



<http://dx.doi.org/10.11646/zootaxa.4033.4.2>

<http://zoobank.org/urn:lsid:zoobank.org:pub:10D02C83-458D-4668-AFA1-AD0A1047492E>

## Areas of endemism in the Southwestern Atlantic Ocean based on the distribution of benthic hydroids (Cnidaria: Hydrozoa)

THAÍS PIRES MIRANDA<sup>1,4</sup>, GABRIEL NESTOR GENZANO<sup>2</sup> & ANTONIO CARLOS MARQUES<sup>1,3</sup>

<sup>1</sup>*Departamento de Zoologia, Universidade de São Paulo, R. Matão, Tr. 14, 101, 05508–090 São Paulo, SP, Brazil.*

*E-mail: thaispmir@ib.usp.br; marques@ib.usp.br*

<sup>2</sup>*Estación Costera Nágera. Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET - UNMdP, Funes 3350, (7600) Mar del Plata, Argentina. E-mail: genzano@mdp.edu.ar*

<sup>3</sup>*Centro de Biología Marinha, Universidade de São Paulo, São Sebastião, Brazil. E-mail: marques@ib.usp.br*

<sup>4</sup>*Corresponding author*

### Abstract

Geographic distributions of 130 species of benthic hydroids were used to infer areas of endemism in the Southwestern Atlantic Ocean (SWAO, between 22°S and 55°S). Endemicity Analysis (EA) was carried out with the software NDM VNDM, using a 2° x 2° grid with different values of F (F = 0.5 and F = 1.0) for inferred presence. Hypothesized areas of endemism (16 with F = 0.5 and 13 with F = 1.0) formed three generalized patterns: (1) Tropical, (2) Subtropical, and (3) disjunctions along Tropical and Subtropical areas. Areas of endemism estimated here were compared with provinces, ecoregions and areas of endemism previously defined (but not based on algorithmic analysis) in the literature. Ecological and historical aspects that are potentially relevant for the SWAO realm were contrasted, related and discussed to areas of endemism. This is the first study to apply NDM VNDM to the marine realm and one of the few that focuses on the SWAO.

**Key words:** polyps, marine realm, Endemicity Analysis, NDM VNDM, Tropical, Subtropical, disjunctions, biogeography

### Introduction

The Southwestern Atlantic Ocean (SWAO) comprises Brazilian, Uruguayan and Argentinean waters, from 22°S to 55°S and from 35°W to 70°W. In terms of oceanography, SWAO has two main and opposing currents: the warm, southbound, Brazil Current that dominates the coast of Brazil (*cf.* Castro & Miranda 1998), and the cold, northbound, Falklands/Malvinas Current that dominates the coast of Argentina (*cf.* Boltovskoy 1981). Where these currents converge, the cold South Atlantic Central Water (SACW) is formed. It flows northward beneath the Brazil Current, and can cause intense thermoclines on the continental shelf of the SWAO (Acha *et al.* 2004). Variable temperatures, wind patterns and shelf topography contribute to the frequent coastal upwellings, and consequent increase in nutrients and recruitment in regional superficial waters (Matsuura 1986; Acha *et al.* 2004). Sea bottoms of the southern Brazilian continental shelf are comprised of varying amounts of sand, mud and gravel that together allow a diverse marine benthic fauna (Amaral *et al.* 2004). Benthic hydroids are a common component of this fauna as epibionts (Genzano & Rodriguez 1998; Migotto *et al.* 2001; Campos *et al.* 2012).

To the south, the mixture of sub-Antarctic waters and the Falklands/Malvinas Current also results in an oceanic front that flows along the continental shelf of Argentina, and brings nutrient-rich waters, allowing a diverse benthic fauna to develop (Acha *et al.* 2004; Acha & Mianzan 2006). In Argentina, dense banks of mussels are common in shallow waters, and dense banks of scallops occur above the 100m isobath (Acha *et al.* 2004; Bremec *et al.* 2008; Genzano *et al.* 2009). As in Brazil, this diversity of benthic species is correlated with loose gravel, rocky outcrops and hard bottoms (Genzano *et al.* 2009), associated with increased recruitment of hydroids on many consolidated substrates of natural or artificial origin.

The SWAO has traditionally been divided into several biogeographical regions and provinces depending upon the number of endemic species, and aspects of oceanography and ecology. Briggs (1974, p. 144) described basic

oceanographic dynamics and some faunal characteristics of the Eastern South America Warm-Temperate Region. Palacio (1982, p. 82) analyzed different oceanographic and zoogeographic studies for the southern region of Brazil and defined the Paulista, N Patagonia, S Patagonia and Malvinas provinces. Spalding *et al.* (2007, p. 579) used more precise spatial resolution and ecological and oceanographic data to divide coastal and shelf areas of the SWAO into two provinces (Warm Temperate Southwestern Atlantic and Magellanic), and seven ecoregions (Southeastern Brazil, Rio Grande, Rio de la Plata, Uruguay–Buenos Aires Shelf, North Patagonian Gulfs, Patagonian Shelf, Malvinas/Falklands). More recently, in a review of the classification of the pelagic oceanic waters of the world, Spalding *et al.* (2012, p. 27) proposed two pelagic provinces for the SWAO: South Central Atlantic and Malvinas Current (driven by the warm Brazil Current and the cold Falklands/Malvinas Current, respectively). Others, using mainly fish distribution data, proposed different provinces for Brazil and Argentina, usually ranging from southeastern Brazil to northern Patagonia in Argentina (*e.g.*, Briggs & Bowen 2012, 2013).

