

## ECHINODERMS AS CLUES TO ANTARCTIC ~ SOUTH AMERICAN CONNECTIVITY

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### ABSTRACT

Isolation and climate change has lead to an Antarctic marine biota rich in endemic taxa. But evidence exists for the occurrence of several shared marine species between the Southern Ocean and other basins. This manuscript reviews on the echinoderm taxa known from the Antarctic and South America, and evaluates some evidences for the connectivity between these continents. Metadata from several studies and data from the Brazilian continental margin were used for the analyses. A total of 602 echinoderm species have been recorded so far at both regions, 101 of those (~17%) are shared between Antarctica and South America, and from these around 47% are typically deep-sea ones. A high species richness was found at the Antarctica Peninsula, South Shetland Is. and South Georgia, possibly resultant from highest sampling effort at these regions. Distinct geological history and the tectonic activities play an important role in regulating the benthic faunal assemblage of these regions. An overlap was found between the echinoderm fauna from the South American cone, and mainly the regions around the Antarctic Peninsula. The echinoderm fauna from the Brazilian margin distinguished from those at the tip of the continent, although a few shared taxa occurred. A species assemblage turnover was identified from the Uruguayan margin. Also, the whole Magellanic region showed more affinities with the Argentinean Atlantic margin and the Falkland/Malvinas Is. than the southern Pacific Chilean margin. South Georgia and South Sandwich Is., as transitions regions between the South American and Antarctic regions, shared species with both continents. The considerably low ratio between the number of shared and total species records from the Antarctic regions revealed that most species are most likely endemic to the Southern Ocean. But future explorations of the South American and Antarctic deep sea margins and basins could reveal a higher number of shared echinoderm species than that reported here. All these comparisons should be backed up by taxonomic calibration and use of molecular tools in order to distinguish cryptic species and evaluate genetic populations' structure, as these would lead to a better understanding of observed biogeographical patterns.

**Keywords:** Zoogeography; echinodermata; biodiversity; polar front; Southern Ocean.

### RESUMO

**EQUINODERMOS COMO INDICADORES DA CONECTIVIDADE ANTÁRTICA ~ AMÉRICA DO SUL.** O isolamento e mudanças climáticas levaram a uma biota marinha antártica rica em táxons endêmicos. Entretanto existem evidências de ocorrência de várias espécies marinhas compartilhadas entre o Oceano Austral e outras bacias oceânicas. Este manuscrito revê os táxons de equinodermos conhecidos para a Antártica e América do Sul e avalia algumas evidências para a conectividade entre estes continentes. Metadados de vários estudos e dados da margem continental brasileira foram utilizados para as análises. Um total de 602 espécies de equinodermos foi registrado até o presente para as duas regiões, 101 das quais (~17%) são compartilhadas entre Antártica e América do Sul e, destas, aproximadamente 47% são tipicamente de oceano profundo. Uma elevada riqueza de espécies foi encontrada na Península Antártica, Ilhas Shetland do Sul e Geórgia do Sul, possivelmente resultante do maior esforço amostral nessas regiões. A distinta história

geológica e atividades tectônicas desempenham um papel importante na regulação das associações faunísticas bentônicas dessas regiões. Foi encontrada uma considerável sobreposição entre a fauna de equinodermos do cone Sul Americano e, especialmente, as regiões no entorno da Península Antártica. Os equinodermos da margem profunda brasileira distinguiram-se daqueles encontrados na extremidade do continente, embora tenham ocorrido algumas espécies compartilhadas. Uma transição das associações de espécies foi encontrada na margem uruguaia. Além disso, a região magelânica apresentou mais afinidades com a margem Atlântica argentina e com as Ilhas Falkland/Malvinas do que com a margem chilena no Pacífico. As Ilhas Geórgia do Sul e Sandwich do Sul apresentaram-se como regiões de transição entre as regiões Sul Americanas e Antárticas, possuindo espécies compartilhadas com os dois continentes. A taxa relativamente baixa entre o número de espécies compartilhadas e o número total de espécies registradas para as regiões na Antártica mostraram que a maioria das espécies é provavelmente endêmica do Oceano Austral. Mas, futuras explorações das margens profundas tanto da América do Sul quanto da Antártica e suas bacias oceânicas podem revelar um número maior de espécies compartilhadas que as registradas aqui. Todas estas comparações devem ser apoiadas por calibração taxonômica e uso de ferramentas moleculares para que se possa distinguir adequadamente espécies crípticas e avaliar a estrutura genética das populações, já que essas informações podem levar a uma melhor compreensão dos padrões biogeográficos observados.

**Palavras-chave:** Zoogeografia; echinodermata; biodiversidade; frente polar; Oceano Austral.

## RESUMEN

**EQUINODERMOS COMO EVIDENCIA DE LA CONECTIVIDAD ANTÁRTICA~SUDAMERICA .** El aislamiento y el cambio climático han llevado a una biota marina Antártica rica en taxones endémicos. Sin embargo, hay evidencia de la ocurrencia de varias especies compartidas entre el Océano Antártico y otras cuencas oceánicas. El presente manuscrito revisa los taxones de equinodermos conocidos en la Antártida y Sudamérica y evalúa algunas evidencias de la conectividad entre estos continentes. Para los análisis fueron usados metadatos de varios estudios y datos del margen continental brasileño. Un total de 602 especies de equinodermos han sido registradas hasta ahora en ambas regiones, de las cuales 101 (~17%) son compartidas por ambas regiones. De éstas, 47% son especies típicas de mares profundos. Se encontró una alta riqueza de especies en la Península Antártica, en las islas Shetland del Sur y Georgia del Sur, posiblemente debido a un mayor esfuerzo de muestreo en estas regiones. Una historia geológica particular y la actividad tectónica juegan un rol importante en la regulación del ensamblaje de la fauna bentónica de estas regiones. Se encontró una superposición en la fauna de equinodermos del Cono Sur y de las regiones alrededor de la Península Antártica. La fauna de equinodermos del margen brasileño se distinguió de aquella del extremo sur del continente, aunque se encontraron algunos taxones compartidos. Se identificó un recambio de la composición de especies desde el margen uruguayo. Por otro lado, la región Magallánica mostró más afinidad con el margen atlántico argentino y las islas Malvinas/Falkland, que con el margen pacífico chileno. Las islas Georgia del Sur y Sandwich del Sur, como transiciones entre Sudamérica y la Antártida, compartieron especies con ambos continentes. La proporción considerablemente baja de especies compartidas sobre registros totales de especies de las regiones antárticas reveló que la mayoría de las especies es endémica del Océano Antártico. Sin embargo, la exploración futura de los márgenes y cuencas del mar profundo de Sudamérica y la Antártida puede revelar un mayor número de especies compartidas de equinodermos que el reportado. Todas estas comparaciones deberían ser soportadas por una revisión taxonómica y el uso de herramientas moleculares para distinguir especies crípticas y evaluar la estructura genética de las poblaciones, ya que esto llevaría a un mejor entendimiento de los patrones biogeográficos observados.

**Palabras clave:** Zoogeografía; echinodermata; biodiversidad; frente polar; Océano Antártico.

## INTRODUCTION

Comparisons between Antarctica and other fragments of Gondwana, the study of climate change, and anthropogenic influences to the Antarctic environment have been critical for understanding the evolution and present biological community structures in Antarctica, and their connexions with the biota outside the Polar Front (Clarke *et al.* 2005, Clarke 2008). The ultimate separation of Antarctica from South America happened during the Oligocene, and was responsible for the Antarctic isolation, formation of the Southern Ocean and Antarctic Circumpolar Current (ACC), northward flow of the Atlantic Antarctic Bottom Water, and numerous geological features observed along the northern end of the Antarctic Peninsula (e.g. an active spreading centre in the Bransfield Strait, ridge trench collision and gas hydrates on modern sediments) (Turner *et al.* 2009). Over an evolutionary time, the combination of isolation and climate change has led to an Antarctic biota rich in endemic taxa (Clarke 2003, 2008, Clarke & Johnston 2003). But evidence exists for the occurrence of several shared marine species between the Southern Ocean and other basins, especially the Magellanic region through the Drake Passage and Scotia Arc (Clarke 2003, Brandt *et al.* 2007a, b). Their evolution and historical biogeography are closely related to major tectonic and climatic changes (González-Wevar *et al.* 2010).

