Antarctic ascidians: an isolated and homogeneous fauna

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Abstract

Several biogeographical studies have already been performed on the ascidians of the Antarctic region. However, new data obtained in the last few years have led us to a revision of the biogeography of this fauna. To examine the biogeographical structure of the Antarctic region, we divided it into 10 sectors, depending on the principal geographical features, and then applied cluster analysis and a multi-dimensional scaling ordination to a presence/absence matrix of species for each biogeographical area. Our study shows that Antarctic ascidians are a very homogeneous fauna, with a high level of endemism in the whole region (25–51% of Antarctic endemic species per sector), but with a low percentage of sector endemism (only up to 10%). This probably results from isolation arising from the Antarctic Convergence, and the vast geographical distances from adjacent regions, as well as from the relative constancy of the hydrographical conditions and the dispersal of organisms through circumpolar currents. In fact, cosmopolitan species represented only 0–7% of the total ascidian fauna in all sectors. Only the Bellingshausen Sea (low sample size), Bouvetøya (young and isolated, with an impoverished ascidian fauna) and the South Sandwich Islands (also young and isolated) are relatively separated. The insular sectors were more closely related to the South America and sub-Antarctic regions than the continental ones, showing a latitudinal gradient.

The geological history and physical and hydrographical characteristics of the Antarctic region are well known (see Arntz et al. 1994; Longhurst 1998; Clarke et al. 2005; Barnes et al. 2006; Knox 2007). In brief, the major geological events that have shaped the ecology and isolation of Antarctica occurred following the break-up of Gondwana. A deep seaway first opened between the South Tasman Rise and East Antarctica about 32 Mya, and the Drake Passage was probably open to deep water flow by 29 Mya (Lawver & Gahagan 2003). These events eventually led to the formation of the West Wind Drift (now commonly termed the Antarctic Circumpolar Current) and the Antarctic Polar Front, or Antarctic Convergence (Barnes et al. 2006). The Antarctic Convergence, which delimits the Antarctic region (Fig. 1), is a circumpolar area where cold superficial water sinks, resulting in an abrupt temperature change (Barnes et al. 2006). Another important feature in this region is the Antarctic Divergence, which separates the West Wind Drift and East Wind Drift currents (Fig. 1). The great depths of the Atlantic, Indic and Pacific basins, and the great distances from adjacent regions, isolate the entire region.

Ascidians have a sessile adult lifestyle and direct development or short-term planktonic larvae (with combined unhatched embryonic and larval periods of up to 16 days in cold regions; Cloney et al. 2002; Strathmann et al. 2006). As a result, they frequently have a restricted geographical distribution characterized by particular ecological conditions, which makes them an excellent group for biogeographical studies.

Although there are several papers on ascidian taxonomy in the Antarctic region (Sluiter 1906; Millar 1960; Kott 1969; Monniot & Monniot 1983; Tatián et al. 1998a, b; Sanamyan & Sanamyan 2002; Tatián et al. 2005; Arntz et al. 2006; among others), and several biogeographical studies with Antarctic, sub-Antarctic and South American ascidians (Ramos-Esplá et al. 2005; Primo & Vázquez 2007a), so far no synthetic biogeographical study considering the relationship among sectors in the Antarctic region, to show how isolated and homogeneous the Antarctic ascidian fauna is, has been carried out. Different zones have been explored in a very uneven way (Monniot & Monniot 1983). For example, areas such as South Georgia, the South Shetland Islands, the western