Areas of endemism are the basic units for biogeographic inference (Morrone 1994; van Soest & Hajdu 1997; Linder 2001), and so provide the basis for hypotheses of primary biogeographic homology (Morrone 2001). The terms ‘endemism’ and ‘endemic’ are historically used in the biological literature under many different meanings (Anderson, 1994). Overall, an ‘endemic species’ is defined as a species restricted to an area (Anderson 1994; Szumik *et al.* 2002; Crother & Murray 2011). The concept of area of endemism, however, is still being strongly debated in the biogeographic literature, with the proposition of several different definitions (*viz.*, Axelius 1991; Harold & Mooi 1994; Morrone 1994; Linder 2001; Humphries & Parenti 2001; Crother & Murray 2011), including discussions about its existence as a natural entity (*viz.*, Hovenkamp 1997, 2014). The historical and traditional sense of areas of endemism considers valid areas as those with overlapping distributional ranges of two or more endemic species (Platnick 1991; Morrone 1994; Crisci *et al.* 2003; Szumik & Goloboff 2004). Alternatively, Crother & Murray (2011) defined areas of endemism as geographic hierarchical areas with at least one unique species, or a unique combination of species, that are spatially and temporally bound to constitute a single unit. They consider areas of endemism as ‘individuals’ and not as ‘classes’, being real and natural entities regardless of human recognition. Thus, areas of endemism are diagnosed by a unique combination of characters, and not intentionally defined by a list of specific characters (Crother & Murray 2011).

Several alternatives can be used to determine areas of endemism, including null models (Mast & Nyffeler 2003; Giokas & Sfenthourakis 2008), area groups (Harold & Mooi 1994; Deo & DeSalle 2006), parsimony analyses (Rosen 1988; Morrone 1994; Morrone & Escalante 2002) and optimization algorithms (Szumik *et al.* 2002; Szumik & Goloboff 2004). Among these, endemism analysis (EA) has been widely used because it reflects both ecological and historical assumptions (Szumik & Goloboff 2004). EA is an optimization method based on an endemism score that includes the number of taxa, and how restricted they are to a given area (Szumik *et al.* 2002, 2006). This method, carried out by the software NDM, follows a heuristic search for the areas, and VNDM allows visualization of the areas of endemism and the contribution of each species to each score (Goloboff 2004; Szumik *et al.* 2002, 2006). NDM VNDM allows customizing different grid sizes within the same dataset, making it easier to compare and evaluate between different options and outputs (*viz.*, Casagrande *et al.* 2009; Szumik *et al.* 2012). Additionally, the three categories of records (absent, present and assumed) and the “evenness rule” (Szumik & Goloboff 2004, p. 969) provide a broader array of efficient options to handle the putative “absences”. This is especially important in marine habitats because sampling is usually fragmented due to the expensive methods required (*e.g.*, oceanographic ships, ROVs, etc.), in particular when involving investigations of remote regions such as the deep-sea. Thus, “absences” in marine distributions may be frequently interpreted as lack of sampling (“unknown”) rather than true (“known”) absence. The “evenness rule” and the use of different values of F can provide a wider range of possibilities to explore different scenarios trying to minimize the misinterpretation of marine “absences”. Finally, incomplete sampling can result in overlooking organisms with patchy distributions driven by specific ecological variables in specific habitats (*e.g.*, thermal vents, seamounts, etc.) or human-mediated dispersals.

Biogeographical studies, especially those considering the dubious “absences” and involving the use of a strict algorithm to infer areas of endemism, are rare for the SWAO, and most “marine provinces” proposed for the region were based on interpretative-narrative scenarios. Despite a recent increase in the number of marine biogeographical studies in areas of endemism (*viz.*, Garraffoni *et al.* 2006; Moreno *et al.* 2006, 2014; Winfield *et al.* 2006; Myers & Lowry 2009; Marques & Peña Cantero 2010; Miranda *et al.* 2013), understanding of marine biogeography is far less-advanced than that of terrestrial environments, and as a consequence, marine conservation policies are often compromised (Marques & Carranza 2013).

On the other hand, EA has been used in many terrestrial studies (*e.g.*, Moline & Linder 2006; Díaz Gómez 2007; Casagrande *et al.* 2009; Carine *et al.* 2009; Aagesen *et al.* 2009; Escalante *et al.* 2009a, 2009b, 2010; Navarro *et al.* 2009; Ferrari *et al.* 2010; Nori *et al.* 2011; Szumik *et al.* 2012). However, this method has not been used for marine regions and its efficacy is therefore unknown for this realm. In addition to considering ecological and historical assumptions, the method evaluates each species according to its geographic position within the area. Therefore, in any hypothetical area, it is possible to evaluate the number of endemic taxa and the degree to which they are endemic (Szumik *et al.* 2006). This is a dynamic strategy that improves the number of hypothesized areas of endemism without discarding ecology in biogeography. Thus, it is necessary to demonstrate the use of EA with marine datasets. Therefore, we infer areas of endemism in the SWAO using EA on a primary dataset of benthic hydroids collected in the region between Cabo Frio (Brazil) and Tierra del Fuego (Argentina), and compared the results with previous biogeographic patterns already delimited for the area.

