioregions, ranging from 16 stations for both Queen Maud Land & Enderby Land (QML&EL) and Ob & Lena seamounts (Ob&Lena) to 993 stations for Campbell and Auckland Is. (Cam&Auc) (Table 1). Similar patterns can be observed for the number of occurrences [from 45 in the Davis Sea & Wilkes Land (DS&WL) to 2,259 in the Weddell Sea (WS)] and the richness at any taxonomic level (the number of orders, families, genera and species ranges from 4 to 7, 9 to 20, 14 to 61, 20 to 128 respectively). Species accumulation curves for each bioregion (Fig. 2a, b) indicate that bioregions Cam&Auc, Ker and Ross are the only ones reaching an asymptote and that many species remain to be discovered in the SO regardless of the location. The steepest curves, reflecting potential high species richness, are all found in the area between South America and the Antarctic Continent (TdF, SG&Sha, SSand, SOrk, AP&SSh and WS). Our final dataset contained 14,005 occurrence records, accounting for 4,512 stations. All seven orders of the class Asteroidea were represented, including 299 species assigned to 28 families and 118 genera (Table 1).

Of the 299 species in the dataset, 196 (*c.* 66%) also occur south of the PF and 123 species (*c.* 41%) have distributions that also extend north of the STF. Thus, a total of 176 species (*c.* 59%) occur exclusively south of the STF and are endemic to the Southern Ocean. Among the 196 species found south of the PF, 56 are restricted to the Antarctic zone (*c.* 29% endemism). In our dataset, 66 species (*c.* 22%) are only found around southern New Zealand and the adjacent regions (Chatham Islands, Tasmania), but not in any other region of the SO. At the scale of a bioregion endemism is low, varying from zero to four endemic species.

### Biogeographic patterns of species

Bioregions are structured into three major groups (Fig. 3a, b): (I) the New Zealand province, composed of Bount&Ant and Cam&Auc bioregions (SP = 6% only with the closest bioregions); (II) South America and the sub-Antarctic Islands (SChi, SArg, Fal, Heard, Ker, Ob&Lena, Cro, PEd&Mar), and is separated from the third group at SP = 36%; and (III) Antarctic bioregions (Bal&Sco, Bouv, PBay, Aland, Ross, AP&SSh, WS, SG&Sha, SOrk, SSand, QML&EL, DS&WL and TdF). Cluster analyses indicate that groups II and III can be subdivided into smaller geographic entities: South America (IIa) and the sub-Antarctic Islands (IIb) (SP = 38%), East Antarctica (bioregions east of the prime