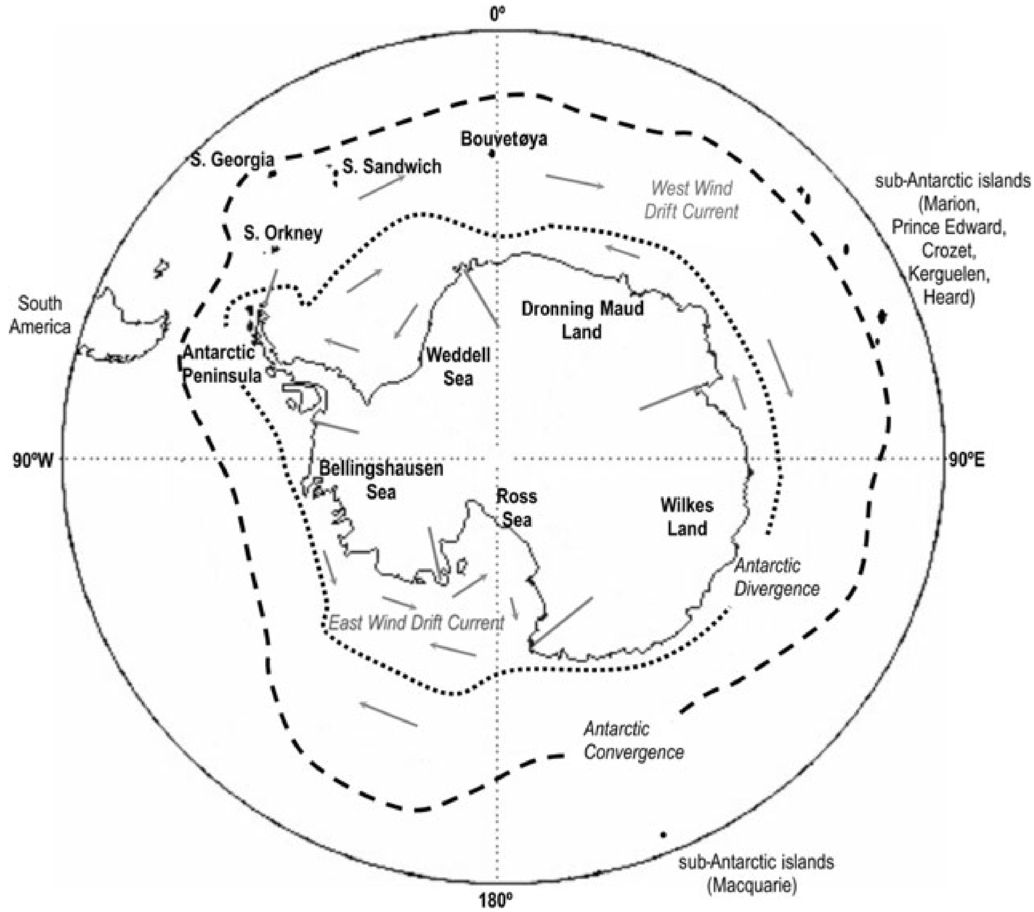

Fig. 1 Outlines of the Antarctic. The sectors considered in this work are marked in boldface.

Antarctic Peninsula, the Ross Sea and the eastern Weddell Sea have been well sampled. In contrast, the coverage of East Antarctica is far from complete, and we know almost nothing of the benthic fauna of the largely inaccessible Amundsen Sea (Clarke et al. 2004). The Bellingshausen Sea has been the object of several recent Spanish oceanographic cruises (BENTART 2003 and BENTART 2006), and the first studies are now starting to appear (molluscs, Troncoso et al. [2007]; soft-bottom community, Saiz et al. [2008]; a new ascidian species, Varela & Ramos-Esplá [2008]). The different sampling efforts make comparisons among different Antarctic sectors difficult; even so, the identification of Antarctic ascidian species is increasing (Primo 2006; Varela 2007; Primo & Vázquez 2007b).

Materials and methods

A presence/absence matrix of 107 species and 32 biogeographical areas was constructed (Table 1). The reported species included most of the known Antarctic ascidians (with inherent limitations resulting from the inaccessibility of certain papers) collected from the intertidal zone to a depth of 1000 m, where the tunicate fauna shows a marked change in species composition (Monniot & Monniot 1982). Species of uncertain identification were excluded. Principally we followed the work of Monniot & Monniot (1983), which was updated with recent data (Monniot & Monniot 1994; Tatián et al. 1998a; Sanamyan & Sanamyan 2002; Ramos-Esplá et al. 2005; Tatián et al. 2005; Arntz et al. 2006; Primo & Vázquez 2007b; Varela & Ramos-Esplá 2008).

As for the biogeographical areas, the Antarctic continent was divided into sectors according to the main Antarctic seas, capes, bays and islands, also taking into consideration the isolation or proximity of the areas (Fig. 1; see sector limits below). Most of the principal islands were taken as independent entities, except for some coastal islands that were included in the continental sectors. The 10 sectors were defined as follows.

- The Antarctic Peninsula sector (PANT), which includes the west coast, from its northern tip to Smiley Cape, and the South Shetlands Islands. The South Shetland

Table 1 Presence/absence matrix of the species recorded in the different areas of the Antarctic considered in this study. The biogeographical areas follow Briggs (1995), and areas beyond the Antarctic are included. The 10 sectors of the Antarctic region are set in boldface. See Fig. 2 for the abbreviations list.

	PANT	**BEL**	**ROS**	**WIL**	**MAU**	**WED**	**SOR**	**SSA**	**SGE**	**BOU**	SAS	SAN	TAS	SNZ	SAF	AS	TG	SAE	SAW	TPE	IPW	SAU	NNZ	JAP	BPW	BPE	CAL	GUI	AM	BAE	CAR	ATW
Aplidium annulatum (Sluiter, 1906)	✓																															
Aplidium aurorae (Harant & Vernières, 1938)	✓		✓	✓	✓																											
Aplidium balleniae Monniot & Monniot, 1983	✓		✓	✓																												
Aplidium bilinguae Monniot & Monniot, 1983				✓					✓	✓																						
Aplidium circumvolutum (Sluiter, 1900)	✓			✓	✓		✓		✓		✓	✓		✓									✓									
Aplidium cyaneum (Sluiter, 1906)	✓		✓	✓	✓	✓	✓			✓																						
Aplidium falklandicum Millar, 1960	✓						✓		✓	✓	✓	✓		✓																		
Aplidium fuegiense Cunningham, 1871				✓			✓		✓		✓	✓																				
Aplidium globosum (Herdman, 1886)	✓						✓	✓			✓	✓																				
Aplidium imbutum Monniot & Monniot, 1983	✓		✓				✓		✓		✓	✓																				
Aplidium longicaudatum (Sluiter, 1912)	✓																															
Aplidium loricatum (Harant & Vernières, 1938)	✓		✓	✓			✓																									
Aplidium meridianum (Sluiter, 1906)	✓		✓	✓		✓	✓	✓	✓		✓	✓																				
Aplidium millari Monniot & Monniot, 1994	✓					✓																										
Aplidium miripartum Monniot & Monniot, 1983	✓																															
Aplidium ordinatum (Sluiter, 1906)	✓			✓																												
Aplidium paessleri (Michaelsen, 1907)									✓		✓																					
Aplidium radiatum (Sluiter, 1906)	✓			✓			✓	✓																								
Aplidium recumbens (Herdman, 1886)	✓						✓	✓			✓	✓																				
Aplidium siderum Monniot & Monniot, 1983	✓																															
Aplidium stanleyi Millar, 1960	✓								✓		✓																					
Aplidium stewartense (Michaelsen, 1924)[a]																																
Aplidium triplex (Sluiter, 1906)	✓										✓																					
Aplidium vanhoeffeni Hartmeyer, 1911[a]																																
Aplidium variabile (Herman, 1886)									✓		✓	✓		✓									✓									
Aplidium vastum (Sluiter, 1912)	✓		✓																													
Placentela translucida Kott, 1969	✓																															
Polyclinum sundaicum (Sluiter, 1909)[a]																																
Ritterella mirifica Monniot & Monniot, 1983	✓		✓																													
Synoicum adareanum (Herdman, 1902)	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓																				
Synoicum georgianum Sluiter, 1932	✓			✓			✓	✓	✓		✓	✓																				
Synoicum giardi (Herdman, 1886)									✓		✓	✓																				
Synoicum hypurgon (Michaelsen, 1924)				✓									✓								✓	✓										
Synoicum ostentor Monniot & Monniot, 1983	✓			✓			✓																									
Synoicum polygyna Monniot & Monniot, 1980	✓		✓			✓																										
Synoicum ramulosum Kott, 1969				✓																												
Cystodytes antarcticus Sluiter, 1912	✓					✓					✓																					
Distaplia colligans Sluiter, 1932	✓		✓	✓	✓	✓	✓		✓		✓																					
Distaplia cylindrica (Lesson, 1830)	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓																					
Polycitor clava (Harant & Vernières, 1938)[a]																																

