

Short Communication

Southern Ocean areas of endemism: a reanalysis using benthic hydroids (Cnidaria, Hydrozoa)

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ABSTRACT. The biogeographic history of the Southern Ocean (SO) fauna is complex and poorly studied, especially the areas of endemism. We reanalyzed the data of Marques & Peña Cantero (2010), along with other geographical records of endemic benthic hydroids below 45°S. A Parsimony Analysis of Endemicity (PAE) based on 5° latitude by 5° longitude matrix with 61 species resulted in eight areas of endemism. We discuss these results in the context of different hypotheses of the evolution of the SO fauna and previously proposed biogeography patterns.

Keywords: Antarctica, barriers, biogeography, endemism, Hydrozoa, PAE, Southern Ocean.

Áreas de endemismo del Océano Austral: un re-análisis basado en datos adicionales de hidroides bentónicos

RESUMEN. La historia biogeográfica de la fauna del océano Antártico (OA) es compleja y está poco estudiada, principalmente en relación a las áreas de endemismo. Se ha reanalizado los datos de Marques & Peña Cantero (2010) junto con otros registros geográficos de hidrozooos bentónicos endémicos de la zona abajo de los 45°S. Una Análisis de Parsimonia de Endemismos (PAE) a partir de una matriz de 5° latitud por 5° longitud con 61 especies, obtuvo ocho áreas de endemismo. Se discute los resultados tomando en cuenta diferentes hipótesis sobre la evolución de la fauna del OA y los patrones biogeográficos de la literatura.

Palabras clave: Antártica, barreras, biogeografía, endemismo, Hydrozoa, PAE, Oceano Austral.

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Marine polar regions are often considered to have low biodiversity, a pattern generally thought to be associated with extreme abiotic factors (Clarke & Crame, 1992). However, several studies on biodiversity, biogeography and paleontology of polar regions (*e.g.*, Beu *et al.*, 1997; Clarke & Johnston, 2003; Adey *et al.*, 2008) revealed greater than expected biodiversity, particularly for the Southern Ocean (SO; *viz.*, Clarke & Johnston, 2003).

The SO is a unique oceanographic system in which the Antarctic Circumpolar Current (ACC) dominates (Barker & Thomas, 2004) and moves around the southern seas with no continental barriers. The ACC originated with the opening of the Drake Passage (*ca.* 30 Ma), thereby causing biogeographically and thermal isolation of the SO (Lawver & Gahagan,

2003). This, in turn, contributed to the isolation and development of endemic marine fauna (Clarke & Crame, 1989; Beu *et al.*, 1997; Barker & Thomas, 2004; Clarke *et al.*, 2004).

On the other hand, there are historical similarities of the Antarctic fauna to those from northern regions (Cañete *et al.*, 1999; Yasuhara *et al.*, 2007; Kaiser *et al.*, 2011), mainly in the Antarctic Peninsula and the subantarctic region of South America (Clarke & Johnston, 2003; Clarke *et al.*, 2005). The connection between both continents is through the Scotia Arc, and since it will have influenced dispersal of their marine fauna, we may question exactly how isolated was the SO (Clarke *et al.*, 2005).

Thus, several hypotheses have been proposed to explain the origin of the SO fauna: (H1) evolution *in*

situ, (H2) derivation from adjacent deep-water basins, (H3) dispersal from South America through the Scotia Arc, and (H4) dispersal from Antarctica through the Scotia Arc (*cf.*, Knox & Lowry, 1977). These not-mutually-independent hypotheses are partially supported by fauna and geography and have been contrasted with abiotic factors of the SO (*viz.*, Beu *et al.*, 1997; Cañete *et al.*, 1999; Yasuhara *et al.*, 2007; Kaiser *et al.*, 2011).

Theoretical and practical frameworks concerning areas of endemism (*cf.* Harold & Mooi, 1994; Morrone, 1994; Szumik *et al.*, 2002) are complicated in marine biogeography. The tridimensional nature of the marine realm, the dynamics of currents and oceanic fronts, the difficulties to establish thresholds in ecophysiological continuums and the amazingly diverse strategies of dispersal, all make for a unique definition of areas, or “volumes,” of endemism (see Miranda & Marques, 2011). Clearly, this will also be an issue in the SO, and in which few studies examine the origin and evolution of all marine organisms, not just endemics (*e.g.*, Clayton, 1994; Brandt, 1999; Clarke *et al.*, 2004).