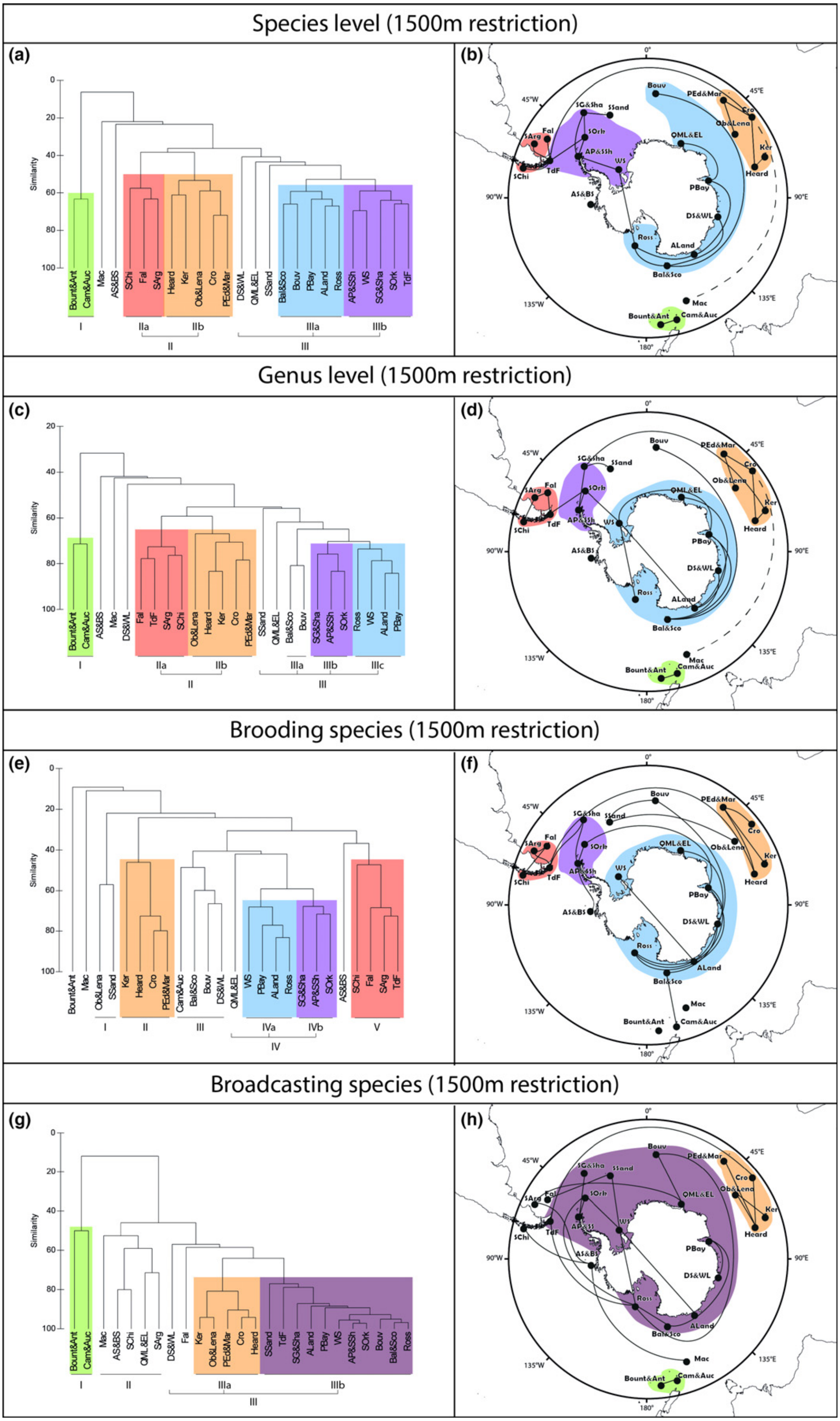
**Table 1** Breakdown numbers of occurrences, stations and taxonomic entities of Asteroidea for each of the 25 investigated bioregions. NA refers to occurrences found outside of the bioregions of interest. Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS).

| Bioregion | No. of occurrences | No. of species | No. of known brooding species | No. of known broadcasting species | No. of genera | No. of families | No. of orders | No. of stations |
|---|---|---|---|---|---|---|---|---|
| ALand | 694 | 47 | 12 | 14 | 30 | 15 | 7 | 141 |
| AP&SSh | 2042 | 128 | 25 | 18 | 61 | 20 | 7 | 618 |
| AS&BS | 49 | 21 | 7 | 4 | 16 | 9 | 6 | 31 |
| Bal&Sco | 202 | 34 | 4 | 15 | 28 | 15 | 6 | 78 |
| Bount&Ant | 245 | 47 | 1 | 2 | 35 | 14 | 7 | 149 |
| Bouv | 128 | 36 | 6 | 15 | 24 | 10 | 5 | 35 |
| Cam&Auc | 1586 | 80 | 3 | 6 | 53 | 19 | 7 | 993 |
| Cro | 489 | 46 | 5 | 9 | 27 | 15 | 5 | 118 |
| DS&WL | 45 | 20 | 6 | 7 | 14 | 9 | 4 | 26 |
| Fal | 232 | 47 | 8 | 9 | 31 | 17 | 6 | 70 |
| Heard | 223 | 31 | 6 | 8 | 20 | 14 | 6 | 85 |
| Ker | 1477 | 52 | 12 | 9 | 31 | 16 | 6 | 422 |
| Mac | 141 | 25 | 5 | 2 | 16 | 13 | 5 | 56 |
| NA | 673 | 126 | NA | NA | 73 | 24 | 7 | 234 |
| Ob&Lena | 68 | 21 | 2 | 8 | 15 | 12 | 5 | 16 |
| PBay | 284 | 44 | 10 | 13 | 31 | 15 | 7 | 106 |
| PEd&Mar | 106 | 36 | 5 | 7 | 25 | 14 | 5 | 29 |
| QML&EL | 111 | 30 | 5 | 9 | 21 | 11 | 6 | 16 |
| Ross | 1257 | 70 | 12 | 16 | 42 | 18 | 6 | 398 |
| SArg | 154 | 42 | 9 | 5 | 27 | 15 | 7 | 63 |
| SChi | 131 | 38 | 3 | 6 | 30 | 18 | 6 | 55 |
| SG&Sha | 405 | 66 | 17 | 16 | 43 | 19 | 7 | 155 |
| SOrk | 421 | 68 | 14 | 17 | 45 | 19 | 7 | 124 |
| SSand | 174 | 48 | 5 | 11 | 34 | 17 | 6 | 68 |
| TdF | 409 | 73 | 13 | 12 | 49 | 19 | 7 | 178 |
| WS | 2259 | 101 | 13 | 16 | 51 | 18 | 7 | 248 |
| Southern ocean | 14005 | 299 | 37 | 22 | 118 | 28 | 7 | 4512 |