Table 1 *Continued*

	PANT	**BEL**	**ROS**	**WIL**	**MAU**	**WED**	**SOR**	**SSA**	**SGE**	**BOU**	SAS	SAN	TAS	SNZ	SAF	AS	TG	SAE	SAW	TPE	IPW	SAU	NNZ	JAP	BPW	BPE	CAL	GUI	AM	BAE	CAR	ATW
Eudistoma magalhaense (Michaelsen, 1907)	✓						✓	✓			✓																					
Sigillina moebiusi (Hartmeyer,1905)	✓														✓						✓											
Sycozoa anomala Millar, 1960							✓																✓									
Sycozoa gaimardi (Herdman, 1886)	✓			✓					✓		✓																					
Sycozoa georgiana (Michaelsen, 1907)	✓	✓	✓	✓		✓			✓			✓																				
Sycozoa sigillinoides Lesson, 1830	✓		✓	✓	✓	✓		✓	✓		✓	✓	✓	✓				✓				✓										
Tetrazona ciemari Primo & Vázquez 2007	✓																															
Tetrazona glareosa (Sluiter, 1906)	✓						✓				✓																					
Didemnum bentarti Varela & Ramos-Esplá 2008		✓																														
Didemnum biglans (Sluiter, 1906)	✓		✓	✓	✓		✓	✓	✓																							
Didemnum studeri Hartmeyer, 1911							✓		✓		✓	✓	✓	✓			✓						✓									
Didemnum tenue (Herdman, 1886)									✓		✓																					
Diplosoma antarcticum Kott, 1969	✓			✓																												
Diplosoma listerianum (Milne-Edwards,1841)				✓									✓	✓	✓			✓			✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Diplosoma longinquum (Sluiter, 1912)	✓								✓																							
Polysyncraton trivolutum (Millar, 1960)	✓		✓			✓	✓		✓		✓	✓																				
Ciona antarctica Hartmeyer, 1911	✓			✓		✓																										
Tylobranchion speciosum Herdman, 1886	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓																				
Cibacapsa gulosa Monniot & Monniot, 1983			✓			✓		✓																								
Megalodicopia hians Oka, 1918[a]																																
Corella eumyota Traustedt,1882	✓		✓	✓		✓	✓		✓		✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓							✓		
Agnezia arnaudi Monniot & Monniot, 1974						✓		✓				✓																				
Agnezia biscoei Monniot & Monniot, 1983	✓			✓		✓	✓	✓														✓										
Caenagnesia bocki Arnback, 1938	✓	✓	✓	✓	✓	✓		✓	✓																							
Caenagnesia schmitti Kott, 1969	✓		✓																													
Corynascidia cubare Monniot & Monniot, 1994						✓																										
Ascidia challengeri Herdman,1882	✓		✓	✓	✓	✓	✓		✓			✓	✓		✓																	
Ascidia meridionalis Herdman,1880	✓						✓		✓		✓							✓														
Ascidia translucida Herdman,1880									✓			✓																				
Alloeocarpa bigyna Monniot, 1978									✓		✓	✓																				
Alloeocarpa incrustans (Herdman, 1886)									✓		✓																					
Cnemidocarpa barbata Vinogradova, 1962				✓								✓										✓				✓						
Cnemidocarpa drygalskii (Hartmeyer, 1911)	✓		✓	✓	✓	✓		✓			✓	✓																				
Cnemidocarpa eposi Moniot & Monniot, 1994						✓																										
Cnemidocarpa pfefferi (Michaelsen, 1898)	✓		✓	✓		✓	✓		✓																							
Cnemidocarpa verrucosa (Lesson, 1830)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓																				
Dicarpa insinuosa (Sluiter, 1912)	✓			✓		✓			✓																							
Dicarpa tricostata (Millar, 1960)	✓		✓			✓			✓																							