The development of the ACC is possibly the most influential stage in the progressive geographic isolation of the Antarctica within oceanic surroundings, forming a continuous hydrographic barrier more than 2000 km from the Antarctic continent (Barker & Thomas 2004). This oceanographic barrier, known as Polar Front, is characterized by abrupt temperature and salinity variations between the Southern Ocean and surroundings waters masses, and is usually considered to represent a limitation for the dispersal of surface marine organisms, especially planktonic larvae (Clarke *et al.* 2005, Turner *et al.* 2009). But it is still unclear the exact effect of the ACC in the distribution of certain invertebrate fauna, as some extinctions occurred millions of years after the establishment of the ACC (Thatje *et al.* 2005, Kim & Thurber 2009). For instance, whether the last occurrence of crabs and lobster was truly at the lower

Miocene, or their absence in younger deposits could be an artifact of non-fossilization or non-preservation (Thomson 2004). Also, *Zygochlamys* bivalve species existed in Antarctic waters until much later, and disappeared only 3 or 4 mya (Jonkers 2003).

The continental shelf and especially the nearshore benthos is directly subject to natural impacts in the Antarctic region related to this seasonal ice formation, which may vary in extent and thickness, and ice melt (Stark *et al.* 2005, Smith *et al.* 2006). But the Antarctic continental shelf is large and generally deep (500–1000m), being strongly influenced by the seasonal sea-ice cover and primary production, factors which may favour strong benthopelagic coupling (Smith *et al.* 2006). This special physical feature of the Antarctic continental shelf combined with the isothermic water column might have led to the extended eurybathy documented for several taxa (Brandt *et al.* 2007a,b). The seasonal temporal and spatial variations from sea ice, local disturbances from iceberg scours and anchor ice, and glacially transported sediments contribute to the patchiness of benthic habitats and communities in the Antarctic regions (Stark *et al.* 2005, Smith *et al.* 2008, Siciński *et al.* 2010).

Some Antarctic benthic organisms are physiologically adapted to these natural changes, but others have shown very limited physiological ability to support slight environmental variations such as temperature (Peck *et al.* 2006). Also, where human activities are more intense, such as near research stations (e.g., sewage, dumps) and more intense scientific activities using trawling, fishing, dredging, a highest stress may be found on benthic communities (Stark *et al.* 2003). The rate at which these variations occur, and the time that it is necessary for phenotypic population to vary, are critical factors related to gradual changes and evolutionary processes (Clarke 2003). Several studies have provided useful information on the Antarctic Peninsula shelf, under-ice and deep basins benthic communities (e.g., Brandt *et al.* 2004, Brandt *et al.* 2007a, b, Gutt 2007, Gutt *et al.* 2007, Smith *et al.* 2008). A more stable benthic community with several sessile and sedentary organisms may be established away from the ice scour effect zones in the deep shelf and continental margin below 400m (Teixidó *et al.* 2007).

Biogeographical studies attempt to explain patterns of distribution and provide useful tools for the identification of species origins based in their phylogenetic relationships (Brandt *et al.* 2004). These are fundamental when taking into account: the rapid warming of the Antarctic Peninsula region with significant glaciers in retreat; its oceanographic relevance in relation to South America; water mass formation and circulation towards the Pacific and Atlantic (Turner *et al.* 2009); the potential role as biodiversity pump towards these oceans (Clarke 2003, Brandt *et al.* 2007a, Clarke 2008, Griffiths *et al.* 2009). Furthermore, as Antarctic benthic communities show high levels of endemism, gigantism, slow growth, longevity, late maturity, adaptive radiations that generated considerable biodiversity in some taxa (Clarke & Johnston 2003), studies on these communities are relevant for understanding the effect of global changes in the marine environment.

Even though most patterns of distribution of marine benthic invertebrates are commonly explained by vicariant speciation caused by plate tectonics, molecular studies have evidenced that long distance dispersion is a plausible explanation for biogeographical patterns in the Southern Ocean (González-Wevar *et al.* 2010). Possibly this is a consequence meso-scale processes (within tens to hundreds of kilometers) at the ACC, which has a very complex structure, is highly variable and dynamic with eddies over a wide range of scales, and could form an important mechanism for transport of organisms across the Polar Front (Clarke *et al.* 2005). According to these authors eddies of cool water surrounding a parcel of warmer water (warm-core rings) might transport sub-Antarctic plankton into Antarctica, and eddies of warmer water surrounding a parcel of colder water (cold-core rings) might carry Antarctic plankton into warmer waters to the north.

The first studies related to the sub-Antarctic and Antarctic regions biogeography (e.g. Ekman 1953, Hedgpeth 1969, Dell 1972) were either based on faunistic and/or oceanographic features. These authors concluded that differences between regions, especially East and West, were possibly a result from the lack of biodiversity data from East Antarctica. The growing knowledge on Antarctic biodiversity in recent years, particularly related to benthic organisms, has allowed the establishment of more

accurate biogeographical patterns, including their relationship with those from South America. For instance, using large data sets, Linse *et al.* (2006) and Griffiths *et al.* (2009) showed that Antarctic mollusks and bryozoans have greater affinity with the southern South American continent than those from New Zealand regions. Häussermann & Fösterra (2005), Montiel *et al.* (2005) and Rodriguez *et al.* (2007) showed that Antarctic and South America (and here mainly the Magellanic region) have a high number of shared anemone and polychaete species. Gutt *et al.* (2003) pointed out the necessity of comparative studies on in the deep sea between the Antarctica and South America, as also in the continental shelves and islands which serve as stepping-stones for the dispersion of shallow fauna (Scotia Arc) to understand the dispersion capability and the effect of isolation of populations on their evolution. Currently, greater multidisciplinary emphasis has been given to understanding how the distribution of species was shaped by geological, oceanographic and biological events since the separation of Antarctica from South America.

Echinoderms are generally conspicuous within Antarctic benthic communities, and they usually occur in fairly high densities and biomass in the deep sea (Gage & Tyler 1991, Brandt *et al.* 2007a, b). In fact, echinoderms are well represented within existing Antarctic datasets, such as in the Scientific Committee on Antarctic Research Marine Biodiversity Information Network (SCAR-MarBIN), with high numbers of georeferenced records (Griffiths 2010). Despite the fact that their species richness is highest on the shelf, they show a rich diversity along the slope and on the deep-sea abyssal plains (Brandt *et al.* 2007b). Below 3000m all the main deep sea regions are directly connected, and as a result there should not be any barrier to the dispersal and establishment of populations to and from the Southern Ocean (Brandt *et al.* 2007a). Generally though, the Southern Ocean benthic shelf faunal composition differs from that of its deep sea as the first is zoogeographically isolated through the ACC, and conversely, the deep-sea fauna can freely migrate in and out of the Polar Front (Brandt *et al.* 2007a). The distribution of water masses in the world oceans will have a strong effect on benthic geographical distribution, allowing potential dispersal and endemism, and also affecting zonation

on bathyal depths along deep sea ocean margins (Tyler & Zibrowius 1992). Clarke (2003) noted that at the generic level there are many similarities between different deep-sea regions in particularly to holothuroids, ophiuroids, some echinoids and pennatulids.

The southern South American and Antarctic continental shelves echinoderm fauna are fairly well studied, and a literature survey plus additional data from the Brazilian deep sea margin provided the basis for testing hypothesis related to biogeographical patterns and their potential connectivity. Despite the fact that both regions have several echinoderm species, at least in shallower waters, mainly on the continental shelves, these would be mostly distinct taking into account physical barriers such as the Polar Front. Conversely, highest proportion of shared species between both continents would be found in deepest waters, possibly as a result from their dispersal over time using deep water masses as their 'highways'. Basically, whilst reviewing the available echinoderm biodiversity data, the main objective of this manuscript has been to substantiate the existence of faunistic overlap, and search for further evidence of the connectivity between the two continents.

## MATERIALS AND METHODS

### SPECIES RECORDS

The South American and Antarctic echinoderm species list used in this study was gathered from the available literature (Appendix 1) and 'Scientific Committee on Antarctic Research Marine Biodiversity Information Network', SCAR-MarBIN (de Broyer *et al.* 2010). This was then checked against major world databases such as World Ophiuroidea (Stöhr & O'Hara 2007), World Asteroidea (Mah 2009), World Echinoidea (Kroh & Mooi 2010) Databases, and complemented with the Antarctic and Subantarctic Marine Invertebrates of the NMNH/Smithsonian Institution Databases (Lemaitre *et al.* 2009).