The hydroids – benthic hydrozoans of the orders Anthoathecata and Leptothecata (*cf.* Marques & Collins, 2004; Collins *et al.*, 2006) – provide an example with many endemics in the SO (Peña Cantero, 2012). For example, a Parsimony Analysis of Endemicity (PAE) for the endemic SO genus *Oswaldella* (a single study using strict endemicity analysis) suggested four areas of endemism: (1) Magellanic Zone, (2) Antarctic Peninsula Zone, (3) Western High Antarctica Zone and (4) Eastern High Antarctica Zone (Marques & Peña Cantero, 2010). In another PAE for the SO, we used additional geographic data of endemic benthic hydroids to test previous hypotheses and to better understand the biogeography of the SO. We used a matrix of 5° latitude by 5° longitude and geographic records of 61 species of the genera *Antarctoscyphus*, *Mixoscyphus*, *Oswaldella* and *Staurotheca* (Table 1). PAE was carried out following Marques & Peña Cantero (2010), but using semistrict consensus trees. Eight areas of endemism were found for the SO, concentrated in the Magellan region, the Antarctic Peninsula, the subantarctic islands, the Ross Sea, the Weddell Sea and Wilkes Land (Figs. 1, 2). Areas I, II and V (Figs. 1, 2) are similar to the previously mentioned Magellanic and Antarctic Peninsula zones (Marques & Peña Cantero, 2010). These areas began with the ACC as a system of deep eastward currents connecting the Magellan region and Scotia Arc to the Weddell Sea, Queen Maud Land and Wilkes Land (Beu *et al.*, 1997; Lawver & Gahagan, 2003; Marques

& Peña Cantero, 2010). These currents caused dispersal towards Queen Maud Land (Marques & Peña Cantero, 2010), thereby supporting the third hypothesis of a South American origin for the SO fauna (Knox & Lowry, 1977).

Areas of endemism I, III, V and VI (Figs. 1, 2) coincide with the Scotia Arc of Marques & Peña Cantero (2010), and may be a transitional region for dispersal events of species distributed both in the Antarctic Peninsula and in the Magellan region (Peña Cantero *et al.*, 1997; Peña Cantero & Vervoort, 2003, 2004 – except the monotypic genus *Mixoscyphus*, which is exclusively in Antarctica (*cf.* Peña Cantero & Vervoort, 2005). These areas support the previously mentioned third and fourth hypotheses (Knox & Lowry, 1977). Nonetheless, this does not refute the hypothesis that vicariance influenced the isolation of the Magellanic (*e.g.*, area V, Figs. 1, 2) from the Antarctic Peninsula (areas I and II, Figs. 1, 2). Thus, evolution *in situ* (hypothesis H1) may have also occurred with a fauna derived from the adjacent deep-water basin (hypothesis H2; *cf.* Knox & Lowry, 1977). Other areas of endemism (I, IV, VI to VIII; Figs. 1, 2) coincide with the Western High Antarctica Zone and Eastern High Antarctica Zone (Marques & Peña Cantero, 2010), and may be due to variations in depth, present oceanic currents and paleocurrents of the SO (Marques & Peña Cantero, 2010).

These results are coherent in part with ecological areas based on earlier informal biogeographic analyses (Hedgpeth, 1969; Briggs, 1974; Spalding *et al.*, 2007). But, these results agree completely with previously hypothesized areas of endemism (Marques & Peña Cantero, 2010, *cf.* their Fig. 2), but now with more detail and defined subregions of those areas. These subregions suggest specific microhabitats for the benthic hydroid fauna of the SO that may be derived from dispersal or vicariant events.

If dispersal, then this suggests the formation of microhabitats, as a consequence of different strategies of larvae transportation, such as rafting of incrusting biota (*e.g.*, on algae, wood) and oceanographic mechanisms (*e.g.*, vortices and oceanic fronts). Both of these mechanisms are important for transportation of subantarctic/Antarctic plankton and benthos (including larvae of benthic or epipelagic organisms) along the southern polar region. If vicariance, historical and ecological barriers may have involved continental drift and climatic changes over time. Nevertheless, vicariance does not imply the absence of dispersal in the formation of the SO benthic hydroid fauna.