## Material and methods

**Taxa.** Our dataset includes 130 species, 29 families and 69 genera of benthic hydroids found over 1,566 geographical locations in the SWAO, covering a broad area between 22–56°S and 0–1,000m depth (Appendix I). We reviewed the taxonomic identification of the species and checked each geographic coordinate of occurrence of the species prior to the inclusion of any point in the dataset. This was strictly necessary because the taxonomic history of Hydrozoa is complicated. The group contains a large number of taxa with intraspecific variation and countless taxonomic issues, involving different life cycle strategies and the consequences of the long time use of a dual classification system for polyps and medusae (Cornelius 1982, 1990; Calder 1988; Cunha *et al.* 2015; Gravili *et al.* 2015). Since then, many phylogenetic classifications for the more inclusive taxa of Hydrozoa were proposed (Collins 2000, 2002; Marques 2001; Marques & Collins 2004; Collins *et al.* 2005, 2006, 2008; Cartwright *et al.* 2008; Leclère *et al.* 2009; Cartwright & Nawrocki 2010; Nawrocki *et al.* 2010). However, the number of taxonomic reviews and phylogenetic studies at family and genus levels remains low for the class Hydrozoa as a whole, which currently comprises ca. 3,700 valid nominal species (Bouillon *et al.* 2006; Gravili *et al.* 2015). Considering the high complexity of Hydrozoa's taxonomy, we preferred to personally review in detail our primary data for the SWAO. We based our taxonomic conclusions on records published exclusively for this area (*viz.*, Genzano *et al.* 2009; Cunha *et al.* 2015), to guarantee the taxonomic accuracy of the dataset and to avoid possible taxonomic and geographic biases.

**Concept of area of endemism.** Here we use the concept of Crother & Murray (2011, p. 1012) on area of endemism, in which it is operationally defined as “an area that contains at least one unique species, or a unique combination of species. Therefore, our search is not limited on the exclusive use of distribution of endemic species of hydroids for the SWAO. Indeed, species of hydroids can have restricted and punctual geographic distribution, living at specific and specialized habitats, such as freshwater, and in interstitial sediments and ice (*e.g.*, Bouillon & Grohmann 1994; Jankowski *et al.* 2008; Piraino *et al.* 2008; Siebert 2009; Salonen *et al.* 2012). However, many taxa have wide geographic distribution and low incidence of endemism (*e.g.*, families Bougainvilliidae, Campanulariidae, Eudendriidae, Hydractiniidae, Sertulariidae, Tubulariidae; Millard 1975; Cornelius 1995; Bouillon *et al.* 2006; Schuchert 2012). Even for the endemic taxa, their distributions are concentrated on wide areas, which sometimes comprehends a whole ocean basin and adjacent seas (*e.g.*, species of *Staurotheca* for the Southern Hemisphere, and species of *Antarctoscyphus*, *Mixoscyphus* and *Oswaldella* for the Southern Ocean; Peña Cantero *et al.* 1997, 1999; Peña Cantero & Vervoort 2003, 2004, 2005). To search for areas of endemism using the distribution of species of hydroids, therefore, should involve as many records of species as possible, allowing a wide variety of contrasting distributions, increasing the biogeographic accuracy of the database studied. In our study, it would be unreasonable to use only endemic species of hydroids for the SWAO because, besides their lower number (only nine of the 130 species are endemic to the SWAO), a search like that would lack representativeness of the main SWAO biota. Also, species sharing a long history in the SWAO, even those non-endemic for the area, might reflect shared historical processes occurring in that time frame because areas of endemism are essentially areas where part of the distribution of a biota was spatially restricted by a common process of isolation (DaSilva 2011). Finally, understanding the distribution of marine taxa is not a simple task because of the complexity of the marine realms, including extreme abiotic gradients, apparent lack of geographic barriers, and great dispersal

potential (Miranda & Marques 2011). Besides, cyclic and acyclic environmental fluctuations (e.g., El Niño, La Niña) directly contribute to these difficulties, since they can shift species distributions for long periods of time, generating seemingly incomparable species lists for the same geographic area (E. Hajdu, pers. comm.).

**Method of search.** We searched for areas of endemism using the optimization algorithm of the software NDM VNDM ver. 2.5 (Goloboff 2004). Analyses were carried out for the 130 species of benthic hydroids (Appendix I), plotted in quadrants of 2° latitude by 2° longitude, with grid origin at 22°S, 70°W. The use of large grids hides the recognition of small and disjunct areas, while the use of small grids increases the spatial discontinuity of the dataset used, decreasing the probability of finding sympatric patterns among the species (Casagrande *et al.* 2009). To avoid under- or overestimating the number of areas of endemism found, we tested several grid sizes through NDM VNDM prior to the analyses, and we chose to work with a grid of 2°X2. With our dataset, larger grids generated a sum of smaller patterns that covered almost the entire SWAO coast, preventing the visualization and establishment of coherent biogeographic areas. Smaller grids, on the other hand, maximized absence quadrants and spatial discontinuity of the dataset, prioritizing “areas” where geographic points were near each other. We used the “swap one cell at a time” heuristic search option and  $F = 0.5$  and  $F = 1.0$  for inference of species distribution. Groups of quadrants with scores greater than 2.0 were saved and considered as areas of endemism.