The SCAR-MarBIN has more than 800 echinoderm species records including geographical information (GIS). Species from the five echinoderm classes (Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea and Crinoidea) were included in this

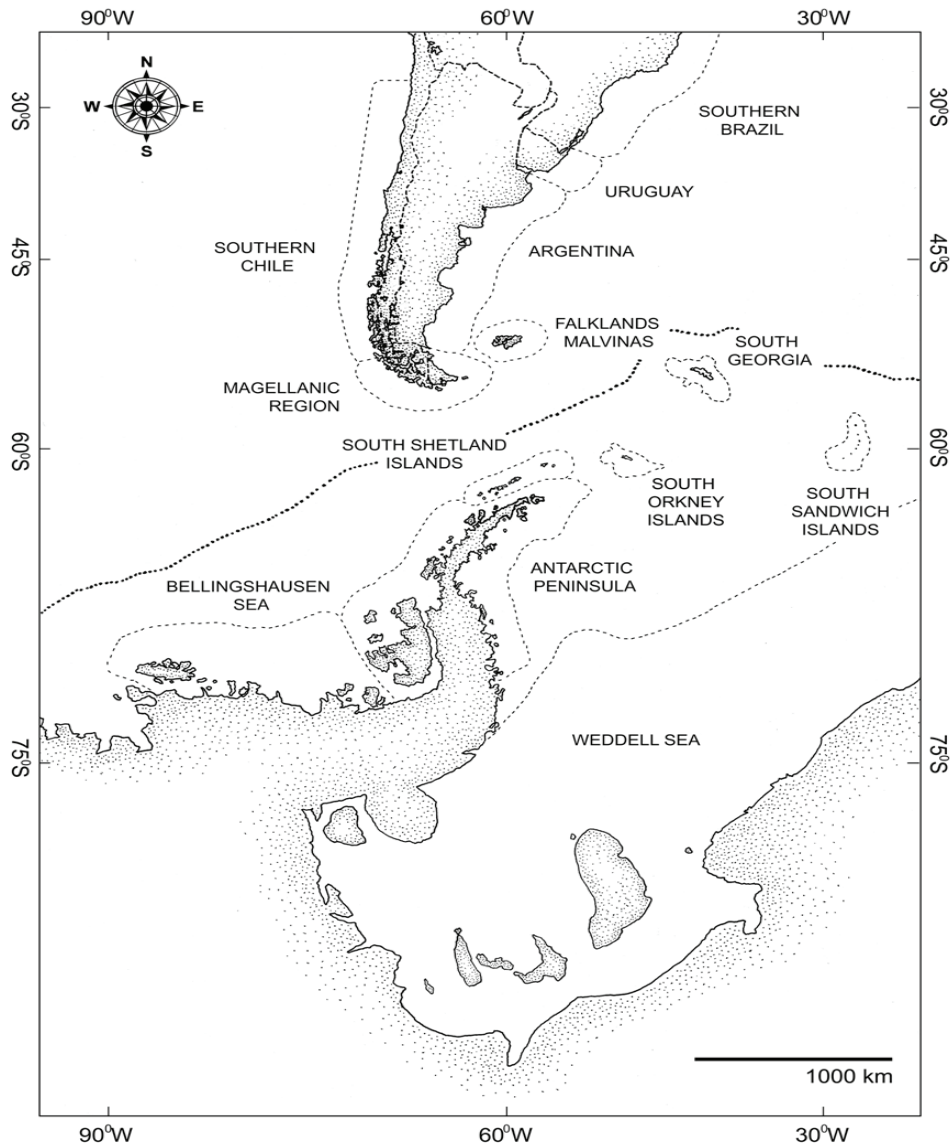
study. All valid species records, from the geographical regions considered, found in the checked data were used regardless of depth distribution. OBIS (Ocean Biogeographic Information Systems) database comprises a powerful tool to identify biodiversity hotspots and large-scale ecological patterns. It includes more than 27 million species records from major oceanographic programs and museum collections of the world (OBIS, 2011). We crossed the species list gathered with the echinoderms records from OBIS in order to complement data from the South American margin and subantarctic regions. Distribution related to each species were accessed, and basic geographical information included in a presence/absence data matrix with additional records from the literature and regions further north in South America (ex. Brazilian margin). Species richness is provided as a total number of species recorded for each region. A species record in the presence/absence matrix for any of the study regions was done only once independently on the number of records found in the literature, SCAR-MarBIN or OBIS.

### REGIONS

In order to create an echinoderm list data matrix the following South American geographic limits were used: 1) Chilean continental margin at the Pacific Ocean (northernmost limit 27° S); 2) Magellanic region (here including the Chilean and Argentinian margin); 3) West Atlantic northernmost limit at Campos Basin off the Brazilian margin (22° S); 4) Uruguayan margin; 5) Argentinean margin; 6) Falkland/Malvinas Is.. The following Antarctic regions (south of the Polar Front) were included in this study: 1) South Georgia (as in Clarke *et al.* 2007 and Griffiths *et al.* 2009); 2) South Orkney Is.; 3) South Sandwich Is.; 4) South Shetland Is.; 5) Antarctic Peninsula; 6) Weddell Sea; 7) Bellingshausen Sea. These 13 regions (Figure 1) were defined mostly based (but modified) on previous (e.g. Hedgpeth 1969) and more recent works by Linse *et al.* (2006) and Clarke *et al.* (2007) on mollusks, and by Griffiths *et al.* (2009) on mollusks and bryozoans. The Magellan Strait and Tierra del Fuego were considered as Magellanic region (here we are interested in the connectivity between this region and the Antarctic continent), and Bellingshausen Sea E and W were

considered just as Bellingshausen Sea region. Here, the northernmost limits in South America were extended compared to those used in all previous

studies above-mentioned. The geographic position of each record was counted if they occurred into these predefined regions.



**Figure 1.** The 13 study regions in Antarctica and South America continents. Black dotted line represents the mean position of the Polar Front

### DATA TREATMENT

The data was analyzed without taking depth into consideration as this information is scattered, not always provided in on line world databases, and would cause restrictions to the data matrix. However, the matrix is far from (> 95%) composed of species records from shallow waters and from the continental margin. The vast majority of the Antarctic sampling effort comes from depths less than 500 m (Griffiths 2010), and contrasts with the area of the deep sea that cover 27.9 million Km<sup>2</sup> (Clarke & Johnston 2003).

The continental shelf and slope cover together an area of 6.94 million Km<sup>2</sup> of the Southern Ocean sea floor (Clarke & Johnston 2003). All shared species between South America and Antarctica were identified and counted. A species was considered shared when recorded at least once in both South American region and in an Antarctic region. The same matrix was then used to verify each South American region common species to those found in each Antarctic region, and vice-versa. This was done to find out which region from each continent had the most number of shared species.

A proportion of shared species (%) was estimated as a ratio between the number of shared species over the total number of species in each region. This was done because, for instance, in two specific regions of South America the same number of shared species with Antarctica may have been recorded, but this value could in fact represent different proportions in relation to the total number of species recorded in each of those regions.

The presence/absence matrix was used to generate a similarity matrix (Bray-Curtis) between regions. The regions faunistic similarity was verified using a nMDS (non multidimensional scaling) analysis of proximity and a cluster analysis (Group Linkage) using PRIMER 6. The hypothesis that the echinoderm assemblages inside and outside the Polar Front are different was tested using the PERMANOVA analyses (Anderson 2005). The Bellingshausen Sea was excluded from this analysis due to low species richness and due a historic scarceness of data. We considered north and south the Polar Front as a two level factor with six replicates regions. PERMANOVA is used for testing the simultaneous response of one or more variables to one or more factors on the basis of any distance measure using permutation methods, in which the matrix includes  $a$

groups and  $n$  observation units (replicates) per group in the simplest situation of a one-way test (Anderson 2005).