Considering the evolutionary history of the SO, an important question to be answered is how important were the intensity and periodicity of changes in sea level and ice (both in extent and quantity) in causing

Table 1. List of the 61 species of benthic hydroids used in PAE and quadrants in which they are present.

Species	Quadrant
<i>Antarctoscyphus admirabilis</i>	70-75°S, 5-10°W
<i>Antarctoscyphus asymmetricus</i>	55-60°S, 25-30°W; 50-55°S, 35-40°W; 50-55°S, 40-45°W; 60-65°S, 45-50°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 90-95°W
<i>Antarctoscyphus elongatus</i>	65-70°S, 5-10°W; 70-75°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 20-25°W; 55-60°S, 25-30°W; 70-75°S, 25-30°W; 75-80°S, 25-30°W; 50-55°S, 35-40°W; 55-60°S, 35-40°W; 50-55°S, 40-45°W; 75-80°S, 45-50°W; 60-65°S, 50-55°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 60-65°W; 70-75°S, 60-65°W; 65-70°S, 65-70°W; 70-75°S, 95-100°W; 75-80°S, 165-170°W; 50-55°S, 0-5°E; 45-50°S, 65-70°E; 65-70°S, 110-115°E; 65-70°S, 135-140°E; 65-70°S, 140-145°E; 75-80°S, 165-170°E; 70-75°S, 170-175°E
<i>Antarctoscyphus encarnae</i>	60-65°S, 55-60°W
<i>Antarctoscyphus fragilis</i>	70-75°S, 25-30°W
<i>Antarctoscyphus grandis</i>	70-75°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 20-25°W; 55-60°S, 25-30°W; 50-55°S, 35-40°W; 60-65°S, 50-55°W; 70-75°S, 50-55°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 90-95°W; 75-80°S, 175-180°W; 65-70°S, 135-140°E; 65-70°S, 140-145°E; 70-75°S, 170-175°E
<i>Antarctoscyphus gruzovi</i>	60-65°S, 50-55°W; 60-65°S, 55-60°W
<i>Antarctoscyphus mawsoni</i>	55-60°S, 25-30°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 65-70°W; 70-75°S, 175-180°W; 65-70°S, 140-145°E; 70-75°S, 170-175°E
<i>Antarctoscyphus spiralis</i>	65-70°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 20-25°W; 55-60°S, 25-30°W; 75-80°S, 25-30°W; 50-55°S, 35-40°W; 60-65°S, 40-45°W; 75-80°S, 45-50°W; 60-65°S, 50-55°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 60-65°W; 70-75°S, 60-65°W; 65-70°S, 85-90°W; 65-70°S, 90-95°W; 70-75°S, 95-100°W; 75-80°S, 170-175°W; 70-75°S, 175-180°W; 75-80°S, 175-180°W; 50-55°S, 0-5°E; 65-70°S, 135-140°E; 65-70°S, 140-145°E; 65-70°S, 160-165°E; 70-75°S, 165-170°E; 75-80°S, 165-170°E; 70-75°S, 170-175°E; 70-75°S, 175-180°E
<i>Mixoscyphus antarcticus</i>	60-65°S, 60-65°W
<i>Oswaldella antarctica</i>	50-55°S, 55-60°W; 60-65°S, 55-60°W; 65-70°S, 90-95°W; 65-70°S, 135-140°E; 65-70°S, 140-145°E
<i>Oswaldella bifurca</i>	75-80°S, 55-60°W; 70-75°S, 60-65°W; 75-80°S, 160-165°W; 70-75°S, 175-180°W; 75-80°S, 175-180°W; 65-70°S, 160-165°E; 70-75°S, 170-175°E
<i>Oswaldella billardi</i>	75-80°S, 30-35°W; 65-70°S, 90-95°E; 65-70°S, 110-115°E; 65-70°S, 135-140°E; 65-70°S, 140-145°E
<i>Oswaldella blanconae</i>	60-65°S, 60-65°W; 70-75°S, 170-175°E
<i>Oswaldella crassa</i>	60-65°S, 55-60°W
<i>Oswaldella curiosa</i>	60-65°S, 55-60°W
<i>Oswaldella delicata</i>	60-65°S, 50-55°W; 70-75°S, 50-55°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 75-80°S, 55-60°W; 60-65°S, 60-65°W; 75-80°S, 165-170°W
<i>Oswaldella elongata</i>	50-55°S, 30-35°W; 50-55°S, 35-40°W; 50-55°S, 50-55°W
<i>Oswaldella encarnae</i>	75-80°S, 45-50°W; 75-80°S, 50-55°W; 75-80°S, 55-60°W
<i>Oswaldella erratum</i>	50-55°S, 0-5°W; 70-75°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 15-20°W; 70-75°S, 20-25°W; 55-60°S, 25-30°W; 70-75°S, 25-30°W; 75-80°S, 25-30°W; 75-80°S, 30-35°W; 60-65°S, 50-55°W; 70-75°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 65-70°W; 50-55°S, 0-5°E; 65-70°S, 10-15°E
<i>Oswaldella frigida</i>	60-65°S, 55-60°W; 60-65°S, 60-65°W
<i>Oswaldella garciacarrascosai</i>	75-80°S, 50-55°W
<i>Oswaldella gracilis</i>	75-80°S, 55-60°W
<i>Oswaldella grandis</i>	75-80°S, 45-50°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W