## Results

The analysis resulted in 16 and 13 overlapped areas of endemism for  $F = 0.5$  and  $F = 1.0$ , respectively (Figures 1, 2). Areas 0 to 3, 5, 7 to 9, 14 (Figure 1), and areas 0 to 3, 5 to 9 (Figure 2), correspond to Tropical areas, occupying the 22–30°S coastal zone. The endemic species supporting each one of these areas are characterized by species well distributed at the shallow waters of the Brazilian coast, commonly occurring between the intertidal zone and 300m depth, mainly on rocky shore zones (Tables 1, 2; Vannucci Mendes 1946; Vannucci 1949; Migotto 1996; Grohmann *et al.*, 2003; Cunha & Jacobucci 2010; Miranda *et al.* 2011). Areas 4, 10 to 12, 15 (Figure 1), and areas 4, 10 to 12 (Figure 2), correspond to Subtropical areas, occupying the zone from 34–44°S. The endemic species supporting these areas are commonly distributed at the Uruguay-Argentine coast, from the intertidal zone to ca. 1,400m depth, although some of them are restricted to zones above 70m depth, such as *Lytocarpia canepa* and *Stegolaria irregularis* (Tables 1, 2; Blanco & Bellusci de Miralles 1971; Stepanjants 1979; Blanco 1994; Genzano *et al.* 2009; El Beshbeeshy & Jarms 2011). Areas 6 and 13 (Figure 1) correspond to areas of disjunction, gathering Tropical and Subtropical areas along the zones from 22–30°S and from 34–44°S. Except for *Eudendrium caraiuru*, which was recorded only for the Brazilian coast (Marques & Oliveira 2003), the endemic species supporting these areas are widely distributed along the Brazilian, Uruguayan and Argentinean coasts, from shallow waters down to 300m depth (Tables 1, 2; Vannucci Mendes 1946; Vannucci 1949; Migotto 1996; Blanco 1994; Genzano *et al.* 2009; El Beshbeeshy & Jarms 2011). The list of species responsible for the determination of each area of endemism is found in Tables 1 and 2.

## Discussion

We find that our areas of endemism reflect relevant ecological and oceanographic processes and areas of disjunction in the SWAO. Typically, areas of endemism are thought to be driven by ecological and historical factors of the region in which they occur (Okolodkov 2010). Here, the three groups of areas of endemism concentrate at 22–30°S, at 34–44°S, or as disjunctions within the same hypothesis of endemism (Figures 1, 2). The Tropical areas of endemism (at 22–30°S; Figures 1, 2) are coincident with the warm Brazil Current flowing region, while the Subtropical areas (at 34–44°S; Figure 2), are coincident with the cold Falklands/Malvinas Current flowing region (Acha *et al.* 2004). The areas of disjunction are influenced by both of these currents. Together, this suggests that the regimen of oceanographic currents of the SWAO have a high influence on the arrangement of these areas, and also on their species composition, which is considerably distinct (Tables 1, 2). These unique species compositions are related to historical processes, such as vicariance and dispersal, since the oceanographic dynamics of the SWAO might be hypothesized as a barrier to some species distributions, or as a way to their dispersion through wider regions.

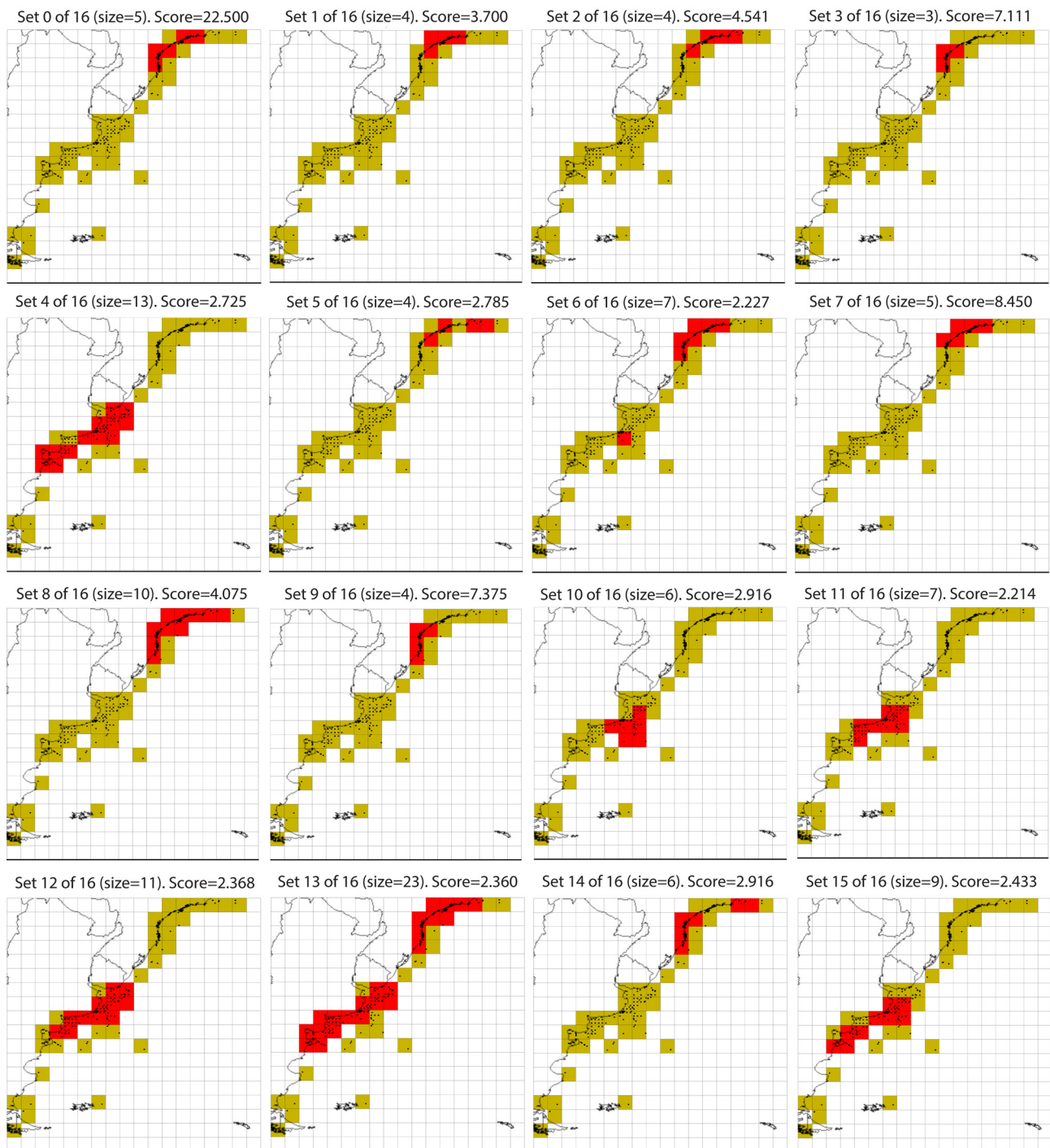
**TABLE 1.** EA sets for quadrants 2°X2° and F = 0.5.