meridian, including Ross) (IIIa) and West Antarctica (bioregions west of the prime meridian) (IIIb) (SP = 52%) respectively. Potential faunal connections among these entities are highlighted by the BSN analysis (See Appendix 2 for BSV) (Fig. 3b). East and West Antarctica are well connected to each other through a particularly strong link between the Weddell (WS) and Ross Seas (BSV = 100%), however no link between WS and the closest other bioregions of East Antarctica is observed. West Antarctica and South America are connected to each other through TdF (BSV = 99.9%). South America shows a strong link with the sub-Antarctic Islands (BSV = 99.8%). Within the sub-Antarctic group, the link is weak (BSV = 63%) between Macquarie and other sub-Antarctic Islands.

The nMDS analysis allows visualizing similarities among bioregions with a low stress value (0.08). The minimum spanning tree (MST) plotted on the graph indicates the shortest path between bioregions (Fig. 4a, b) and confirms

**Figure 3** Cluster analyses (average linkage) of the percentage faunal similarity (a), (c), (e) and (g) using the Bray–Curtis index and bootstrapped spanning networks (b), (d), (f) and (h) performed for species and genus level as well as for brooding and broadcasting species for the class Asteroidea among the studied bioregions: Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS). Links with BSV < 70% correspond to dashed lines, links with BSV < 50% are not shown. Corresponding groups based on the cluster analyses display a similar colour. Green: New Zealand – Red: South America – Orange: Sub-Antarctic Islands – Blue: High Antarctica or East Antarctica – Purple: West Antarctica – Burgundy: Circumpolar Pattern.


Species level (1500m restriction)
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Cam&Auc