Continuation

Species	Quadrant
<i>Oswaldella herwigi</i>	50-55°S, 55-60°W; 50-55°S, 70-75°W
<i>Oswaldella incognita</i>	55-60°S, 40-45°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 160-165°W
<i>Oswaldella laertesi</i>	70-75°S, 170-175°E
<i>Oswaldella medeae</i>	60-65°S, 50-55°W; 70-75°S, 175-180°W; 70-75°S, 175-180°E
<i>Oswaldella monomammillata</i>	60-65°S, 50-55°W
<i>Oswaldella niobae</i>	60-65°S, 55-60°W
<i>Oswaldella obscura</i>	70-75°S, 5-10°W; 70-75°S, 20-25°W; 75-80°S, 45-50°W
<i>Oswaldella rigida</i>	70-75°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 15-20°W; 70-75°S, 20-25°W; 75-80°S, 25-30°W
<i>Oswaldella shetlandica</i>	55-60°S, 40-45°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W; 50-55°S, 60-65°W; 55-60°S, 60-65°W; 60-65°S, 60-65°W; 65-70°S, 60-65°W
<i>Oswaldella stepanjantsae</i>	70-75°S, 5-10°W; 70-75°S, 10-15°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 75-80°S, 170-175°W; 65-70°S, 110-115°E; 65-70°S, 160-165°E; 75-80°S, 165-170°E; 70-75°S, 170-175°E; 70-75°S, 175-180°E
<i>Oswaldella terranova</i>	70-75°S, 170-175°E
<i>Oswaldella tottoni</i>	70-75°S, 10-15°W; 75-80°S, 160-165°E
<i>Oswaldella vervoorti</i>	55-60°S, 40-45°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 50-55°S, 0-5°E
<i>Staurorthea abyssalis</i>	55-60°S, 55-60°W
<i>Staurorthea affinis</i>	50-55°S, 35-40°W
<i>Staurorthea amphorophora</i>	50-55°S, 35-40°W; 50-55°S, 40-45°W
<i>Staurorthea antarctica</i>	70-75°S, 0-5°W; 70-75°S, 10-15°W; 70-75°S, 15-20°W; 75-80°S, 25-30°W; 50-55°S, 35-40°W; 75-80°S, 45-50°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 60-65°W; 65-70°S, 65-70°W; 50-55°S, 70-75°W; 65-70°S, 70-75°W; 70-75°S, 80-85°W; 75-80°S, 160-165°W; 75-80°S, 170-175°W; 70-75°S, 175-180°W; 75-80°S, 175-180°W; 65-70°S, 5-10°E; 65-70°S, 10-15°E; 65-70°S, 110-115°E; 65-70°S, 135-140°E; 65-70°S, 140-145°E; 75-80°S, 165-170°E; 70-75°S, 170-175°E
<i>Staurorthea australis</i>	65-70°S, 5-10°E; 65-70°S, 10-15°E
<i>Staurorthea compressa</i>	55-60°S, 25-30°W; 60-65°S, 50-55°W; 55-60°S, 55-60°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 140-145°W; 65-70°S, 160-165°W; 65-70°S, 140-145°E; 65-70°S, 160-165°E; 70-75°S, 165-170°E
<i>Staurorthea cornuta</i>	60-65°S, 45-50°W; 60-65°S, 55-60°W
<i>Staurorthea densa</i>	60-65°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 160-165°W; 70-75°S, 170-175°E; 70-75°S, 175-180°E
<i>Staurorthea dichotoma</i>	70-75°S, 5-10°W; 55-60°S, 25-30°W; 70-75°S, 25-30°W; 50-55°S, 30-35°W; 55-60°S, 30-35°W; 50-55°S, 35-40°W; 50-55°S, 40-45°W; 60-65°S, 45-50°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 70-75°S, 80-85°W; 65-70°S, 90-95°W; 75-80°S, 170-175°W; 70-75°S, 175-180°W; 50-55°S, 0-5°E; 65-70°S, 5-10°E; 65-70°S, 10-15°E; 45-50°S, 35-40°E; 65-70°S, 160-165°E; 75-80°S, 160-165°E; 75-80°S, 165-170°E; 70-75°S, 170-175°E
<i>Staurorthea echinocarpa</i>	45-50°S, 65-70°E; 45-50°S, 70-75°E
<i>Staurorthea frigida</i>	70-75°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 20-15°W; 55-60°S, 25-30°W; 50-55°S, 30-35°W; 55-60°S, 30-35°W; 50-55°S, 35-40°W; 55-60°S, 35-40°W; 50-55°S, 40-45°W; 60-65°S, 40-45°W; 60-65°S, 45-50°W; 60-65°S, 60-65°W; 65-70°S, 65-70°W; 75-80°S, 160-165°W; 65-70°S, 5-10°E; 65-70°S, 110-115°E; 70-75°S, 170-175°E
<i>Staurorthea glomulosa</i>	70-75°S, 0-5°W; 70-75°S, 10-15°W; 70-75°S, 20-25°W; 55-60°S, 25-30°W; 50-55°S, 35-40°W; 60-65°S, 40-45°W; 75-80°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 60-65°W; 65-70°S, 70-75°W; 65-70°S, 160-165°W; 75-80°S, 160-165°W; 75-80°S, 175-180°W; 65-70°S, 0-5°E; 65-70°S, 5-10°E; 65-70°S, 10-15°E; 65-70°S, 110-115°E; 65-70°S, 160-165°E; 70-75°S, 170-175°E; 70-75°S, 175-180°E