Polyzoa opuntia Lesson,1830								✓	✓	✓	✓	✓		✓				✓														
Styela glans Herdman, 1881	✓		✓			✓						✓						✓														
Styela materna Monniot & Monniot,1983								✓	✓						✓																	
Styela squamosa Herdman 1881	✓		✓			✓	✓		✓		✓		✓	✓	✓			✓	✓	✓					✓	✓	✓	✓				✓
Styela wandeli (Sluiter, 1911)	✓	✓					✓		✓																							
Theodorella arenosa Michaelsen, 1922									✓					✓																		
Bathypera splendens Michaelsen, 1904	✓		✓	✓	✓	✓	✓				✓																					
Pyura bouvetensis (Michaelsen, 1904)	✓		✓	✓	✓	✓	✓		✓	✓				✓																		
Pyura discoveryi (Herdman, 1910)	✓		✓	✓	✓	✓	✓		✓																							
Pyura georgiana (Michaelsen, 1898)			✓					✓	✓																							
Pyura legumen (Lesson, 1830)									✓		✓																					
Pyura lycoperdon Monniot & Monniot,1983	✓																															
Pyura obesa Sluiter, 1912	✓						✓																									
Pyura paessleri (Michaelsen, 1900)									✓		✓																					
Pyura setosa (Sluiter, 1905)	✓		✓	✓	✓		✓																									
Pyura squamata Hartmeyer 1911	✓		✓	✓		✓	✓					✓		✓																		
Pyura tunica Kott, 1969				✓																												
Eugyra kerguelenensis (Herdman, 1881)	✓							✓			✓	✓																				
Eugyra polyducta (Monniot & Monniot,1983)	✓	✓				✓	✓	✓	✓																							
Molgula enodis (Sluiter, 1912)	✓			✓			✓																									
Molgula euplicata Herdman, 1922	✓		✓	✓	✓	✓	✓		✓																							
Molgula georgiana Michaelsen, 1900								✓	✓			✓																				
Molgula hodgsoni Herdman, 1910	✓		✓	✓	✓	✓	✓		✓																							
Molgula longivascula Millar, 1982									✓			✓																				
Molgula marioni Millar, 1960									✓		✓	✓																				
Molgula mortenseni (Michaelsen, 1922)									✓		✓		✓	✓									✓									
Molgula pedunculata Herdman, 1881	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓							✓													
Molgula pulchra Michaelsen, 1900									✓		✓	✓																				
Molgula pyriformis Herdman, 1881									✓		✓							✓														
Molgula robini Millar, 1960			✓			✓			✓																							
Molguloides bathybia (Hartmeyer, 1912)					✓																											
Molguloides coronatum Monniot, 1978						✓						✓																				
Pareugyrioides arnbackae (Millar, 1960)	✓	✓	✓			✓		✓																								
Paramolgula gregaria (Lesson, 1830)									✓		✓							✓														

[a]Excluded from the analysis because of uncertain identification.

Table 2 Description of the biogeographical categories under consideration.

Biogeographical component	Distribution
Sector endemisms	Considered sector
Antarctic endemisms	Antarctic region (two or more sectors)
Antarctic–South American	Antarctic and South America regions, sometimes extending their distribution to the sub-Antarctic region
Cosmopolitan	Most of the global regions
Southern Hemisphere	Broad distribution in the Southern Hemisphere
Cold regions	Cold and cold–temperate regions in the Southern Hemisphere
Antarctic–sub-Antarctic	Antarctic and sub-Antarctic regions
Antarctic–southern New Zealand	Antarctic and southern New Zealand regions, sometimes extending their distribution to the sub-Antarctic region
Antarctic–Tasmanian	Antarctic and Tasmanian regions, sometimes extending their distribution to the sub-Antarctic region
Antarctic–southern African	Antarctic and southern Africa regions, sometimes extending their distribution to the sub-Antarctic region

Islands were grouped with the Antarctic Peninsula because of their close geographical proximity, and because it has been shown that the two areas are similar in terms of their ascidian faunistic composition (Monniot & Monniot 1983; Ramos-Esplá et al. 2005).

- The Bellingshausen Sea sector (BEL), from the PANT limit to the Shirase Coast, including Peter I Øy (Peter I Island) and the Amundsen Sea.
- The Ross Sea sector (ROS), from the BEL limit to Cape Adare.
- The Wilkes Land sector (WIL), from the ROS limit to the Amery Ice Shelf; this sector includes the Davis Sea.
- The Dronning Maud Land sector (MAU), from the WIL limit to Cape Norvegia.
- The Weddell Sea sector (WED), from the MAU limit to the northern tip of the Antarctic Peninsula; i.e., comprising the east coast of the Antarctic Peninsula.
- The South Orkney Islands sector (SOR).
- The South Sandwich Islands sector (SSA).
- The South Georgia Islands sector (SGE).
- The Bouvetøya (Bouvet Island) sector (BOU).

Each record was assigned to the sector or sectors where it was cited. In addition, we reviewed the worldwide distribution of each species, and assigned them to the regions proposed by Briggs (1995). Regions with no records were not included in the analysis.