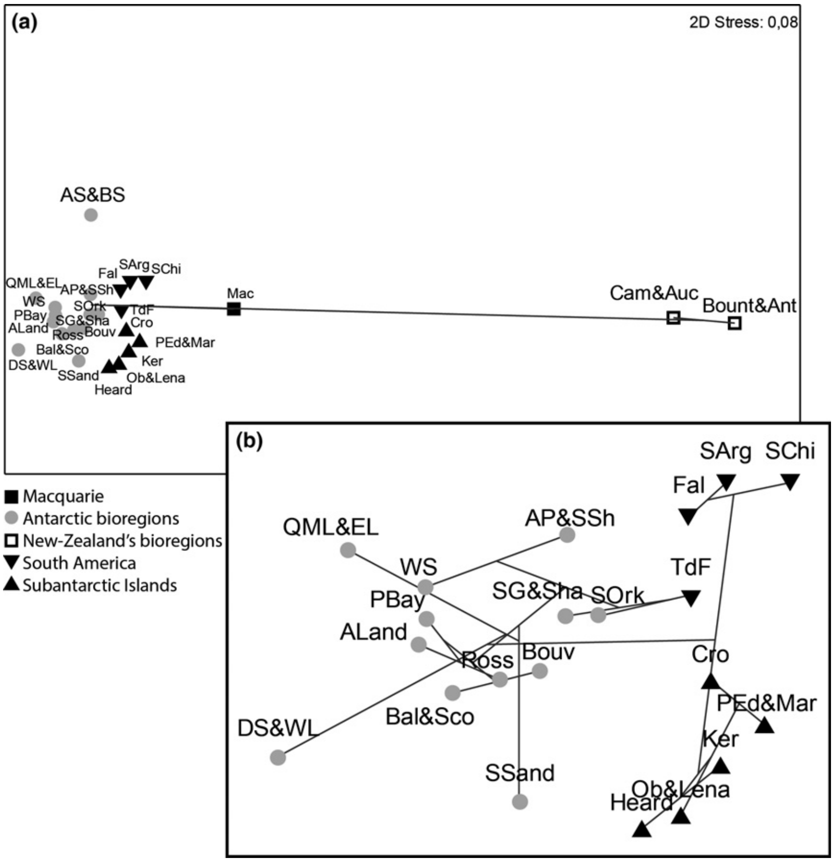

**Figure 4** Non-metric multidimensional scaling map with superimposed minimum spanning tree (partial representation to ease the reading) for the class Asteroidea among the 25 studied bioregions: Adélie Land (ALand); Antarctic Peninsula & the South Shetland Is. (AP&SSh); Amundsen & Bellingshausen Sea (AS&BS); Balleny & Scott Is. (Bal&Sco); Bounty & Antipodes Is.(Bount&Ant); Bouvet Is. (Bouv); Campbell & Auckland Is. (Cam&Auc); Crozet Is. (Cro); Davis Sea & Wilkes Land (DS&WL); Falkland Is. (Fal); Heard Is. (Heard); Kerguelen Is. (Ker); Macquarie Is. (Mac); Ob & Lena seamounts (Ob&Lena); Prydz Bay (PBay); Prince Edward & Marion Is. (PEd&Mar); Queen Maud Land & Enderby Land (QML&EL); Ross Sea (Ross); South Argentina (SArg); South Chile (SChi); South Georgia & Shag Rocks (SG&Sha); South Orkney Is. (SOrk); South Sandwich Is. (SSand); Tierra Del Fuego (TdF) and Weddell Sea (WS). (a) All bioregions. (b) Close-up without AS&BS, Mac, Cam&Auc and Bount&Ant.

that bioregions from New Zealand are well differentiated from others. Two other bioregions, AS&BS and Mac, are also well discriminated. Other bioregions (Fig. 4b) are plotted together following a north–south differentiation: sub-Antarctic and South American bioregions on one side, Antarctic bioregions and the Scotia Arc on the other, with the exception of Tierra del Fuego that shows affinities with Antarctic bioregions (note the shortest path between TdF and SOrk).

## Brooders versus broadcasters

Information about reproductive strategies was available for 59 species with occurrence data shallower than 1,500 m: 37 brooding species (accounting for 2,403 occurrences) and 22 broadcasting species (4,608 occurrences). Cluster analysis of brooding species (Fig. 3e) indicates five groups: (I) Ob & Lena seamounts (Ob&Lena) and the South Sandwich Island (SSand) (SP = 22% with the remaining groups); (II) sub-Antarctic Islands (Ker, Heard, Cro and PEd&Mar) (SP = 24% with the remaining groups); (III), four New Zealand, sub-Antarctic and Antarctic bioregions (Cam&Auc, Bal&Sco, Bouv and DS&WL); (IV) eight Antarctic bioregions (SP = 40% between group III and IV) differ from the fifth group; and (V) South American bioregions (SChi, Fal, SArg and TdF) at SP = 30%. The Antarctic group is subdivided into two subgroups: high Antarctica (IVa) (WS, PBay, ALand and Ross) and West Antarctica (IVb) (SG&Sha, AP&SSh and SOrk) (SP = 59%). BSN connections (Fig. 3f) indicate the occurrence of a link between New Zealand and Balleny & Scott Is. (Bal&Sco) (BSV = 86%) as well as strong affinities among all bioregions of the high Antarctica (continental Antarctica excluding the Antarctic peninsula). South America is strongly linked to the West Antarctica to the south and the sub-Antarctic Islands to the east through South Georgia & Shag Rocks (SG&Sha) (BSV = 98.5% and 85.7% respectively).