Continuation

Species	Quadrant
<i>Staurrotheca jaderholmi</i>	50-55°S, 50-55°W; 50-55°S, 55-60°W; 50-55°S, 60-65°W; 50-55°S, 65-70°W; 50-55°S, 70-75°W; 50-55°S, 75-80°W; 60-65°S, 90-95°W; 65-70°S, 135-140°E; 65-70°S, 140-145°E
<i>Staurrotheca juncea</i>	70-75°S, 95-100°W
<i>Staurrotheca multifurcata</i>	55-60°S, 25-30°W; 50-55°S, 30-35°W; 55-60°S, 30-35°W; 50-55°S, 35-40°W; 55-60°S, 35-40°W; 50-55°S, 40-45°W
<i>Staurrotheca nonscripta</i>	70-75°S, 0-5°W; 70-75°S, 5-10°W; 70-75°S, 10-15°W; 60-65°S, 55-60°W; 75-80°S, 60-65°W; 75-80°S, 165-170°W; 75-80°S, 170-175°W; 65-70°S, 0-5°E; 65-70°S, 5-10°E; 65-70°S, 10-15°E; 75-80°S, 160-165°E; 70-75°S, 165-170°E; 75-80°S, 165-170°E; 70-75°S, 170-175°E
<i>Staurrotheca pachyclada</i>	70-75°S, 5-10°W; 70-75°S, 10-15°W; 70-75°S, 20-25°W; 55-60°S, 25-30°W; 75-80°S, 25-30°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 160-165°W; 75-80°S, 160-165°W; 75-80°S, 175-180°W; 70-75°S, 170-175°E
<i>Staurrotheca plana</i>	70-75°S, 5-10°W; 70-75°S, 10-15°W
<i>Staurrotheca polarsteni</i>	70-75°S, 10-15°W; 70-75°S, 15-20°W; 70-75°S, 20-25°W; 75-80°S, 25-30°W; 70-75°S, 30-35°W; 60-65°S, 60-65°W; 65-70°S, 0-5°E; 65-70°S, 5-10°E; 65-70°S, 10-15°E
<i>Staurrotheca profunda</i>	50-55S 55-60W
<i>Staurrotheca stolonifera</i>	70-75°S, 5-10°W; 70-75°S, 80-85°W
<i>Staurrotheca undosiparietina</i>	50-55°S, 30-35°W; 50-55°S, 35-40°W; 50-55°S, 40-45°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W
<i>Staurrotheca vanhoeffeni</i>	70-75°S, 0-5°W; 70-75°S, 5-10°W; 70-75°S, 10-15°W; 60-65°S, 50-55°W; 60-65°S, 55-60°W; 60-65°S, 60-65°W; 65-70°S, 5-10°E; 50-55°S, 70-75°E; 70-75°S, 170-175°E
<i>Staurrotheca vervoorti</i>	50-55°S, 30-35°W; 50-55°S, 55-60°W