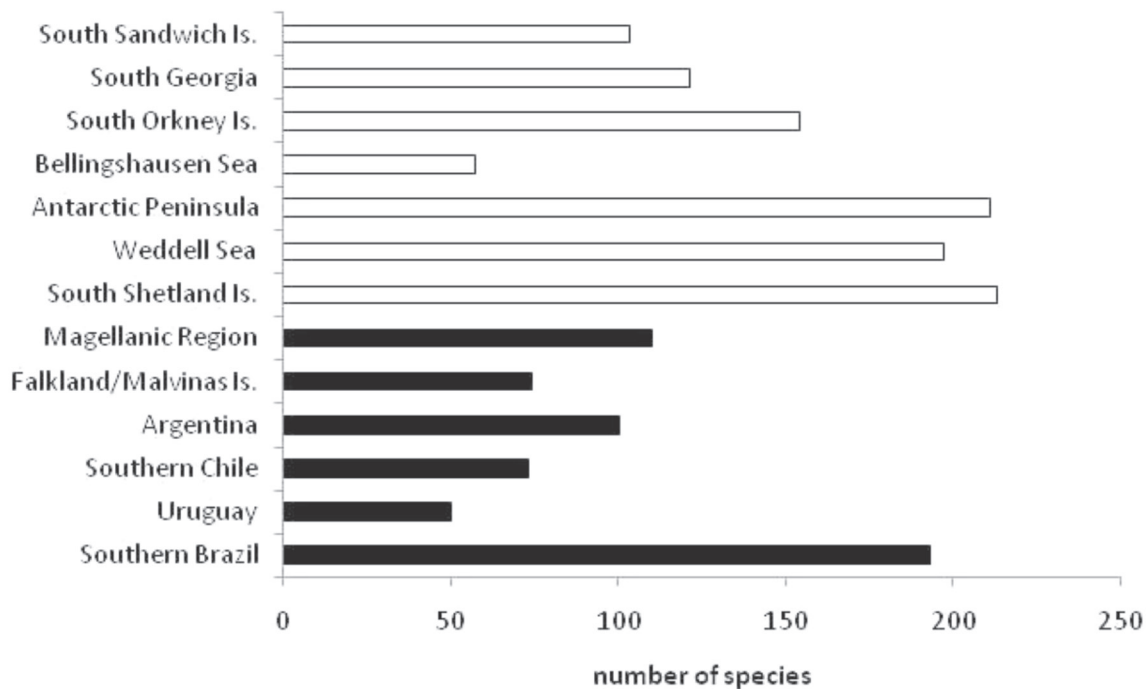
## RESULTS

### *SPECIES RICHNESS*

A total of 602 species of echinoderms were recorded in this study: 185 ophiuroids (brittle stars and basket stars), 176 asteroids (sea stars), 138 holothuroids (sea cucumbers), 82 echinoids (sea urchins) and 21 crinoids (sea lilies and comatulids).

The South Shetland Is. and Antarctic Peninsula were the regions with the highest numbers of species, 213 and 211 respectively (Figure 2).

The Weddell Sea and the Brazilian margin had the second highest species richness values. It is relevant to note the fairly high echinoderm species richness recorded for the South Orkney Is. ( $n=154$ ) and South Georgia ( $n=121$ ), especially taking into account its size. Its number of species was higher than most extensive areas such as the Chilean and Argentinean coasts (Figure 2). Considering the Antarctic regions studied here, a low number of species was found in the Bellingshausen Sea.



**Figure 2.** Number of echinoderm species recorded at each region of the Antarctica and South America continent. Empty bars represent Antarctic regions and black bars represent the South American regions.

*SHARED SPECIES*

About 17% (n=102) of the total number of species studied were shared between South America and Antarctica. And from these, there were 40 asteroids,

22 ophiuroids, 21 holothuroids, 16 echinoids, and only two crinoid species. Amongst these shared species, 47% occur at depths greater than 800 m, and these are represented by the 18 asteroid, 10 ophiuroid, 10 holothuroid, 8 echinoid, and 2 crinoid species (Table I).

**Table I.** List of shared echinoderm species between South America and Antarctica, including the regions of occurrence for each species. (SB) Southern Brazil; (URU) Uruguay; (SC) Sothern Chile; (AR) Argentina; (F/MI) Falkland Is.; (MR) Magellanic Region; (SSI) South Shetland Is.; (WS) Weddell Sea; (AP) Antarctic Peninsula; (BS) Bellingshausen Sea; (SOI) South Orkney Is.; (SG) South Georgia; (SSandI) South Sandwich Is. (\*) species that occur at depths deepest than 800 m (Source Appendix I).

Echinoids	> 800 m	Regions
Family Arbacidae		
<i>Arbacia dufresnii</i> (Blainville, 1825)		SC, AR, F/MI, MR, SSI
Family Cidaridae		
<i>Austrocidaris spinulosa</i> Mortensen, 1910		AR, F/MI, MR, SG
Family Ctenocidaridae		
<i>Aporocidaris milleri</i> (A.Agassiz, 1898)	*	SC, SSI, WS, AP, SOI, SG, SSandI
Family Echinidae		
<i>Sterechinus agassizi</i> Mortensen, 1910	*	AR, F/MI, MR, SG
<i>Sterechinus diadema</i> Studer, 1876		AR, SSI
<i>Sterechinus neumayeri</i> (Meissner, 1900)	*	MR, SSI, WS, AP, BS, SOI, SG
Family Paleopneustina ( <i>incertae sedis</i> )		
<i>Delopatagus brucei</i>	*	MR, SSI, WS, AP
Family Prenasteridae		
<i>Tripylus excavatus</i> Philippi, 1845		SC, AR, MR, SG
<i>Tripylus reductus</i> (Koehler, 1912)		AR, MR, SSI, AP, SOI
Family Schizasteridae		
<i>Abatus agassizii</i> Mortensen, 1910		MR, SSI, WS, SG
<i>Abatus cavernosus</i> (Philippi, 1845)	*	AR, MR, SSI, AP, BS, SOI, SG
<i>Abatus curvidens</i> Mortensen, 1836		F/MI, MR, SSI, AP, SOI, SG
<i>Abatus philippii</i> Loven, 1871	*	AR, SSI, WS, AP, BS, SG
<i>Brisaster moseleyi</i> (A. Agassiz, 1881)	*	SC, F/MI, MR, SOI
<i>Tripylaster philippii</i> (Gray, 1851)		SC, AR, F/MI, MR, SG
Family Temnopleuridae		
<i>Pseudechinus magellanicus</i> (Philippi, 1857)		URU, SC, AR, F/MI, MR, AP



Continuation of Table 1

Asteroids	> 800 m	Regions
Family Asteroidea		
Family Asteroidea		
<i>Anasterias antarctica</i> (Lütken, 1857)		MR, SSI, AP
<i>Anasterias pedicellaris</i> Koehler, 1923		URU, AR, F/MI, MR, AP, SOI
<i>Cosmasterias lurida</i> (Philippi, 1858)		SC, AR, MR, SSI, AP, SOI
<i>Diplasterias brandti</i> (Bell, 1881)	*	SB, AR, F/MI, MR, SSI, AP, SOI, SG
<i>Diplasterias meridionalis</i> (Perrier, 1875)		MR, SSI
<i>Diplasterias octoradiata</i> (Studer, 1885)	*	F/MI, SG
<i>Diplopteraster verrucosus</i> (Sladen, 1882)		SC, AR, F/MI, MR, AP, SOI
<i>Lysasterias perrieri</i> (Studer, 1885)		MR, SSI, AP, SOI, SSandI
<i>Psalidaster mordax</i> Fisher 1940	*	AR, F/MI, MR, AP, SOI, SSandI
<i>Smilasterias scalprifera</i> (Sladen, 1889)	*	F/MI, SSI, AP, SOI, SSandI
Family Astropectinidae		
<i>Bathybiaster loripes</i> Sladen, 1889	*	SB, URU, AR, F/MI, MR, SSI, AP, SOI, SG, SSandI
<i>Mimastrella cognata</i> (Sladen, 1889)		MR, SSI
Family Benthoplectinidae		
<i>Cheiraster (Luidiaster) planeta</i> (Sladen, 1889)		MR, SSI, SOI
<i>Cheiraster (Luidiaster) gerlachei</i> (Ludwig, 1903)	*	F/MI, MR, SSI, WS, AP, SOI
Family Brisingidae		
<i>Odinella nutrix</i> Fisher, 1940		MR, SSI, SOI, SG
Family Ctenodiscidae		
<i>Ctenodiscus australis</i> Lütken, 1871	*	SB, URU, AR, F/MI, MR, AP, SOI
<i>Ctenodiscus procurator</i> Sladen, 1889	*	SC, AR, MR, SSI, AP
Family Echinasteridae		
<i>Henricia obesa</i> (Sladen, 1889)		URU, SC, AR, F/MI, MR, WS, AP
<i>Henricia studeri</i> Perrier, 1891		F/MI, MG, AP, SOI
Family Ganeriidae		
<i>Cycethra verrucosa</i> (Philippi, 1857)		URU, SC, AR, F/MI, MR, SSI, WS, AP, SOI, SG
<i>Cycethra verrucosa verrucosa</i> (Philippi, 1857)		URU, AR, SSI, AP, SOI, SG
<i>Ganeria falklandica</i> Gray, 1847		URU, SC, AR, MR, SSI, SOI
Family Goniasteridae		
<i>Ceramaster patagonicus</i> (Sladen, 1889)	*	SB, AR, F/MI, MR, SSI, AP, SOI