Set	Number of quadrants	Score	Number of endemic species	Endemic species
0	5	22.500	36	<i>Aglaophenia latecarinata</i> , <i>Bougainvillia rugosa</i> , <i>Campanularia hincksii</i> , <i>Cladocoryne floccosa</i> , <i>Clytia hummelincki</i> , <i>C. linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Diphasia tropica</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Eudendrium carneum</i> , <i>Halecium bermudense</i> , <i>H. dyssymetrum</i> , <i>H. lightbourni</i> , <i>H. tenellum</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Idiellana pristis</i> , <i>Lafoeina amirantensis</i> , <i>Lytocarpia tridentata</i> , <i>Macrorhynchia philippina</i> , <i>Monothecha margaretta</i> , <i>Orthopyxis caliculata</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Pycnotheca mirabilis</i> , <i>Scandia mutabilis</i> , <i>Sertularella areyi</i> , <i>Sertularia loculosa</i> , <i>S. marginata</i> , <i>S. rugosissima</i> , <i>S. turbinata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i> , <i>Zyzyzus warreni</i>
1	4	3.700	12	<i>Clytia linearis</i> , <i>Dynamena crisioides</i> , <i>Halopteris diaphana</i> , <i>Idiellana pristis</i> , <i>Lafoeina amirantensis</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Sertularia marginata</i> , <i>S. notabilis</i> , <i>S. rugosissima</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i>
2	4	4.541	10	<i>Aglaophenia trifida</i> , <i>Halecium bermudense</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Lafoeina amirantensis</i> , <i>Nemalium lighti</i> , <i>Plumularia floridana</i> , <i>Sertularia marginata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i>
3	3	7.111	15	<i>Clytia linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Idiellana pristis</i> , <i>Macrorhynchia philippina</i> , <i>Monothecha margaretta</i> , <i>Orthopyxis caliculata</i> , <i>Pennaria disticha</i> , <i>Scandia mutabilis</i> , <i>Sertularia loculosa</i> , <i>S. rugosissima</i> , <i>S. tumida</i> , <i>S. turbinata</i>
4	13	2.725	4	<i>Aglaophenia acacia</i> , <i>Campanularia agas</i> , <i>Halecium beanii</i> , <i>Syntheicum protectum</i>
5	4	2.785	6	<i>Aglaophenia trifida</i> , <i>Dynamena dalmasi</i> , <i>Halecium bermudense</i> , <i>Halopteris polymorpha</i> , <i>Lafoeina amirantensis</i> , <i>Nemalium lighti</i>
6	7	2.227	3	<i>Eudendrium caraiuru</i> , <i>Hebella scandens</i> , <i>Sertularella conica</i>
7	5	8.450	22	<i>Clytia hummelincki</i> , <i>C. linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Idiellana pristis</i> , <i>Macrorhynchia philippina</i> , <i>Monothecha margaretta</i> , <i>Orthopyxis caliculata</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Scandia mutabilis</i> , <i>Sertularia loculosa</i> , <i>S. marginata</i> , <i>S. notabilis</i> , <i>S. rugosissima</i> , <i>S. turbinata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i>
8	10	4.075	6	<i>Aglaophenia latecarinata</i> , <i>Dynamena dalmasi</i> , <i>Eudendrium carneum</i> , <i>Halecium bermudense</i> , <i>Halopteris polymorpha</i> , <i>Lafoeina amirantensis</i>
9	4	7.375	16	<i>Clytia linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Macrorhynchia philippina</i> , <i>Monothecha margaretta</i> , <i>Orthopyxis caliculata</i> , <i>Parawrightia robusta</i> , <i>Pennaria disticha</i> , <i>Pycnotheca mirabilis</i> , <i>Scandia mutabilis</i> , <i>Sertularia loculosa</i> , <i>S. rugosissima</i> , <i>S. tumida</i> , <i>S. turbinata</i>
10	6	2.916	4	<i>Gonothyraea loveni</i> , <i>Grammaria abietina</i> , <i>Lytocarpia canepa</i> , <i>Stegolaria irregularis</i>
11	7	2.214	4	<i>Campanularia agas</i> , <i>Gonothyraea loveni</i> , <i>Halecium beanii</i> , <i>Phialella belgicae</i>
12	11	2.368	4	<i>Aglaophenia acacia</i> , <i>Campanularia agas</i> , <i>Halecium beanii</i> , <i>Phialella belgicae</i>
13	23	2.360	3	<i>Bougainvillia muscus</i> , <i>Clytia gracilis</i> , <i>Obelia dichotoma</i>
14	6	2.916	7	<i>Aglaophenia latecarinata</i> , <i>Dynamena dalmasi</i> , <i>Eudendrium carneum</i> , <i>Halecium bermudense</i> , <i>Halopteris polymorpha</i> , <i>Hincksella cylindrica</i> , <i>Lafoeina amirantensis</i>
15	9	2.433	5	<i>Aglaophenia acacia</i> , <i>Campanularia agas</i> , <i>Halecium beanii</i> , <i>Monothecha pulchella</i> , <i>Syntheicum protectum</i>