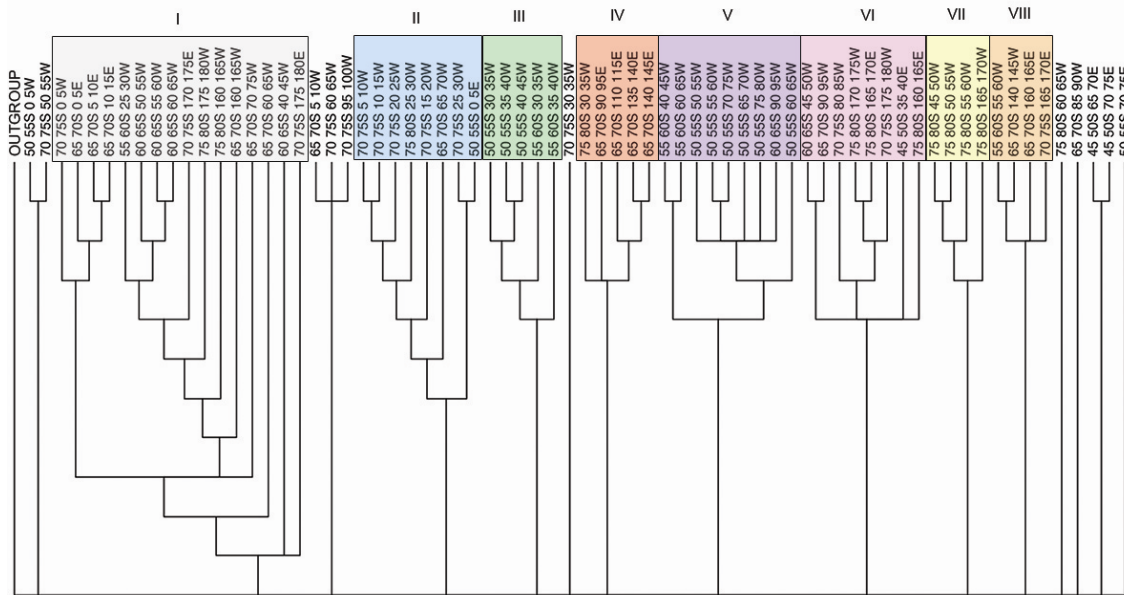


Figure 1. Semistrict consensus of the PAE in the 5° x 5° matrix grid. Codes I to VIII indicate the resultant areas of endemism. Colors are as in Figure 2.

the depth and occupation of habitats along the Antarctic continental shelf (Clarke & Crame, 1989; Clarke *et al.*, 2004). These phenomena influence marine areas of endemism because they contribute to

the formation of new habitats and the availability of ecological niches, which in turn may alter the geographic distribution of the species. The SO biota has a complex evolutionary history associated with