Areas were classified by cluster analysis, using the Bray-Curtis similarity coefficient for binary data and the unweighted pair-group method with arithmetic mean (UPGMA) aggregation algorithm; the results of the classification were combined with multi-dimensional scaling (MDS) ordination to confirm the groups obtained. The Bray-Curtis similarity coefficient for binary data (also known as the Sørensen similarity coefficient) gives less weighting to outliers (McCune & Grace 2002), thereby minimizing the errors derived from the different quantities of data. Analyses were run using PRIMER 5 (Plymouth Routines in Multivariate Ecological Research). In addition, a similarity matrix was constructed using the Kulczynski-2 index, to compare our results with those previously obtained by Monniot & Monniot (1983) and Tatián et al. (2005). The data set was therefore slightly modified, as Monniot & Monniot (1983) only considered WIL to be the coast of the Antarctic continent, between 130–170°E, because of the low sampling effort in the remaining areas, and they did not include BEL, MAU and BOU for the same reason. This matrix was constructed using SPSS 16.0 (Statistical Package for the Social Sciences).

The percentage abundance of species per biogeographical category was also calculated from the presence/absence matrix (Table 1). The biogeographical categories are defined here as faunistic groups, depending on the world distribution of the species beyond the limits of the biogeographical regions considered in the present study. The categories included in the analysis are shown in Table 2.

Results

The classification analysis of all marine biogeographical areas (Fig. 2) showed all of the Antarctic sectors to be clustered together. However, most of the continental sectors were grouped with a high similarity index (55%), whereas BOU and BEL were less closely related (20% similarity). The SGE showed a relationship (60% similarity) with the South America and sub-Antarctic regions: with the first region comprising the South American coast from the Chiloé Islands to Peninsula Valdés, including the Falkland Islands, and the second region comprising the Kerguelen, Heard, Crozet, Marion, Prince Edward and Macquarie islands (Briggs 1995) (Fig. 1). The SSA also appeared to be related to this group, but with a lower similarity (40%). All other biogeographical areas appeared to be clustered together; these regions were not at all related to the Antarctic region (Fig. 2), and were not included in the following analysis.

The MDS ordination (Fig. 3) was carried out to compare the clusters obtained in the classification analysis. The classification analysis on its own can lead to misleading results, as it will give rise to a hierarchy (clusters) whether the variables are hierarchically interrelated

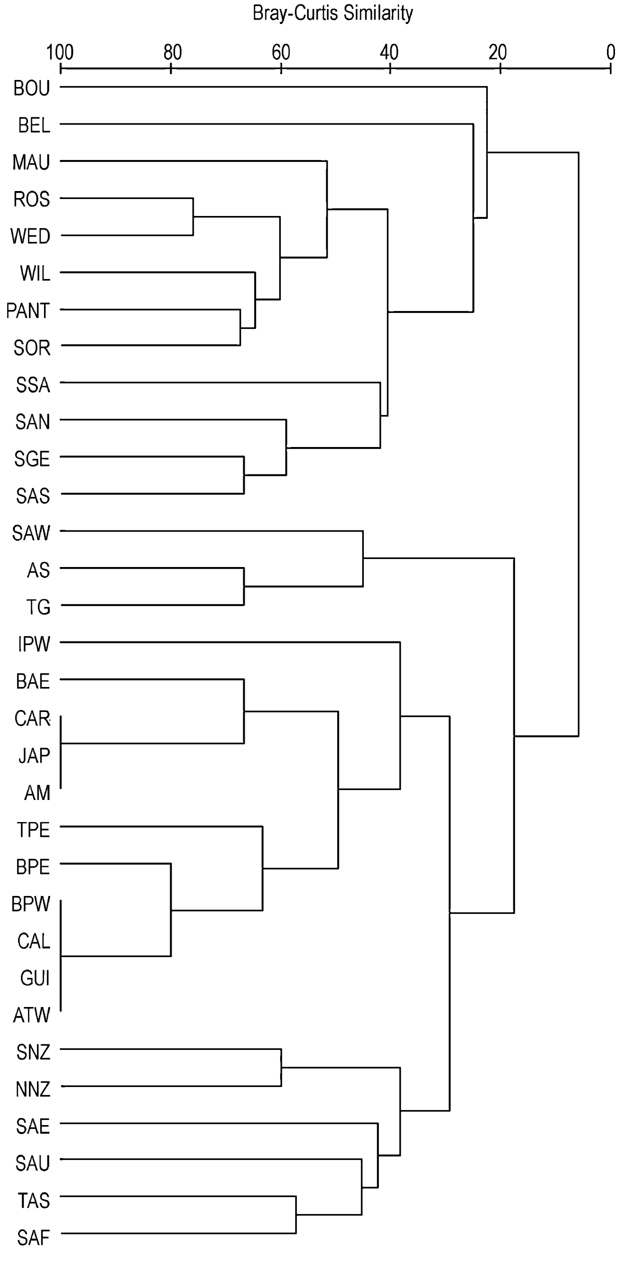

Fig. 2 Bray-Curtis classification analysis. Abbreviations: BOU, Bouvetøya; BEL, Bellingshausen Sea; MAU, Dronning Maud Land; ROS, Ross Sea; WED, Weddell Sea; WIL, Wilkes Land; PANT, Antarctic Peninsula; SOR, South Orkney Islands; SSA, South Sandwich Islands; SAN, sub-Antarctic region; SGE, South Georgia Islands; SAS, South America Region; SAW, western South America Region; AS, Amsterdam–Saint Paul; TG, Tristan da Cunha; IPW, Indo-West Pacific region; BAE, eastern Atlantic Boreal region; CAR, Carolina region; JAP, Japan region; AM, Mediterranean–Atlantic region; TPE, eastern Pacific region; BPE, eastern Pacific Boreal region; BPW, western Pacific Boreal region; CAL, California region; GUI, eastern Atlantic region; ATW, western Atlantic region; SNZ, southern New Zealand region; NNZ, northern New Zealand region; SAE, eastern South America region; SAU, southern Australia region; TAS, Tasmania region; SAF, southern Africa region.