Continuation of Table 1

<b>Asteroids</b>	<b>&gt; 800 m</b>	<b>Regions</b>
<i>Ceramaster grenadensis</i> (Perrier, 1881)		F/MI, MR, SOI
<i>Cladaster analogus</i> Fisher, 1940		URU, AR, MR, SSI, SO, SG
<i>Hippasteria falklandica</i> Fisher, 1940		AR, F/MI, SSI, SOI
<i>Pseudarchaster discus</i> Sladen, 1889	*	F/MI, MR, SSI, AP, SOI, SG, SSandI
Family Korethrasteridae		
<i>Peribolaster folliculatus</i> Sladen, 1889	*	SC, MR, F/MI, SSI
Family Labiateridae		
<i>Labidiaster radiosus</i> Lütken, 1871		AR, F/MI, MR, SSI, SG
Family Odontasteridae		
<i>Acodontaster elongatus</i> (Sladen, 1889)		AR, F/MI, MR, SSI, AP, SOI, SG, SSandI
<i>Odontaster meridionalis</i> (E.A. Smith, 1876)	*	MR, SSI, AP, SOI
<i>Odontaster penicillatus</i> (Philippi, 1870)	*	SC, AR, F/MI, MR, SSI, AP, SOI
Family Pedicellasteridae		
<i>Anteliaster australis</i> Fisher, 1940		F/MI, MR, SSandI
Family Poranidae		
<i>Porania (Porania) antarctica</i> E.A. Smith, 1876	*	SC, AR, F/MI, MR, SSI, WS, AP, SOI, SG, SSandI
<i>Porania (Porania) antarctica magellanica</i> Studer, 1876		MR, AP, SG
Family Pterasteridae		
<i>Pteraster affinis</i> Smith, 1876	*	MR, SSI, WS, AP
<i>Pteraster stellifer</i> Sladen, 1882	*	F/MI, MR, SSI, WS, AP, SG
Family Porcellanasteridae		
<i>Eremicaster vicinus</i> Ludwig, 1907	*	SC, SSI, SOI, SG, SSandI
Family Solasteridae		
<i>Lophaster stellans</i> Sladen, 1889		SC, F/MI, MR, SSI, WS
<i>Solaster regularis</i> Sladen, 1889	*	URU, AR, F/MI, MR, SSI, AP, SOI
<b>Ophiuroids</b>	<b>&gt; 800 m</b>	<b>Regions</b>
Family Amphiuridae		
<i>Amphioplus perigrinator</i> (Koehler, 1912)	*	F/MI, SSI, WS, AP, SOI, SG, SSandI
<i>Amphiura belgicae</i> Koehler, 1900	*	AR, F/MI, SSI, WS, AP, SOI, SG, SSandI

Continuation of Table 1

Ophiuroids	> 800 m	Regions
<i>Amphiura eugeniae</i> Ljungman, 1867		URU, AR, MR, WS, SSandI
<i>Amphiura joubini</i> Koehler, 1912	*	SB, URU, AR, SSI, WS, AP, BS, SOI, SG, SSandI
<i>Amphiura protecta</i> Hertz, 1926		F/MI, MR, SSI, WS, AP, BS, SG, SSandI
Family Gorgonocephalidae		
<i>Astroclamys bruneus</i> Koehler, 1911	*	MR, SSI, WS, AP, SOI, SG, SSandI
<i>Astrotoma agassizii</i> Lyman, 1875	*	SC, AR, F/MI, MR, SSI, WS, AP, SG, SSandI
<i>Gorgonocephalus chilensis</i> (Philippi, 1858)		SB, URU, SC, AR, F/MI, MR, WS, AP, SG, SSandI
Family Hemieuryalidae		
<i>Ophiochondrus stelliger</i> Lyman, 1879		AR, MR, SSI, WS, AP, SOI, SSandI
Family Ophiacanthidae		
<i>Ophiacantha antarctica</i> Koehler, 1900	*	MR, SSI, WS, SOI, SG, SSandI
<i>Ophiacantha cosmica</i> Lyman, 1878		SB, WS, SOI
<i>Ophiacantha vivipara</i> Ljungman, 1870		SC, AR, F/MI, MR, SSI, WS, AP, SOI, SG, SSandI
<i>Ophiomitrella conferta</i> (Koehler, 1922)		AR, F/MI, MR, SSI, WS, AP
<i>Ophioscolex nutrix</i> Mortensen, 1936	*	SB, MR, AP, BS
Family Ophiactidae		
<i>Ophiactis asperula</i> (Philippi, 1858)		URU, SC, AR, F/MI, MR, SSI, AP
Family Ophiuridae		
<i>Ophiocten amitinum</i> Lyman, 1878	*	SC, AR, F/MI, MR, SSI, WS, AP, SG, SSandI
<i>Ophiogona doederleini</i> (Koehler, 1901)	*	MR, SSI, WS, AP, BS, SOI, SSandI
<i>Ophiolimna antarctica</i> (Lyman, 1879)		MR, SSI, WS, AP, SOI, SG, SSandI
<i>Ophioplinthus inornata</i> (Lyman, 1878)		AR, F/MI, WS
<i>Ophiura ambigua</i> (Lyman, 1878)	*	MR, WS
<i>Ophiura (Ophiuroglypha) lymani</i> (Ljungman, 1871)		SC, AR, F/MI, MR, WS, SG
<i>Ophiura meridionalis</i> (Lyman, 1879)		MR, SSI, AP, SG
Holothuroids	> 800 m	Regions
Family Chiridotidae		
<i>Taeniogyrus contortus</i> (Ludwig, 1874)	*	SC, AR, F/MI, MR, SSI, WS, AP, SG, SSandI
<i>Trochodota purpurea</i> (Lesson, 1830)		SC, AR, F/MI, MR, SSI, SOI, SG, SSandI
Family Cucumariidae		
<i>Cladodactyla crocea</i> Lesson, 1830		SC, AR, F/MI, MR, SOI, SG

Continuation of Table 1

<b>Holothuroids</b>	<b>&gt; 800 m</b>	<b>Regions</b>
<i>Cucumaria georgiana</i> Lampert, 1886		F/MI, SSI, WS, AP, SOI, SG, SSandI
<i>Heterocucumis steineni</i> (Ludwig, 1898)		F/MI, SSI, SOI, WS, AP, SG
<i>Trachythyone parva</i> (Ludwig, 1874)		SC, AR, F/MI, WS, AP, SOI, SG
Family Deimatidae		
<i>Oneirophanta mutabilis mutabilis</i> Théel, 1879	*	AR, SG, SSI, SSandI
Family Elpidiidae		
<i>Scotoplanes globosa</i> (Théel, 1879)	*	URU, SSI, WS, AP, SOI, SG, SSandI
Family Molpadidae		
<i>Molpadia antarctica</i> (Théel, 1886)	*	SC, AP, BS
<i>Molpadia musculus</i> Risso, 1826	*	SC, F/MI, SSI, WS, AP, BS, SOI, SG
Family Psolidae		
<i>Neopsolidium convergens</i> (Hérouard, 1901)		SC, AR, F/MI, SG
<i>Psolidium incertum</i> Ludwig & Heding, 1935		F/MI, WS
<i>Psolus antarcticus</i> (Phillippi, 1857)	*	SB, SC, F/MI, MR, WS, AP, BS, SOI, SG, SSandI
<i>Psolus koehleri</i> Vaney, 1914	*	F/MI, SSI, AP, BS, SOI, SG, SSandI
<i>Psolus patagonicus</i> Ekman, 1925		SB, SC, AR, MR, AP, SG
<i>Psolus squamatus</i> (Koren, 1844)		SC, AR, AP
Family Synaptidae		
<i>Anapta fallax</i> Lampert, 1889		SC, AR, MR, SG
Family Synallactidae		
<i>Bathyplores natans</i> (Théel, 1886)		SC, SSI, AP, BS, SOI
<i>Mesothuria bifurcata</i> Hérouard, 1906	*	SC, MR, SSI, WS, AP, BS, SSandI
<i>Molpadiodemas violaceus</i> (Théel, 1886)	*	SC, AR, SSI, SOI, SSandI
<i>Molpadiodemas involutus</i> (Sluiter, 1901)	*	AR, F/MI, SSandI
<b>Crinoids</b>	<b>&gt; 800 m</b>	<b>Regions</b>
Family Antedonidae		
<i>Isometra vivipara</i> Mortensen, 1917	*	SB, AR, F/MI, MR, WS, SG
<i>Promachocrinus kerguelensis</i> Carpenter, 1888	*	MR, SSI, WS, AP, SOI, SG, SSandI

The number of shared echinoderm species between the study regions is provided in Table II. The Magellanic Region has showed the highest number of shared species ( $n=74$ ) with the Antarctic, being this more than half of the total number of species found in this South American region (67%). Further north along the Chilean coast the percentage of shared species was much lower. The Falkland Is. and Argentinean margin showed the second highest values of shared species, and also here these represent the majority of echinoderm species found in these regions (equivalent to 78 and 54%, respectively, see Table II). Only 5% of species found off South and Southeast Brazil have also been recorded in Antarctica so far. This is expectedly a much lower proportion than that found for the Uruguayan margin.