Faunal affinities for broadcasting species (Fig. 3g) show higher similarity values than brooders, except for New Zealand (I) which is isolated at 12% of SP. A second group (II) formed by Antarctic (AS&BS, QML&EL) and South American bioregions (SChi and SArg) is distinguished from the remaining bioregions (III) (SP = 46%) structured into two subgroups (SP = 64%): the sub-Antarctic Islands (IIIa) and Antarctic bioregions with TdF (IIIb). The BSN network for broadcasting species (Fig. 3h) highlights the isolation of New Zealand from SO bioregions. Sub-Antarctic Islands are all strongly linked to each other and to South America through Tierra del Fuego (TdF) (BSV = 98.8%). Brooder and broadcaster networks (Table 2) were not correlated ($r_s = 0.296$; $P = 0.067$).

## Biogeographic patterns of genera

At genus level, bioregions are structured in three distinct geographic groups (Fig. 3c, d): (I) New Zealand (SP = 32%),

**Table 2** Results of the Mantel test between BSN structure matrices using the Spearman coefficient. $r_s$ is the correlation value and p the associated probability. The symbol * underlines significant values ($P < 0.05$).

| Situation | $r_s$ | $P$ |
|---|---|---|
| Brooders versus broadcasters | 0.296 | 0.067 |
| Brooders versus genus | 0.641* | 0.0002 |
| Broadcasters versus genus | 0.444* | 0.0142 |
| Genus versus species | 0.728* | 0.0001 |

(II) South America (including TdF) and the sub-Antarctic Islands together, separated from a last group composed of (III) Antarctic bioregions (SP = 55%). At regional scale, group II can be split into two smaller entities: South America (IIa) and the sub-Antarctic Islands (IIb) (SP = 59%). The structure of Antarctic bioregions follows a more complex pattern of three distinct subgroups (SP = 65 to 70%): Antarctic Islands (IIIa) (Bal&Sco and Bouv), West Antarctic bioregions (IIIb) (SG&Sha, AP&SSh and SOrk) and high Antarctica (IIIc) (Ross, WS, ALand and PBay). BSN connections among these subgroups (Fig. 3d) highlight the isolation of New Zealand from other bioregions of the SO and in contrast, strong links between Antarctic bioregions. Bioregions of South America are linked to West Antarctic through the South Orkney bioregion (BSV = 98.2%). Sub-Antarctic Islands are connected to West Antarctica through South Georgia & Shag Rocks (Sg&Sha; BSV = 86%) to the west and to Macquarie Island (BSV = 66%) to the east. A strong circumpolar connection is present without the gap observed at species level between the Weddell Sea (WS) and the closest other bioregions of East Antarctica (BSV = 99.4%) (Fig. 3d). There is a significant correlation (Table 2) between genus and species networks ($r_s = 0.\ 728$; $P < 0.0005$), between genus and brooder networks ($r_s = 0.641$; $P = 0{<}0.0005$), and a moderate but significant correlation between the genus and broadcaster networks ($r_s = 0.444$; $P = 0.0142$).

## DISCUSSION

### Main patterns of SO asteroid biogeography

At species level, high levels of endemism reflect the isolation of marine biogeographic units due to oceanographic barriers to dispersal or environmental filters. We found low values of endemism for each bioregion when considered in isolation in contrast to the high levels of endemism for the SO (59%) and Antarctic region (29%). These levels are similar to those previously reported for the SO (Moles *et al.*, 2015) and high compared to other regions, possibly due to the ancient isolation of the SO by the ACC front system associated to speciation and radiation events within Antarctic waters (Watling & Thurston, 1989; Lecointre *et al.*, 2013; De Broyer & Jażdżewska, 2014).