or not. It can also create different configurations from the same similarity matrix (Legendre & Legendre 1998). The MDS ordination was carried out only considering the Antarctic sectors, and the sub-Antarctic and South America regions (Fig. 3). The MDS ordination (stress 0.03) revealed a latitudinal gradient. Except for BEL, the continental sectors appeared to be closely related and associated with the Antarctic Peninsula that links the continent with the insular sectors of SOR and SGE. The SGE neither grouped with the other Antarctic sectors, nor with the South America and sub-Antarctic regions (although it was more closely related to these). It may represent a link between both groups. Again, the BOU was separated from the rest, and the SSA was also quite distant, although it was closer to the other Antarctic sectors than BOU.

Excepting BEL and BOU, which both had a very low number of ascidian citations (10 and eight, respectively), the Antarctic sectors had similar abundance percentages for all of the biogeographical categories (Table 3). The Antarctic endemic species category was one of the best represented groups in every case (25–51%), whereas the percentage of sector endemism was small or null, thereby corroborating the ascidian fauna homogeneity in the Antarctic continent. It is remarkable that despite the Antarctic region as a whole having 44% of endemic species (Primo & Vázquez 2007a), the number of endemic species in each sector was always lower than 10%. The Antarctic–South American group was also well represented in all of the sectors considered (especially in the Scotia Arc islands), indicating a close relationship between both regions.

Using the Kulczynski-2 similarity index, faunistic affinities were calculated and compared with those obtained by Monniot & Monniot (1983) and Tatián et al. (2005), in order to assess the evolution of the ascidian fauna in the Antarctic region (Table 4). We found an increase in the affinity between sectors in all instances. The affinity between WED and all other sectors was particularly high, as was the affinity between SGE and SOR.

Discussion

The most obvious pattern observed in the dendrogram (Fig. 2), and in the three-dimensional diagram (Fig. 3), is the separation of the sectors BEL, BOU and SSA from the other Antarctic sectors. The low sampling effort in the Bellingshausen Sea is the most probable reason for the separation of this sector. Collections made from recent Spanish cruises on board the RV *Hespérides* (BENTART 2003 and BENTART 2006) would help to elucidate the biogeographical relationships, but no results have yet been published for ascidians, except for the description of

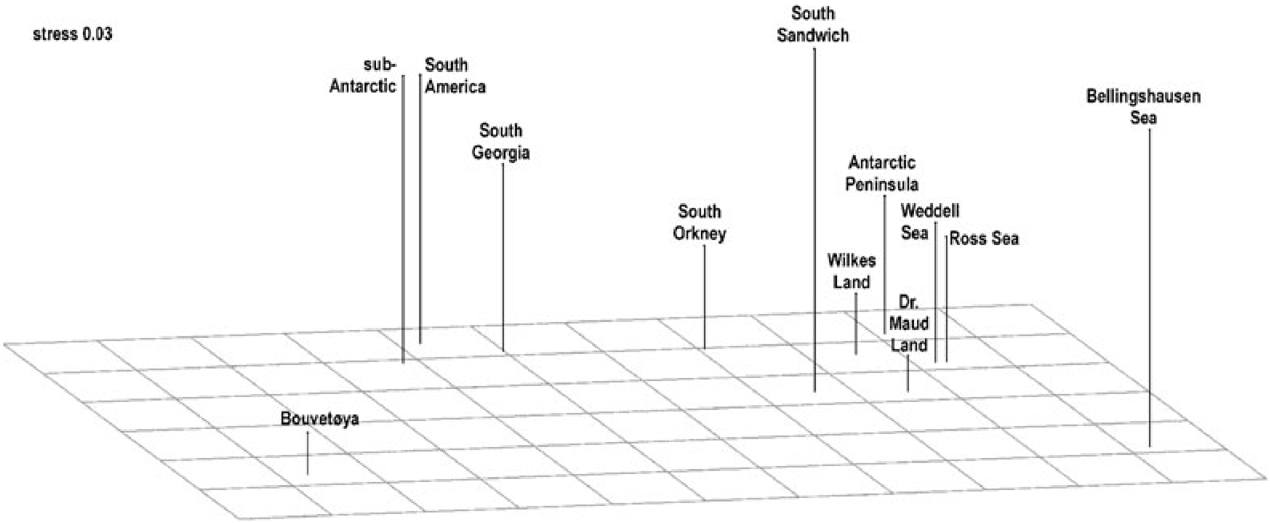

Fig. 3 Multi-dimensional scaling ordination analysis of Antarctic sectors, the sub-Antarctic region and the South America region.

Table 3 Percentage of the biogeographical categories in the 10 Antarctic sectors considered. Abbreviations: SE, sector endemism; AE, Antarctic endemism; A–SAM, Antarctic–South American; C, cosmopolitan; SH, Southern Hemisphere; CR, cold regions; A–SAN, Antarctic–sub-Antarctic; A–TAS, Antarctic–Tasmanian; A–SNZ, Antarctic–southern New Zealand; A–SAF, Antarctic–southern African.