**TABLE 2.** EA sets for quadrants 2°X2° and F = 1.0.

Set	Number of quadrants	Score	Number of endemic species	Endemic species
0	6	29.800	36	<i>Aglaophenia latecarinata</i> , <i>Bougainvillia rugosa</i> , <i>Campanularia hincksii</i> , <i>Cladocoryne floccosa</i> , <i>Clytia hummelincki</i> , <i>C. linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Diphasia tropica</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Eudendrium carneum</i> , <i>Halecium bermudense</i> , <i>H. dyssymetrum</i> , <i>H. lightbourni</i> , <i>H. tenellum</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Idiellana pristin</i> , <i>Lafoeina amirantensis</i> , <i>Lytocarpia tridentata</i> , <i>Macrorhynchia philippina</i> , <i>Monothea margaretta</i> , <i>Orthopyxis calculata</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Pycnotheca mirabilis</i> , <i>Scandia mutabilis</i> , <i>Sertularella areyi</i> , <i>Sertularia loculosa</i> , <i>S. marginata</i> , <i>S. rugosissima</i> , <i>S. turbinata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i> , <i>Zyzyzus warreni</i>
1	4	5.666	10	<i>Aglaophenia trifida</i> , <i>Halecium bermudense</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Lafoeina amirantensis</i> , <i>Nemalium lighti</i> , <i>Plumularia floridana</i> , <i>Sertularia marginata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i>
2	7	30,500	35	<i>Aglaophenia latecarinata</i> , <i>Bougainvillia rugosa</i> , <i>Campanularia hincksii</i> , <i>Cladocoryne floccosa</i> , <i>Clytia hummelincki</i> , <i>C. linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Diphasia tropica</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Eudendrium carneum</i> , <i>Halecium bermudense</i> , <i>H. dyssymetrum</i> , <i>H. tenellum</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Idiellana pristin</i> , <i>Lafoeina amirantensis</i> , <i>Lytocarpia tridentata</i> , <i>Macrorhynchia philippina</i> , <i>Monothea margaretta</i> , <i>Orthopyxis calculata</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Pycnotheca mirabilis</i> , <i>Scandia mutabilis</i> , <i>Sertularella areyi</i> , <i>Sertularia loculosa</i> , <i>S. marginata</i> , <i>S. rugosissima</i> , <i>S. turbinata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i> , <i>Zyzyzus warreni</i>
3	3	8.333	15	<i>Clytia linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Idiellana pristin</i> , <i>Macrorhynchia philippina</i> , <i>Monothea margaretta</i> , <i>Orthopyxis calculata</i> , <i>Pennaria disticha</i> , <i>Scandia mutabilis</i> , <i>Sertularia loculosa</i> , <i>S. rugosissima</i> , <i>S. tumida</i> , <i>S. turbinata</i>
4	13	3.428	4	<i>Aglaophenia acacia</i> , <i>Campanularia agas</i> , <i>Halecium beanii</i> , <i>Syntheicum protectum</i>
5	4	3.714	6	<i>Aglaophenia trifida</i> , <i>Dynamena dalmasi</i> , <i>Halecium bermudense</i> , <i>Halopteris polymorpha</i> , <i>Lafoeina amirantensis</i> , <i>Nemalium lighti</i>
6	5	11,000	22	<i>Clytia hummelincki</i> , <i>C. linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Halopteris diaphana</i> , <i>H. polymorpha</i> , <i>Idiellana pristin</i> , <i>Macrorhynchia philippina</i> , <i>Monothea margaretta</i> , <i>Orthopyxis calculata</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Scandia mutabilis</i> , <i>Sertularia loculosa</i> , <i>S. marginata</i> , <i>S. notabilis</i> , <i>S. rugosissima</i> , <i>S. turbinata</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i>
7	10	5.500	6	<i>Aglaophenia latecarinata</i> , <i>Dynamena dalmasi</i> , <i>Eudendrium carneum</i> , <i>Halecium bermudense</i> , <i>Halopteris polymorpha</i> , <i>Lafoeina amirantensis</i>
8	4	9.666	16	<i>Clytia linearis</i> , <i>C. noliformis</i> , <i>Dentitheca bidentata</i> , <i>Dynamena crisioides</i> , <i>D. quadridentata</i> , <i>Macrorhynchia philippina</i> , <i>Monothea margaretta</i> , <i>Orthopyxis calculata</i> , <i>Parawrightia robusta</i> , <i>Pennaria disticha</i> , <i>Pycnotheca mirabilis</i> , <i>Scandia mutabilis</i> , <i>Sertularia loculosa</i> , <i>S. rugosissima</i> , <i>S. tumida</i> , <i>S. turbinata</i>
9	5	4.500	15	<i>Cladocoryne floccosa</i> , <i>Clytia linearis</i> , <i>Dynamena crisioides</i> , <i>Halecium dyssymetrum</i> , <i>Halopteris diaphana</i> , <i>Idiellana pristin</i> , <i>Lafoeina amirantensis</i> , <i>Monothea margaretta</i> , <i>Pennaria disticha</i> , <i>Plumularia floridana</i> , <i>Sertularia marginata</i> , <i>S. notabilis</i> , <i>S. rugosissima</i> , <i>Turritopsis nutricula</i> , <i>Ventromma halecioides</i>
10	7	3.000	4	<i>Campanularia agas</i> , <i>Gonothyrea loveni</i> , <i>Halecium beanii</i> , <i>Phialella belgicæ</i>
11	11	3.111	4	<i>Aglaophenia acacia</i> , <i>Campanularia agas</i> , <i>Halecium beanii</i> , <i>Phialella belgicæ</i>
12	10	3.222	5	<i>Aglaophenia acacia</i> , <i>Campanularia agas</i> , <i>Halecium beanii</i> , <i>Monothea pulchella</i> , <i>Syntheicum protectum</i>