Our quantitative analyses highlighted the relatively weak biogeographic connectivity of New Zealand to SO bioregions at all taxonomic levels and reproductive strategies. The influence of New Zealand cold temperate fauna on its southernmost areas is shown by the high level of endemism observed within and around New Zealand waters. The uniqueness of the New Zealand's benthic fauna compared to the rest of the SO benthos has been demonstrated in many studies on diverse taxa (e.g. molluscs: Linse *et al.*, 2006; bryozoans: Barnes & Griffiths, 2007; and echinoids: Pierrat *et al.*, 2013).

The faunal affinities between East Antarctica and the Macquarie Island suggest that faunal connections may occur through the southern Macquarie ridge, as demonstrated for other echinoderms (asteroids and ophiuroids) (O'Hara, 1998; O'Hara *et al.*, 2013). An additional link was observed between Macquarie and the sub-Antarctic islands, supporting a pattern already established for echinoderms (asteroids, ophiuroids and holothuroids: O'Hara, 1998). Passive transport of adults and juveniles by kelp rafting may explain this affinity (Edgar, 1987) as well as a long-distance transport of larvae.

Distribution patterns of asteroids are strongly structured within the SO. Antarctic and sub-Antarctic provinces are well differentiated from each other with bioregions of East and West Antarctica grouped together to the south, bioregions of South America and the sub-Antarctic Islands to the north. Asteroid distribution is therefore strongly structured according to latitude. This may be a result of the PF acting as a biogeographic barrier to the dispersal of asteroids leading to distinct species assemblages between the two provinces. Northern bioregions are clustered together following an additional, longitudinal segregation between South American bioregions to the west and sub-Antarctic islands to the east.

The role of the PF as a barrier to gene flow between Antarctic and sub-Antarctic benthic fauna has been frequently discussed (Clarke *et al.*, 2005; Fraser *et al.*, 2012), although it can be relatively permeable to certain species (Convey *et al.*, 2009; Sands *et al.*, 2015; Fraser *et al.*, 2016). This is supported by the BSN analyses where there is no obvious faunal connection between the sub-Antarctic and Antarctic bioregions, but through the Scotia Arc bioregions. This last area constitutes a potential gateway to Antarctica for northern fauna, as demonstrated in previous research (e.g. IBMANT: Arntz, 2005). Explanations for this include the role of mesoscale eddies (Glorioso *et al.*, 2005; Chown *et al.*, 2015) and stepping-stone dispersal through islands of the Scotia Arc (e.g. Tatiàn *et al.*, 2005; Fortes & Absalão, 2011). Our results also show faunal affinities between Magellanic and sub-Antarctic assemblages, supporting previous studies on sponges (Downey *et al.*, 2012), molluscs (Griffiths *et al.*, 2009) and echinoids (Pierrat *et al.*, 2013). This pattern is probably driven by the westward flowing ACC allowing long-distance dispersal of propagules (see Waters, 2008 for discussion).

West and East Antarctica bioregions are well differentiated from each other, confirming previous studies (e.g. Griffiths *et al.*, 2009; Pierrat *et al.*, 2013; De Broyer & Jażdżewska, 2014). Here, the geological/glacial history of Antarctica can be invoked as a possible cause as the Weddell, Amundsen and Ross Seas may have been connected by a trans-Antarctic seaway (Lawver & Gahagan, 2003; Pollard & DeConto, 2009) that separated East Antarctica from continental fragments of West Antarctica (Linse *et al.*, 2006; Pierrat *et al.*, 2013). Molecular studies partially support this hypothesis (Strugnell *et al.*, 2012), although data from East Antarctica are needed for confirmation. The east–west pattern may also have originated from the contrasting environmental conditions that prevail between East and West Antarctica (David & Saucè, 2015). The affinity of asteroid faunas between Tierra del Fuego and West Antarctic bioregions is a novel result, highlighting the importance of connections between South America and Antarctica.