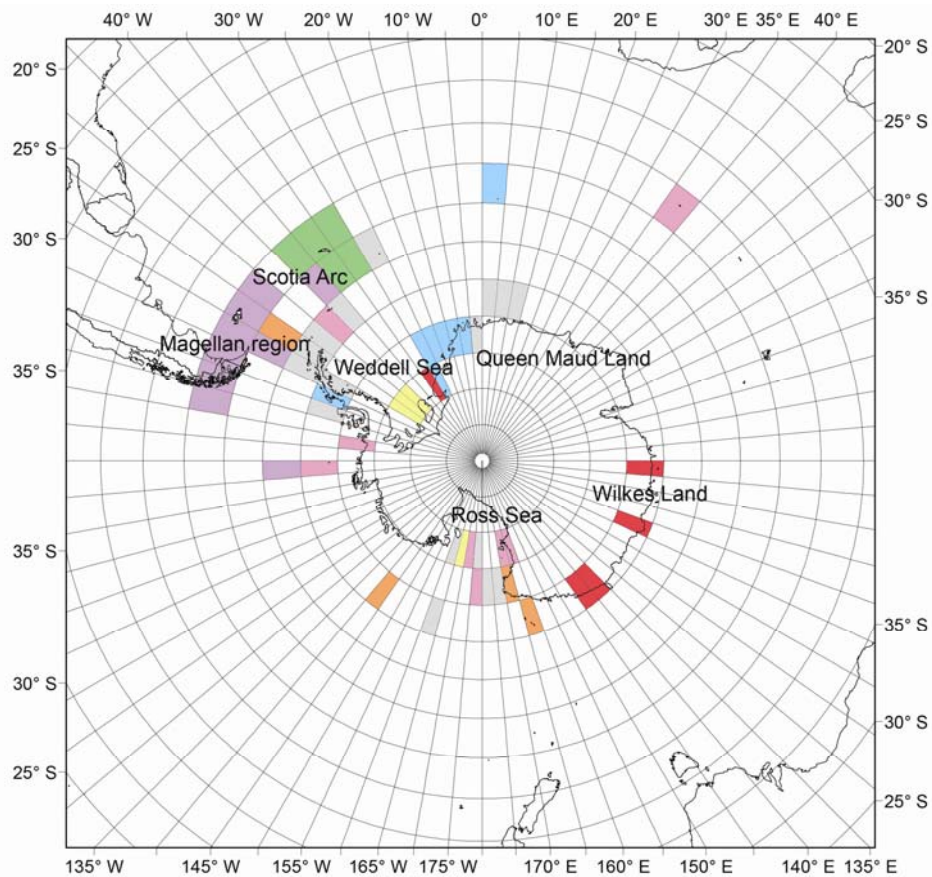


Figure 2. Areas of endemism from PAE for the 5° x 5° matrix grid. Colors indicate monophyletic groups delimited in the semistrict consensus from Figure 1 and are the same for the clades in Figure 1.

dispersal, vicariance and subsequent processes of oceanic restructuring. The use of different data sets and multiple evolutionary hypotheses will increase the explanatory power for understanding the peculiar processes leading to endemism and biogeographic patterns in the SO realm.

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REFERENCES

- Adey, W.H., S.C. Lindstrom, M.H. Hommersand & K.M. Müller. 2008. The biogeographic origin of Arctic endemic seaweeds: a thermogeographic view. *J. Phycol.*, 44: 1384-1394.
- Barker, P.F. & E. Thomas. 2004. Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. *Earth-Sci. Rev.*, 66: 143-162.
- Beu, A.G., M. Griffin & P.A. Maxwell. 1997. Opening of Drake Passage gateway and Late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. *Tectonophysics*, 281: 83-97.
- Brandt, A. 1999. On the origin and evolution of Antarctic Peracarida (Crustacea, Malacostraca). *Sci. Mar.*, 63: 261-274.
- Briggs, J.C. 1974. *Marine zoogeography*. McGraw-Hill Book Company, New York, 475 pp.
- Cañete, J.I., G.L. Leighton & F.F. Aguilera. 1999. Polychaetes from Aysén Fjord, Chile: distribution, abundance and biogeographical comparison with the