	SE	AE	A–SAM	C	SH	CR	A–SAN	A–TAS	A–SNZ	A–SAF
Antarctic Peninsula	10	42	26	3	11	1	3	0	3	0
Belligshausen Sea	10	40	20	0	10	0	20	0	0	0
Ross Sea	0	51	23	5	10	0	5	0	5	0
Wilkes Land	5	43	23	7	14	0	5	0	5	0
Dronning Maud Land	5	37	32	0	16	0	5	0	5	0
Weddell Sea	5	40	23	5	13	0	10	0	5	0
South Orkney Islands	0	36	33	5	18	3	3	0	5	0
South Sandwich Islands	0	32	40	0	12	0	12	0	0	4
South Georgia Islands	0	25	36	4	20	2	9	0	4	2
Bouvetøya	0	25	25	0	25	13	0	0	13	0

Table 4 Kulczynski-2 similarity index (percentage) between different sectors. Abbreviations: MM, Monniot & Monniot (1983); TA, Tatián et al. (2005); PS, present study; nd, no data.

	Antarctica Peninsula			Ross Sea			Wilkes Land			Weddell Sea			S. Orkney			S. Sandwich		
	MM	TA	PS	MM	TA	PS	MM	TA	PS	MM	TA	PS	MM	TA	PS	MM	TA	PS
Ross Sea	65	nd	72	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wilkes Land	64	nd	62	61	nd	54	—	—	—	—	—	—	—	—	—	—	—	—
Weddell Sea	54	nd	67	59	nd	76	52	nd	45	—	—	—	—	—	—	—	—	—
S. Orkney	65	69	73	61	nd	58	65	nd	59	43	nd	53	—	—	—	—	—	—
S. Sandwich	44	45	52	33	nd	43	42	nd	36	26	nd	42	43	41	42	—	—	—
S. Georgia	47	48	51	47	nd	52	41	nd	49	40	nd	49	44	45	58	49	47	43

a new Didemnidae species (Varela & Ramos-Esplá 2008). Bouvetøya is a geologically young and isolated island, located to the south of the Polar Front, and was separated from neighbouring areas in the analysis because of the low sampling effort in this sector (Primo & Vázquez 2007a). However, a recent expedition to this island confirmed the impoverished ascidian fauna—only seven species were found (Arntz et al. 2006)—whereas in other taxonomical groups the number of species has increased substantially in recent years. The South Sandwich Islands is a relatively young archipelago of volcanic origin, just south of the Polar Front, and is the most remote Scotia Arc archipelago from both South America and Antarctica (Zelaya 2005). This could explain the separation of this sector in the analyses. The separation of the SSA was already observed for ascidians by Monniot & Monniot (1983), who suggested a decrease in Antarctic influence without a rise in South American influence as the most likely reason for this result. Recent papers (Ramos-Esplá et al. 2005; Tatián et al. 2005) have also reported a difference in the species composition of this archipelago, although this appeared to be more closely related to the South Georgia Islands than is found in the present work.

The remaining areas appear to be more closely related. Moreover, there appears to be a difference in the specific composition between continental and insular sectors (Fig. 3), and the geographical distance is the most likely reason for this. On the other hand, the insular sectors, and especially South Georgia Island, are closer to the South America and sub-Antarctic regions. Similarly, Tatián et al. (2005) assumed that the Polar Front was situated south of this archipelago. South Georgia Island seems to be an overlapping area for ascidian fauna (Monniot & Monniot 1983; Ramos-Esplá et al. 2005; Primo & Vázquez 2007a), although it appears to be more closely connected to the Antarctic region (Primo & Vázquez 2007a).

The grouping of most of the Antarctic sectors suggests a great homogeneity of the Antarctic ascidian fauna, especially in the continental sectors. Even the ascidian fauna of the Ross and Weddell seas appear to be closely related to each other, in spite of the presence of the Antarctic Peninsula and Bellingshausen Sea between them. A possible explanation for this similarity is the presence of a seaway linking both seas, but separating them from the micro-continental fragments that would later form the Antarctic Peninsula and Scotia Arc islands (Lawver & Gahagan 2003; Linse et al. 2007). The homogeneity of the Antarctic ascidian fauna could also be a consequence of the relative constancy of the physical conditions (except for light) in the Antarctic region (Arntz et al. 1994), as well as the effect of the circum-Antarctic currents (the East and West Wind drifts), which favour the dispersal of organisms around the whole region (Linse et al. 2007; Barnes & Griffiths 2008). In addition to this, the isolation by deep sea and the Antarctic Convergence, which impedes the mixing with fauna from other regions, may also contribute to the unification of the Antarctic ascidian fauna. Nevertheless, the faunistic exchange is not equal across the entire region (Arntz et al. 1994). The insular sectors show a closer relationship with the South American fauna, probably because of geographical proximity.