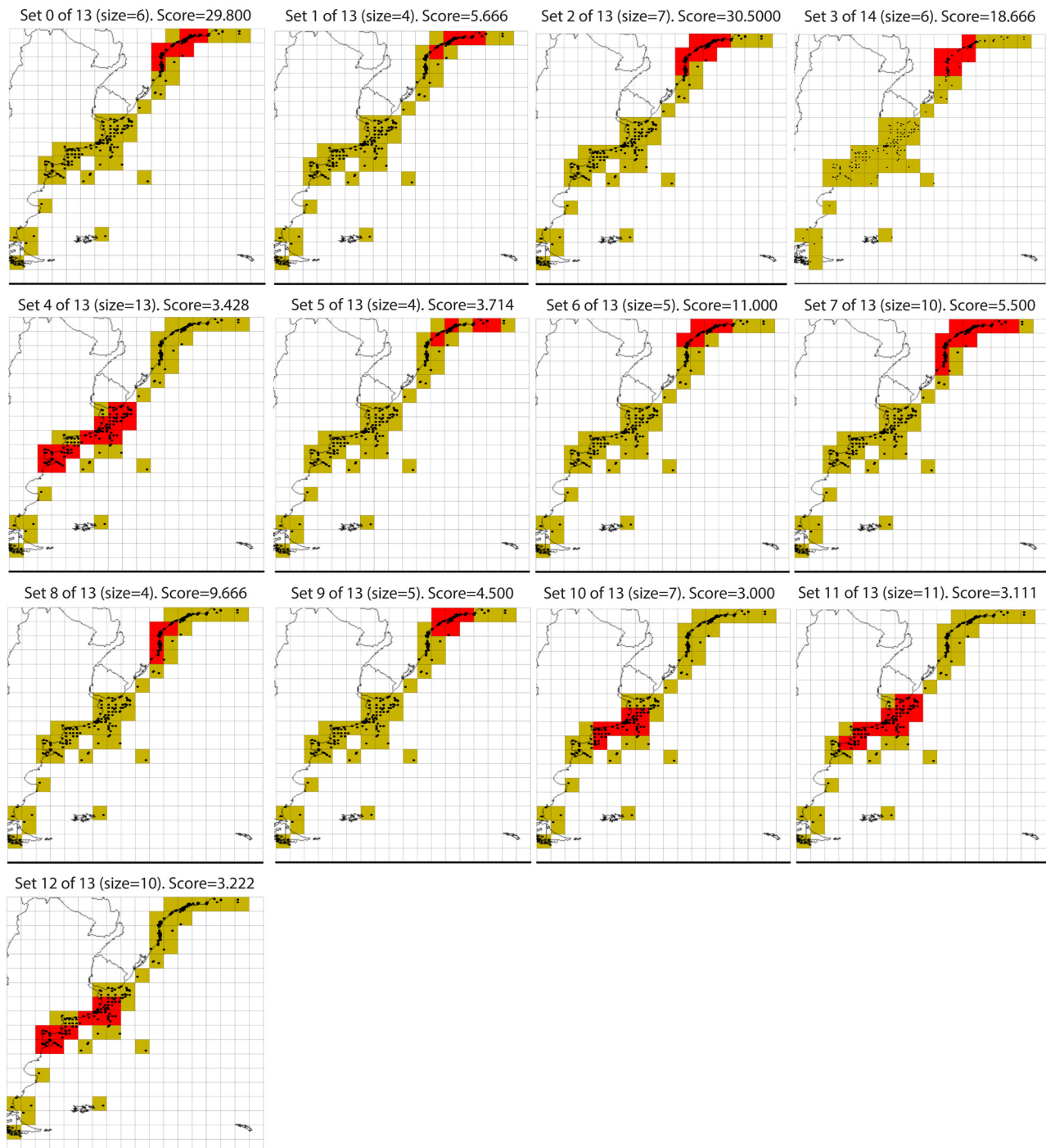




**FIGURE 1.** Areas of endemism (in red), their number of quadrants (size) and their score, in sets 0 to 15 resulting from the EA with NDM VNDM for quadrants  $2^{\circ}\times 2^{\circ}$  and  $F = 0.5$ . In yellow are the quadrants with benthic hydroids occurrences considered by the NDM VNDM for the EA.