West Antarctica is surprisingly rich in asteroid species, even when compared to other well-sampled areas (Table 1; Fig. 2). As previously discussed (Barnes, 2005; Barnes *et al.*, 2006; Linse *et al.*, 2007b), this can be accounted for by the ACC hypothesis (see Pearse *et al.*, 2009) that suggests that recurrent (but sporadic) transport of brooding species by the ACC caused their establishment in the Scotia Arc region. The hypothesis predicts the "existence of many species in clades of varied divergence times, at a wide range of depths, but with highest diversity downstream of the Drake Passage (passage between Cape Horn and the Antarctic peninsula), in the Scotia Arc and Weddell Sea" (Pearse *et al.*, 2009). Here, the high number of brooding species and strong species:genus ratio in the Scotia Arc area supports this hypothesis.

## The importance of reproductive strategies for asteroid biogeography

Pappalardo & Fernández (2014) recently reported a poleward increasing number of direct developers in crustaceans and molluscs. They linked this to low temperatures and food availability in the highest latitudes, emphasizing the importance of life-history traits such as larval development in determining patterns of species richness in marine taxa. The high number of brooding asteroid species in the SO can also be explained by vicariance and allopatry, and not solely as a consequence of adaptation (Poulin *et al.*, 2002; Pearse *et al.*, 2009).

The ecological uniqueness of the New Zealand asteroid fauna can be explained by the geographic position of New Zealand, which limits faunal exchange and larval dispersal to the south. Surprisingly, with only three brooding species reported in New Zealand waters (among which two are found in the Antarctic region), our results show a connection with East Antarctica (Fig. 3f). This weak link might be an artefact due to the very small number of species, but could also reflect an existing relationship such as that proposed for cheilostomatid bryozoa (Griffiths *et al.*, 2009).

The diversity of asteroids from the sub-Antarctic Islands region appears to have been shaped by a complex evolutionary history. Here, reproductive strategy significantly contributes to our understanding of large-scale distribution patterns. Asteroids of the sub-Antarctic Islands show fewer affinities with South American species than with those of both West and East Antarctic regions. The low capacity of brooders to disperse over large distances (around 7,000 km between South America and the sub-Antarctic Islands) partly explains this delineation, given the absence of stepping stones between the sub-Antarctic Islands. In contrast, the high dispersal capacity of broadcasters reduces the impact of geographic isolation on faunal exchange between provinces. In summary, an original fauna evolved *in situ* around the islands, with some species arriving from South America and others from the Antarctic region. This scenario explains the interrelationships of the fauna of Tierra del Fuego (Fig. 3h), which is highly influenced by both South America and the West Antarctic region. Only brooding species show a clear structuring of Antarctic bioregions. In contrast, broadcasting species show weak spatial structure with a clear circumpolar continuity and no distinct biogeographic boundary.

More information is required to fully understand the role of reproductive strategy in asteroid biogeography. Larval ecology of sea stars in the SO takes a variety of different forms (Bosch & Pearse, 1990), with planktonic (planktotrophic or lecitotrophic) larvae for broadcasters. The pelagic larval duration may also vary among species, up to 165 days for *Odontaster validus* (Bosch & Pearse, 1990) which allows a huge potential for long-distance dispersal. Brooding biology also varies with some broods developing within suboral maternal brood chambers and others beginning their development in the stomach pouch (McClintock *et al.*, 2006). Broods can be carried for several months before releasing a fully developed juvenile. So far there has been little research on species in the SO (Agüera *et al.*, 2015), and most of these focus on near-shore shallow-water species. Overall, brooders account for low fecundity, high survival and a limited dispersal capacity. On the contrary, broadcasters have a high fecundity and a low survival rate of their larvae. Another potentially important (and understudied) factor is variation in habitat suitability for larvae along the dispersal routes. Such suitability depends on many factors including diet of larvae, the dynamics of planktonic life (Byrne *et al.*, 2016), substrate availability and biotic interactions (i.e. competition). New modelling techniques based on experimental data (Dynamic Energy Budget – Functional Trait and Distribution Models) are starting to produce insights into these mechanisms, and can even generate predictive scenarios of migration or invasion (e.g. Byrne *et al.*, 2016).