The South Shetland Is. and the Antarctic Peninsula had the highest number of echinoderm shared species records with South America (Table II). Even though this number was similar to those found for some South American regions, such as in Falkland Is., its proportion in relation to the total number of species in these Antarctic regions is much lower than the others. The number of shared species between the Weddell Sea and South America was similar to that found between South Orkney Is. and South Georgia. However, proportionally, the Weddell Sea showed a lower percentage of shared species than these islands. The Bellingshausen Sea had only 10 species in common with South America but represented around 23% of the total species (Table II).

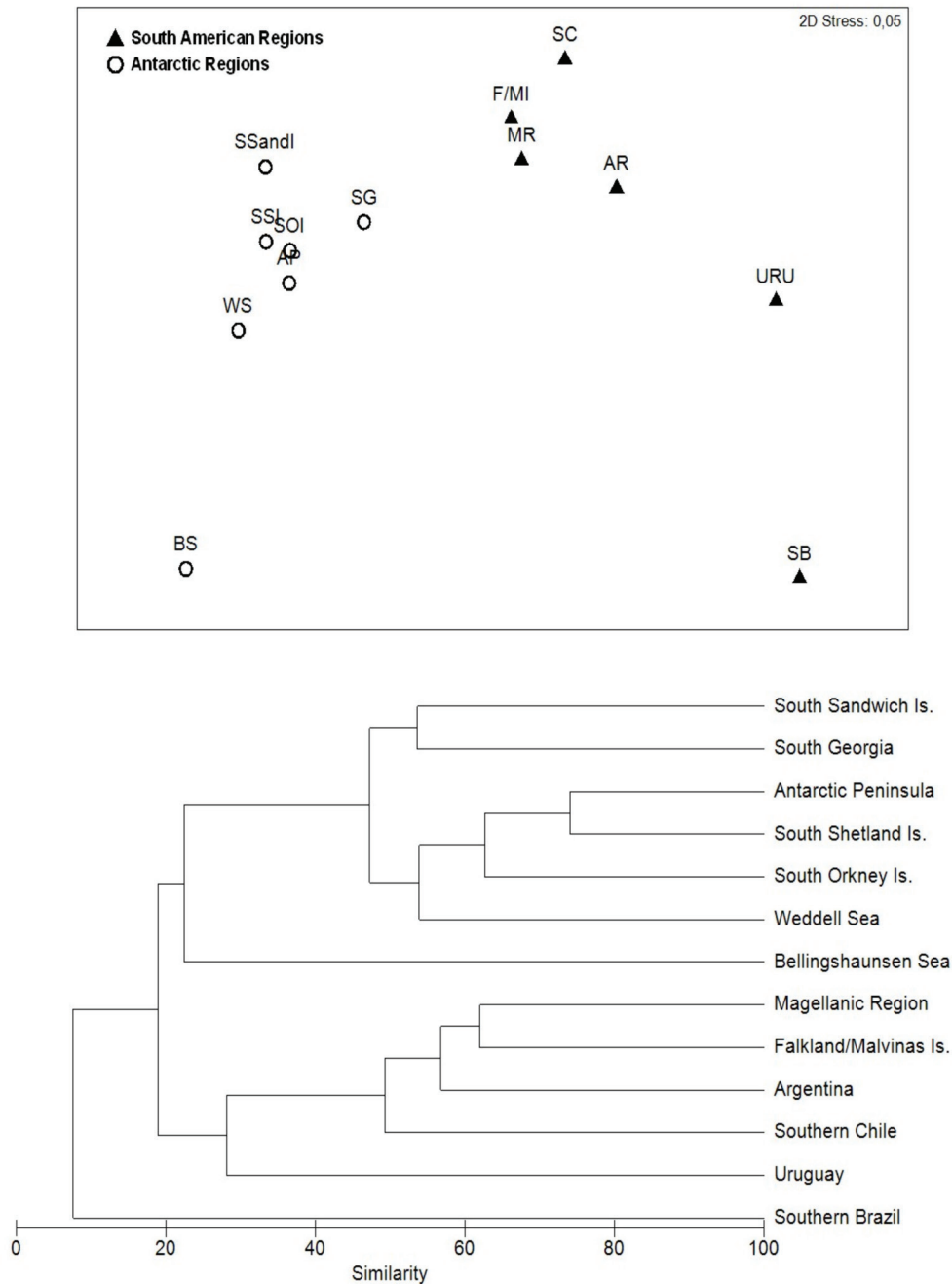
**Table II.** Number of shared species between the South American and Antarctica regions and the percentage of shared species in relation to the total species records of each region.

Regions	Antarctic - South America shared species	% shared species / total species
Southern Brazil	10	5.18
Uruguay	16	32.00
Argentina	54	54.00
Falkland/Malvinas Islands	58	78.38
Southern Chile	39	53.42
Magellanic region	74	67.27
South Georgia	54	44.63
South Orkney Islands	54	35.06
South Sandwich Islands	39	37.86
South Shetland Islands	66	30.99
Antarctic Peninsula	63	29.85
Weddell Sea	43	21.83
Bellingshausen Sea	13	22.81

### REGIONAL RELATIONSHIPS

The nMDS diagram clearly separated the South American and Antarctic regions. Two major groups were identified through the: 1) South American regions excluding the Brazilian margins, but with less than 30% similarity; and 2) all the Antarctic

regions (Figure 3). The South Orkney Is., South Shetland Is., Antarctic Peninsula, and the Weddell formed a well defined cluster with more the 50% similarity between these regions. The South Georgia and South Sandwich Is. were grouped as a separate cluster with about 53% of similarity. The Bellingshausen Sea stood as a separate group from these two groups of Antarctic regions.



**Figure 3.** Similarity between regions using a non-metric multidimensional scaling (nMDS) and cluster analysis of 602 echinoderms species from Antarctica and South America. (SB) Southern Brazil; (URU) Uruguay; (SC) Southern Chile; (AR) Argentina; (F/MI) Falkland/Malvinas Is.; (MR) Magellanic Region; (SSI) South Shetland Is.; (WS) Weddell Sea; (AP) Antarctic Peninsula; (BS) Bellingshausen Sea; (SOI) South Orkney Is.; (SG) South Georgia; (SSandI) South Sandwich Is.

Despite being outside the Polar Front, the Uruguay margin, the southern Chile, Magellanic Region, Argentinean margin, and Falkland/Malvinas Is. showed higher similarity with the Antarctic regions than to the Brazilian margins. These three latter regions showed great affinities and were grouped with over 50% of faunistic similarity. Southern

Chile was grouped with this concise cluster with more than 45% of similarity. The Uruguay margin stood as a separate region. The PERMANOVA tests (Table III) showed that the South America and Antarctica regions groups are statically strong and can be considered to have different echinoderms assemblages.

**Table III.** Results of PERMANOVA analyses (10000 permutations) between Antarctica and South American regions.

	DF	SS	MS	F	p	p (MC)
Antarctic X South America	1	11598.36	11598.36	6.52	<b>0.003</b>	<b>0.001</b>
Residual	10	17778.58	1711.86			
Total	11	29376.94				

p (MC) Monte Carlo permutation

## DISCUSSION

The assessment of Antarctic biodiversity, the knowledge about its role in the ecosystem functioning, and requirement for its conservation are of particular importance in the context of global environmental changes (Brandt *et al.* 2004). Although Polar regions have long been regarded as areas of low marine diversity, recent reviews (ex. Clarke & Johnston 2003) showed that the Southern Ocean benthos is considerably rich and diverse, despite variations across major groups. Many of the species currently known from Antarctica were described in the early 20<sup>th</sup> century, and around the turn of the century significant additions were made (Clarke 2008).