- shallow soft-bottom polychaete fauna from Antarctica and the Magellan Province. *Sci. Mar.*, 63: 243-252.
- Clarke, A. & J.A. Crame. 1989. The origin of the Southern Ocean marine fauna. In: J.A. Crame (ed.). *Origins and evolution of the Antarctic biota*, 47. Geol. Soc. Spec. Publ., London, pp. 253-268.
- Clarke, A. & J.A. Crame. 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Philos. T. Roy. Soc. B*, 338: 299-309.
- Clarke, A. & N.M. Johnston. 2003. Antarctic marine benthic diversity. In: R.N. Gibson & R.J.A. Atkinson (eds.). *Oceanography and marine biology: an annual review*. Taylor & Francis, London, pp. 47-114.
- Clarke, A., R.B. Aronson, J.A. Crame, J.M. Gili & D.B. Blake. 2004. Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf. *Antarct. Sci.*, 16: 559-568.
- Clarke, A., D.K.A. Barnes & D.A. Hodgson. 2005. How isolated is Antarctic? *Trends Ecol. Evol.*, 20: 1-3.
- Clayton, M.N. 1994. Evolution of the Antarctic marine benthic algal flora. *J. Phycol.*, 30: 897-904.
- Collins, A.G., P. Schuchert, A.C. Marques, T. Jankowski, M. Medina & B. Schierwater. 2006. Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Syst. Biol.*, 55: 97-115.
- Harold, A.S. & R.D. Mooi. 1994. Areas of endemism: definition and recognition criteria. *Syst. Biol.*, 43: 261-266.
- Hedgpeth, J.W. 1969. Distribution of selected groups of marine invertebrates in waters south of 35°S latitude. *Antarct. Map folio Ser.*, 11: 1-9.
- Kaiser, S., H.J. Griffiths, D.K.A. Barnes, S.N. Brandão, A. Brandt & P.E. O'Brien. 2011. Is there a distinct continental slope fauna in the Antarctic? *Deep-Sea Res. II*, 58: 91-104.
- Knox, G.A. & J.K. Lowry. 1977. A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and the Polychaeta. In: M.J. Dunbar (ed.). *Polar oceans*. Proceedings of the Polar Ocean Conference, Calgary, pp. 432-462.
- Lawver, L.A. & L.M. Gahagan. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeogr. Palaeoclimatol.*, 198: 11-37.
- Marques, A.C. & A.G. Collins. 2004. Cladistic analysis of Medusozoa and cnidarian evolution. *Invertebr. Biol.*, 123: 23-42.
- Marques, A.C. & A.L. Peña Cantero. 2010. Areas of endemism in the Antarctica case study of the benthic hydrozoan genus *Oswaldella* (Cnidaria, Kirchenpaueriidae). *J. Biogeogr.*, 37: 1-7.
- Miranda, T.P. & A.C. Marques. 2011. Abordagens atuais em biogeografia marinha. *Rev. Biol.*, 7: 41-48.
- Morrone, J.J. 1994. On the identification of areas of endemism. *Syst. Biol.*, 43: 438-441.
- Peña Cantero, A.L. 2012. Filling biodiversity gaps: benthic hydroids from the Bellingshausen Sea (Antarctica). *Polar Biol.*, 35: 851-865.
- Peña Cantero, A.L. & W. Vervoort. 2003. Species of *Staurotheca* Allman, 1888 (Cnidaria: Hydrozoa: Sertulariidae) from US Antarctic expeditions, with the description of three new species. *J. Nat. Hist.*, 37: 2653-2722.
- Peña Cantero, A.L. & W. Vervoort. 2004. Species of *Oswaldella* Stechow, 1919 (Cnidaria: Hydrozoa: Kirchenpaueriidae) from US Antarctic expeditions, with the description of three new species. *J. Nat. Hist.*, 38: 805-861.
- Peña Cantero, A.L. & W. Vervoort. 2005. *Mixoscyphus antarcticus* gen. nov., sp. nov. (Cnidaria, Hydrozoa, Sertulariidae), the first truly endemic genus of Antarctic benthic hydroids. *Polar Biol.*, 28: 956-963.
- Peña Cantero, A.L., A.M. García Carrascosa & W. Vervoort. 1997. On *Antarctoscyphus* (Cnidaria, Hydrozoa), a new genus of antarctic hydroids and the description of two new species. *Polar Biol.*, 18: 23-32.
- Spalding, M.D., H.E. Fox, G.R. Allen, N. Davidson, Z.A. Ferdeña, M. Finlayson, B.S. Halpern, M.A. Jorge, A. Lombana, S.A. Lourie, K.D. Martin, E. McManus, J. Molnar, C.A. Recchia & J. Robertson. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience*, 57: 573-583.
- Szumik, C.A., F. Cuzzo, P.A. Goloboff & A.E. Chalup. 2002. An optimality criterion to determine areas of endemism. *Syst. Biol.*, 51: 806-816.
- Yasuhara, M., M. Kato, N. Ikeya & K. Seto. 2007. Modern benthic ostracodes from Lützow-Holm Bay, East Antarctica: paleoceanographic, paleobiogeographic, and evolutionary significance. *Micropaleontology*, 53: 469-496.

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