## Across taxonomic levels and time-scales

Analysing biogeographic patterns at high taxonomic levels can bring insights about upstream patterns of distribution and, in particular, the legacy of past processes for present-day biogeography (Pierrat *et al.*, 2013). Our genus-level analysis revealed that some SO distribution patterns are ancient and probably linked to major processes that occurred in the past. For instance, the Antarctic versus sub-Antarctic pattern is probably due to the long history of isolation of Antarctic waters. The setting up of the PF and of the ACC in the early Oligocene (30 Ma BP) (Lawver & Gahagan, 2003; Lawver *et al.*, 2014) and of other biogeographic barriers resulting from past geological activity were accompanied by vicariant processes. However, the use of molecular markers is needed to build robust phylogenies and increase the accuracy of divergence times between clades to infer the potential impact of past geological events on the evolution of the fauna. For example, González-Wevar *et al.* (2012) used the COI marker in various taxa (*Sterechinus, Nacella* and *Yoldia*) to demonstrate that the barrier between Antarctic and sub-Antarctic areas formed 3.7 to 5 Mya. This barrier reflects the recent impact of Plio-Pleistocene glaciations more than the ancient oceanographic history of the ACC. Janosik *et al.* (2011) drew a similar conclusion using data on asteroids, and proposed that mixing was still possible during the Last Glacial Maximum (21,000 years ago) due to changing and moving boundaries of the PF. In contrast, the molecular phylogeny of the sea star superorder Valvatacea (Mah & Foltz, 2011a) suggests a possible ancestry of the Antarctic fauna from the adjacent sub-Antarctic regions and a diversification of the Antarctic Asteriidae associated with the isolation of the SO fauna and the formation of the ACC. Another molecular study on the asteroid superorder Forcipulatacea (Mah & Foltz, 2011b) also supports the hypothesis of diversification of Antarctic clades when the ACC first started to flow.

At the generic level, the circum East Antarctic versus West Antarctic pattern can be accounted for by the existence of a past trans-Antarctic pathway linking the Weddell and Ross seas (Linse *et al.*, 2006; Pierrat *et al.*, 2013). The closure of this pathway and the existence of the Weddell Sea Gyre might explain the absence of strong faunal similarities between the Weddell Sea and the close bioregions of East Antarctic at the species level (Linse *et al.*, 2006; Pierrat *et al.*, 2013). Finally, in contrast to the species-level analysis, dissimilarities between the asteroid genera of Tierra del Fuego and the West Antarctic region might reflect the recent mixing of species between South America and West Antarctica.

Surprisingly, the biogeographic patterns shown for brooding species are very similar to those of all asteroid genera. New Zealand apart, the two patterns fit almost perfectly and are statistically the most similar to each other (Table 2). This may simply illustrate the conservative biogeographic patterns of brooders compared to broadcasters that are able to disperse over long distances, which is supported by the circumpolar patterns shown in many species (35% of the species found south of the PF in this study) from many taxonomic groups. Such an ability to disperse may also explain the counter-intuitive presence of multiple lineages of certain circumpolar broadcasting species at the same locations (see Hemery *et al.*, 2012). If broadcasting species were isolated into refugia during glacial maxima, their populations may have evolved independently and merged again after conditions warmed to form the current biogeographic patterns.

## CONCLUSIONS

The biogeographic patterns observed for sea stars in the SO are consistent with those of other taxonomic groups. Our result highlights the important role of reproductive strategy to understand large-scale spatial patterns of faunal distribution of asteroids. We therefore recommend that, whenever possible, reproductive strategy should be taken into account in large-scale biogeographic studies. Finally, more effort is needed to fill data shortfalls and to date the diverse origins of biogeographic patterns in the SO. Using molecular tools in studies of asteroid species with contrasted reproductive strategies should bring new insights and help to gain a comprehensive understanding of historical legacy on present-day biogeography of the SO.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Data source and quality control for Southern Ocean Asteroidea.

**Appendix S2.** Bootstrap Spanning Values for each Bootstrap Spanning Network.

## BIOSKETCH

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Author contribution: C.M., T.S. and B.D. wrote the manuscript; C.M., Q.J., A.A. and A.B. performed the analyses; C.M. collected the data.

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