Comparisons between different continents and their oceans may be limited by the general lack of marine richness data from all regions and realms (i.e., shelf, margin and abyssal plains). The Register of Antarctic Marine Species (RAMS) and SCAR-MarBIN have brought together over 1 million distribution records for the Southern Ocean species, and is a good illustration of the large gaps or a complete lack of information in some Antarctic areas like the Bellingshausen Sea (Griffiths 2010).

The northern Antarctic Peninsula and the South Shetland Is. were the focus of a high number of oceanographic expeditions and an intensive effort in taxonomic resolution during the last decades. Also, Clarke *et al.* (2007) demonstrated that current knowledge on mollusks Antarctic continental shelf species richness is constrained strongly by sampling intensity. These facts must be taken into account, when considering the high diversity found in these areas. But taking into account a cross-section of major macro-invertebrate groups, the

species richness of the Antarctic continental shelf is comparable with the shelf faunas of Hawaii or northwest Europe (Clarke 2008).

The idea that species richness typically increases with geographical area and decreases with isolation (e.g., MacArthur & Wilson 1967) is frequently assumed in ecological studies comparing the diversity from regions with different dimensions. For instance, in analyzing biogeographic patterns of Antarctic regions and surrounding oceans, Griffiths *et al.* (2009) showed that the relationship between area and species numbers for Gastropoda and Cheilostomata was highest in biggest areas, but this was not the case for Bivalvia and Cyclostomata. In this study, we have shown that the number of echinoderms species at the small islands of South Georgia and the South Orkneys were comparable, and in some cases higher than other larger areas, such as the temperate margin of Argentina, Southern Chile and the sub-tropical margin of southern Brazil. In fact, three of the four regions that had the highest echinoderm species records were within the Polar Front.

The echinoderm fauna from the southern South American and Antarctic continental shelves are relatively well studied. This provided the basis for examining in more detail their distribution patterns, verifying the existence of faunistic overlap, and providing further evidence for the connectivity between the two continents. Around 17% of all echinoderms species known for South America and Antarctica are shared between these two continents. Similar overlaps were found for different invertebrate groups, such as Actinaria and Corallimorpharia (Häuserman & Fösterra 2005), bivalves (Zelaya 2005) and polychaetes (Montiel *et al.* 2005). More recently, Rodriguez *et al.* (2007) found that 15% of the anemone fauna are shared.

Knox & Lowry (1977) proposed that Antarctic continental shelf fauna originates from three different sources: 1) a relict autochthonous fauna; 2) a fauna derived by migration into shallow water from adjacent deep sea; and 3) a fauna dispersing into Antarctica from South America along the islands of the Scotia arc. Furthermore, Clarke (2008) proposed a fourth possibility that some taxa would have migrated out of Antarctica in the reverse direction along the Scotia arc.

Here, the relationship between the shared and total numbers of echinoderm species found in each region was lowest in Antarctica. Despite the fact that the Antarctic regions in this study had 101 echinoderm species shared with South America, a greater proportion of species was only known from the Southern Ocean, representing a relict autochthonous fauna. Conversely, in South America (e.g., Argentina, Falkland/Malvinas Is., and the Magellanic Region) the number of shared species represents more than half of the total species records in its regions, showing the great affinity with the Antarctic fauna.

The hypothesis about the existence of a connection between South America and the Antarctic Peninsula dates back to Arctowski in 1895 in which the Scotia arc lying between the southern tip of South America and the northern tip of the Antarctic Peninsula would serve as stepping stones for dispersion (Barth & Holmsen 1939, Thomson 2004). The Scotia Arc is composed of a number of islands, seamounts and ocean deeps that evolved over the last 40 mya since the split of the two continents (Pearse *et al.* 2001, Thomson 2004). Arntz *et al.* (2005) suggested that the development of the faunal structure known today was triggered by exchanges along the Scotia Arc, which would possibly be the most likely migration route between South America and Antarctica. For instance, this was the case for eurybathic ophiuroid species (Dahm 1999), and appears to have been the case for other echinoderm species with widespread distribution that occur on the southern South American shelf, especially in the Magellanic Region, and Antarctic Peninsula (e.g., the echinoids *Arbacia dufresnii*, *Austrocidaris spinulosa*, and *Abatus philipii*, the asteroids *Anasterias pedicellaris*, *Ganeria falklandica* and *Henricia obesa*, the ophiuroids *Gorgonocephalus chilensis*, *Ophiactis asperula* and the holothuroids *Cladodactyla crocea* and *Trochodota purpurea*).

Amongst the echinoderm shared species 47% are characteristically from deeper waters, found below 800m. In this review, 44-50% of the shared species in each echinoderm classes (excluding crinoids) occur in the deep sea. It is interesting to note that this proportion can be higher due to our gap of knowledge on the biodiversity of the deep sea in these regions. It is known that the deepest portions of the Southern Ocean are well connected to other oceans, and in the Atlantic section below 800-1000m a branch from the Circumpolar Deep Water flows northwards within the Malvinas Current (Piola & Mantano 2001). Below this, a warmer water mass (the North Atlantic Deep Water) flows southwards towards Antarctica, and further down the Antarctic Bottom Water flows northwards reaching regions as far the North Atlantic (Rintoul *et al.* 2001). Similar oceanographic processes occur between the Southern Ocean, the Pacific and Indian Oceans. This potentially enables strong deep sea faunal exchange between Antarctica and other continents (Brandt *et al.* 2007a,b). As South America was the last to separate from the Gondwana, and being the closest to Antarctica, this high proportion of echinoderm shared species found at slope depths support the connectivity hypothesis, and it is very likely that as sampling efforts increase at deepest zones, more shared species should be found in future. Major questions remain though related to the ecosystem functioning, species source and rates of gene flow, these latter also dependant on each taxon biological features such as reproductive and development traits (e.g., Hunter & Halanych 2008, Thornhill *et al.* 2008).

Similarities between the fauna from the Antarctic continental shelf and typical deep-sea (bathyal to abyssal) have been reported before (e.g., Gage 2004, Brandt *et al.* 2007b, Clarke 2008). Aronson *et al.* (2007) emphasizes the importance of echinoderms in benthic communities and the evolutionary connection between the faunas of the Antarctic continental shelf and the adjacent deep sea. Studies on other groups have shown similar evolutionary paths, for instance, whilst some isopod groups have moved from the continental shelves into the deep sea, others have colonized the shelves from the deep sea (Menziés *et al.* 1973; Brandt 1992). Invasion of Antarctic species into the deep sea, and then dispersion northwards seems to be the case for the ascidian *Bathypeva*, the crinoid



genus *Florometra*, the ophiuroid genus *Ophiacantha* and the cidaroids *Aporocidaris* (Pearse & Lockhart 2004). The species *Aporocidaris milleri* occurs in the Antarctic deep sea, and its northern distribution extends along the western coast of Americas as far as Alaska (Pearse & Lockhart 2004). The ophiuroid *Ophioscolex nutrix* occurs in Antarctic shelves (Mortensen 1936) and in the Brazilian continental margin at depths greater than 1000m (Campos *et al.* 2010).

Evidence exists of fauna that entered the Southern Ocean deep regions from South America. For instance, Diaz *et al.* (2010) proposed that a possible scenario to explain the *Sterechinus* spp. evolutionary pathways between shallow and deep sea could have involved an initial separation between the Antarctic and Subantarctic species by the end of the Miocene (~5 mya), and a later colonization of the deep ocean from the Subantarctic zone via Scotia Arc. Conversely, the Antarctic Circumpolar Current, the overall circulation complexity around the Antarctic Peninsula region, and the formation of Antarctic water masses that outflow from that region northwards (e.g., AIW and ADW) would allow pathways in reverse, providing grounds for Antarctic species to expand towards the north as proposed by some authors (Knox & Lowry 1977, Pearse & Lockhart 2004). This South American 'invasion' from Antarctic fauna through the deep ocean may have occurred principally during glacial maxima, where the continental ice sheets extended to the edge of the continental shelf in many areas of Antarctica (Thatje *et al.* 2005, Clarke 2008, Kaiser *et al.* 2010).