The distribution of biogeographical categories in the sectors considered confirmed the results of the classification and ordination analyses. First, a high percentage of endemic species in the whole Antarctic region and a low percentage of sector endemism (Table 3) corroborate the hypothesis of a very homogeneous Antarctic ascidian fauna. The fact that every sector (except BEL and BOU, which both have a low number of species) has similar percentages of biogeographical elements also seems to support this theory. Evolution may be extremely slow under cold Antarctic conditions (Ingels et al. 2006), where animals live long and reproduce slowly (Arntz et al. 1994), and there may not have been enough time for a significant endemic fauna to develop in these sectors (Glasby & Alvarez 1999; Barnes & Griffiths 2008). Even the proportion of Antarctic–South American species, although slightly higher in the island sectors, is also similar in all sectors, confirming the homogeneity of this fauna, and refuting the grouping of South Georgia with the South America and sub-Antarctic regions observed in the classification analysis.

The general increase of faunistic affinities between sectors through time (Table 4) also seems to confirm the idea of a very homogeneous Antarctic ascidian fauna. The more we learn about this fauna, the more homogenous it seems to be. This idea is also supported by the decrease in the percentage of sector endemism, from a maximum of 15% in the Antarctic Peninsula, found by Monniot & Monniot (1983), to 10% in the present study. Nevertheless, the fact that there is a greater increment of faunistic affinities in the WED than in other sectors may be a consequence of our improved knowledge of this sector (from 11 species cited by Monniot & Monniot [1983] to 40 species in the present study). On the other hand, the substantial similarity of the SGE to the SOR, when compared with Monniot & Monniot (1983) and Tatián et al. (2005), seems to support the idea that the South Georgia ascidian fauna is more closely related to that of the Antarctic region than is shown in the cluster analysis, although we observed a gradient along the Scotia Arc, as did Tatián et al. (2005).

Several recent studies on the zoogeography of the Antarctic region have been carried out, although different methods of analyses were used for different taxa: comparing them is not easy. Most of these studies considered the Antarctic region as the whole area south of the Antarctic Convergence, but very different divisions were chosen, ranging from no divisions at all (mysids, Brandt et al. [1998]; hydroids, Peña-Cantero & García Carrascosa [1999]) to seven, 12 or 15 subregions (cumaceans, Mühlenhardt-Siegel [1999]; molluscs, Linse et al. [2006]; bryozoans, Barnes & Griffths [2008]), with different limits. Some of the studies excluded all or part of the Scotia Arc islands (isopods, Brandt et al. [1999]; ascidians, Ramos-Esplá et al. [2005]), or included the sub-Antarctic islands in some of the analyses (Barnes & Griffiths 2008). Although the results differ among the studies, in general, the Antarctic continent (or continental sectors) and Scotia Arc islands were grouped together, whereas Bouvetøya, South Georgia and the South Sandwich islands have an uncertain position in some cases (Ramos-Esplá et al. 2005; Linse et al. 2006).

The percentage of endemic species in the Antarctic region for benthic invertebrates is usually high. It varies from 35% (scleractinian corals; Arntz et al. [1997]) to 95% (pycnogonids, Jazdzewski et al. [1991]), although a decreasing percentage has been found for the same taxa over time. For example, Jazdzewski et al. (1991) reported 95% endemism for amphipods, and De Broyer et al. (2007) reported 72% endemism for the same group of animals. Barnes & De Grave (2000) reported 83% endemism among bryozoans; this figure went down to 57% eight years later (Barnes & Griffiths 2008). The decrease of endemism could indicate that Antarctica has been less isolated over geological time than was once thought (Barnes & Griffiths 2008). This is not the case for ascidians, as the percentage of endemic species seems to remain quite constant, ranging from 51% (Monniot & Monniot 1983) to 44% (Primo & Vázquez 2007a).

As for the sector endemism, Barnes & Griffiths (2008) also found a low level of endemism for bryozoans, and suggested the West Wind Drift current as the most probable agent of dispersion that may explain this pattern. Other groups showed a completely different pattern, with a high level of endemism in some sectors, and lower endemism in others (Brandt et al. 1999; Mühlenhardt-Siegel 1999; Linse et al. 2006).

As a final point, we should not forget the potential contribution of anthropogenic introductions to the Southern Ocean. Several ascidian species that are found in Antarctic waters have a wide distribution (e.g., *Sigillina moebiusi*, *Diplosoma listerianum*, *Corella eumyota* and *Styela squamosa*), and it may not be appropriate to assume that these species (or any other marine species) are natives. Although little is known about the present rate of establishment of non-indigenous marine species in the Southern Ocean, shipping has the potential to introduce non-native species into a marine environment that is known to have very high degrees of endemism. The probability of transport of invasive species into the Southern Ocean may increase in the future, as a consequence of the growth in tourism, fisheries and science activities in the region (Lewis et al. 2003), and fouling organisms would seem to be the likely first candidates (Barnes & Griffiths 2008). Ascidians, as a common component of the fouling communities on the hulls of ships (Carlton 1989; Coutts 1999; Gollasch & Leppakoski 1999; Floerl et al. 2005; Lambert 2007), are one of the most probable taxa to be introduced in this region. Also, as factors limiting successful invasions are frequently related to physical characteristics such as temperature, a future global warming would enable new taxa to become established (Lewis et al. 2003; Clarke et al. 2005). The growth of some invasive ascidian species is affected by temperature (Agius 2007), so a rise in sea-surface temperatures may facilitate the invasion of non-native ascidian species; a significant warming has been already detected around the Antarctic Peninsula (Meredith & King 2005; Turner et al. 2005). However, no marine non-indigenous animal species have yet been proven to have become successfully established in Antarctic waters (Thatje 2005; Barnes et al. 2006).

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