Little detail is known about the majority of Antarctic benthic organisms, and only a few studies exist evaluating populations connectivity between the Southern Ocean and South American species (Hunter & Halanych 2008). In this sense, the shared species list shown here could be considered as target benthic taxa for molecular investigations of gene flows between populations from both continents.

The multivariate analyses showed that the overall echinoderm community from South America is statistically different from that of Antarctic regions. These communities' differences are expected considering the unique Southern Ocean oceanographic features, such as the Polar Front as a dispersal barrier for many shallow benthic species. Conversely, the

Drake Passage, its very deep ocean basins and the Scotia Arc combined with circulation patterns may enable free faunal exchange of eurybathic species.

A higher similarity was found between the echinoderm fauna from the South American tip and northern portion of western Antarctica than that observed between the southern Brazilian region and the tip of South America. This result suggests a clear turnover of species along the Atlantic South American margin from the Brazilian subtropical region towards temperate areas, mainly at Uruguay. This was supported by the cluster analysis, which showed that even though the Uruguayan margin grouped with the other regions from the South American cone, the similarity between them is less than 30%.

The Magellan Strait and Magellanic Atlantic shelf, which extends from Rio de la Plata to Tierra del Fuego, have different topographic and oceanographic conditions, but also, both are different from the southern Chilean region from the Pacific coast (Montiel *et al.* 2005). Biogeographical studies using benthic invertebrates have also shown a turnover of species along the Chilean margin between the warm-temperate Province, that extends until 42°S, and the cold-temperate Province, that extends until the Cape Horn 56°S in the Pacific Ocean (e.g., Garth 1957, Bernasconi 1964, Desqueyroux-Faúndez 1994). Considering the Magellanic Region a single province, our results show that the echinoderm fauna from this region had more affinities with the fauna from the Falkland/Malvinas Is. and the Argentinean Margin than that from the Southern Chilean. The continental margin from the South American cone is influenced by the Cape Horn Current, which surrounds the Magellanic Region and flows northwards reaching the Burdwood Banks and the Falkland shelf (Riemann-Zürneck 1991). These flows generate a relative homogeneous water mass pathway through these areas that could partly explain the distribution patterns observed, and so the northward flow of Cape Horn Current towards South America may transport echinoderm larvae and adults associated with algal wisps. This could be an important dispersal mechanism of echinoderm species as proposed by Fell (1962) and Smirnov (1990, 1992).

Our data revealed that the Antarctic Peninsula, the South Shetland Is., South Orkney Is. and the Weddell Sea formed an outstanding group from other

Antarctic regions evaluated here. Similar results were found for mollusks species by Linse *et al.* (2006) in which South Georgia and South Sandwich stood as separate branch from that regions. An exclusive distribution of many anemone species represented a remarkable singularity in the Antarctic Peninsula and Weddell Sea regions (Rodríguez *et al.* 2007). Nevertheless, this was not the case for bryozoans and bivalves (Griffiths *et al.* 2009). It was evident from our study that the South Georgia, South Sandwich Is. represented transitions regions between Antarctica and South America.

The faunal resemblance of the Antarctic and South American continents and South Georgia was subject to debate in the literature. Zelaya (2005), using bivalves, included the South Georgia with the Antarctic regions. This was supported by Linse *et al.* (2006) and Griffiths *et al.* (2009) using mollusks and combined data of bryozoan and mollusks, respectively. Lovrich *et al.* (2005) studying decapods, and Ramos-Esplá *et al.* (2005) and Tatián *et al.* (2005) analyzing ascidian fauna suggested that the South Georgia would stand a transient position between South America and Antarctica. Our results support findings from these latter authors. Even though the island was grouped with the other Antarctic regions, it stood, with the South Sandwich Is., an outgroup from the Weddell Sea, South Orkney Is., South Shetland Is. and Antarctic Peninsula cluster. This resulted from a non-restricted Antarctic species composition, including a South American signature in the echinoderm fauna of these islands, revealed by the proportions of shared species with the South American regions. The South Sandwich Is. are very young islands, probably no more than 5 mya (Baker 1990), tectonically active and surrounded by very deep trenches (Thomson 2004). Kim and Thurber (2007) showed that the asteroids fauna from South Sandwich appear to be distinctively different from other Antarctic regions, but the result could be due the fact that the stations from these islands were deeper than others.

Our results showed that the Bellingshausen Sea outgrouped is possibly related to the scarceness of data from this region, a fact that was attempted by Griffiths *et al.* (2010). The Bellingshausen Sea is older than the Scotia Sea and areas around the Antarctica Peninsula (Thomson 2004), so we should expect a higher number of species than these areas. The fact

that the split of the Bellingshausen Sea is due a lack of data are also supported by the relative high proportion of shared species with the South American continent. This proportion was higher than the Weddell Sea (but probably because the far less number of species) and revealed that the region is not composed by a strict unique fauna. Future explorations probably will reveal that the Bellingshausen Sea has also a high number of species that are, in part, shared with other Antarctic regions and the South American continent.

## CONCLUSIONS

This study assessed the connectivity between the Antarctic and South American continents using the echinoderm fauna. Around 17% of the Antarctic species were shared with South America. The percentage of shared species in South American regions (ex. Falkland/Malvinas Is., the Argentina margin and the Magellan Region) were sometimes more than half of the total species records. This result underlined the great overlap between the echinoderm fauna from the South American cone and, principally, the regions around the Antarctic Peninsula. The considerably low ratio between the number of shared and total species records from the Antarctic regions revealed that most of those species are most likely endemic to the Southern Ocean. The high species richness of the Antarctica Peninsula, South Shetland Is. and South Georgia is possibly a result from the highest sampling effort in these regions, a fact which may lead to mistakenly conclusions that these regions are definitely diversity hot spots, as reported for several invertebrate groups. And results shown here, in principal, would support this hypothesis. But care should be taken when analyzing metadata that were originally sampled from any region at different depths, using different gears, and different sampling designs. Besides, the Antarctic Peninsula and surrounding regions are tectonically active and their benthic communities more subject to frequent disturbances compared to other areas of Antarctica that split from the Gondwana at earlier stages, e.g., the East Antarctica in the Pacific section, which might effectively have highest diversity.

The echinoderm fauna from the Brazilian margin were considered different from the tip of the continent, the latter showing more faunistic affinities

with the Antarctic regions. The Uruguayan margin represented a region of species assemblage turnover along the South American Atlantic margin. Also, the whole of the Magellanic region showed more affinities with the Argentinean Atlantic margin and the Falkland/Malvinas Is. than the southern Pacific Chilean margin.

South Georgia and the South Sandwich Is. are transitional positions between South American and Antarctic regions sharing species with both continents. The Weddell Sea, the South Shetland Is., the Antarctic Peninsula and the South Orkney Is. formed a well defined group within Antarctica. Distinct geological history and the tectonic activities play an important role in regulating the benthic faunal assemblage of these regions. The Bellingshausen Sea represented an isolated outgroup, possibly because of lowest sampling efforts in this region.

Future explorations of the South American and Antarctic deep sea margins and basins could reveal a higher number of shared echinoderm species than that reported here. But, in any case, these comparisons should be backed up by taxonomic calibration and the use of molecular tools in order to distinguish cryptic species and evaluate genetic populations' structure. These would lead to a better understanding of processes that determine biogeographical patterns.

**ACKNOWLEDGEMENTS:** This is a contribution to the Census of Antarctic Marine Life (CAML) and Continental Margins Ecosystems (COMARGE). We are grateful to the Antarctic Marine Biodiversity Information Network (SCARMarBIN) and the Antarctic and Subantarctic Marine Invertebrates of the NMNH/ Smithsonian Institution Databases, which provided useful data used in this manuscript. Brazilian continental margin data have been gathered through the "Campos Basin-Deep Sea Environmental Project/PETROBRAS". The authors are grateful to the Research and Development Center of PETROBRAS (CENPES) for the opportunity of sampling and studying this material. Brazilian Antarctic data was acquired through several CNPq financed projects including GEAMB (Process No. 55.0356/2002-9), MABIREH (Process No. 52.0293/2006-1, International Polar Year), INCT-APA (Process No. 574018/2008-5), and FAPERJ INCT-APA (Process No. E-26170.023/2008), and supported by the Ministry of Environment, Ministry of Science and Technology, and the Secretariat for the Marine Resources Interministerial Committee (SECIRM). The authors are grateful to the anonymous referees and the Editorial Team for their useful comments and contributions to this manuscript.

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## APPENDIX 1

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Submetido em 15/11/2010

Aceito em 26/01/2011