The Tropical and Subtropical areas (i.e., at  $22\text{--}30^{\circ}\text{S}$  and at  $34\text{--}44^{\circ}\text{S}$ , respectively, *viz.* Figures 1, 2) are associated with zones defined by precise abiotic factors (*e.g.*, temperature, salinity, nutrient concentration) and oceanic front regimes. The Tropical areas (at  $22\text{--}30^{\circ}\text{S}$ , Figures 1, 2) are included in the Warm Temperate Southwestern Atlantic province that encompasses the Southeastern Brazil and Rio Grande ecoregions (*cf.* Spalding *et al.* 2007). These ecoregions are considered to be transitional between the tropical and temperate southwest Atlantic. They are influenced by the warm Brazil Current and by the convergence zone of the Brazil Current with the cold Falkland/Malvinas Current, and thus have high seasonal variation in surface water temperatures and dry winters (Palacio 1982; Acha *et al.* 2004). The Subtropical areas (at  $34\text{--}44^{\circ}\text{S}$ , Figures 1, 2) include the Uruguay-

Buenos Aires Shelf and North Patagonian Gulf ecoregions (*cf.* Spalding *et al.* 2007) which are strongly influenced by the cold Falkland/Malvinas Current and, less so, by its convergence with the Brazil Current. Variable abiotic factors in these areas may act as ecological barriers for benthic hydroids, which can be seen in the particular species assemblages that characterize these areas of endemism (*viz.*, Tables 1, 2). It is interesting to note that Medel & López-González (1998) already recorded a similar pattern of distribution for Atlantic benthic hydroids. The authors found that their “Brazilian Subregion” is oceanographically more closely related with the warm regions of the North American and Caribbean Provinces, and that their “Magellanic Province” is more closely related with colder areas of the Antarctic region.



**FIGURE 2.** Areas of endemism (in red), their number of quadrants (size) and their score, in sets 0 to 12 resulting from the EA with NDM VNDM for quadrants  $2^{\circ}\times 2^{\circ}$  and  $F = 1.0$ . In yellow are the quadrants with benthic hydroids occurrences considered by the NDM VNDM for the EA.



Moreno *et al.* (2014) carried out a parsimony analysis for ascidians using latitudinal/longitudinal gradients as sampling units, revealing interesting patterns in the Atlantic Ocean, clearly delimiting areas of endemism at the western and eastern sides of this ocean. Our Tropical and Subtropical areas (at 22–30°S and at 34–44°S, Figures 1, 2) overlap with previous areas of endemism delimited for ascidians in the SWAO (Moreno *et al.* 2014). Tropical areas (at 22–30°S, Figures 1, 2) correspond to their bioregion 7 (at 21–30°S), inserted into the wider bioregion 2, while our Subtropical areas (at 34–44°S, Figures 1, 2) are inserted into bioregions 8, 9 and 10 (*viz.*, Moreno *et al.* 2014).

Our analysis showed areas of disjunction (sets 5, 6, 13, 14, Figure 1, and set 5, Figure 2) in the SWAO, in contrast with inshore/offshore areas and latitudinal gradients of biodiversity already documented for the marine realm in biogeographic studies (*e.g.*, Searless 1984; Calder 1992; Liuzzi *et al.* 2011; Fautin *et al.* 2013). Areas of disjunction, recognized by EA, are common in nature (Casagrande *et al.* 2012), and can be related to several ecological and historical aspects of the SWAO. Here, our areas of disjunction (sets 5, 6, 13, 14, Figure 1, and set 5, Figure 2) are the result of concatenated but disjunct distribution of sets of species in different sub-areas within a larger area. Interpreting these patterns is not simple and a variety of hypotheses could explain them.

Hypothesis 1: this disjunct pattern is the result of an algorithmic artifact related to the uneven distribution of benthic hydroid species in the SWAO, since EA is sensible and would perform well to identify areas of disjunction (*viz.*, Casagrande *et al.* 2012).

Hypothesis 2: the identity of each sub-area is derived from spurious processes, such as bioinvasions (*e.g.*, human mediated) that are currently being examined (*e.g.*, Bardi & Marques 2009; Rocha *et al.* 2013). If so, these sets of sub-areas would not be historical areas *per se*.

Hypothesis 3: discontinuity reflects incipient vicariance, in which case a wide barrier is separating biota that recently split evolutionarily.

Hypothesis 4: dispersal over a barrier, even though barriers are seldom hypothesized or tested in marine scenarios, which renders such hypotheses difficult to characterize and understand (Miranda & Marques 2011).

For sets 6 and 13 (Figure 1) along the SWAO coast, for instance, possible barriers could be the convergence zone of the Brazil and Falklands/Malvinas currents, which occurs along the 30°S to 36°S region and produces "an extended region of interrelated fronts" (Acha *et al.* 2004, p. 90) with wide variation in temperature, salinity, and nutrient concentration. This potential barrier might hinder larval transportation/advection (or survival) between regions, restraining colonization. Another putative barrier is the La Plata River, though this freshwater input does not seem to be a real barrier in more recent times, including different populations of hydroids (*e.g.*, Imazu *et al.* 2014). Last but not least, a potential barrier would be the availability of hard substrate at the southern Brazilian coast, mainly between 30–34°S, which is a region characterized by the lack of rocky shores. The availability of substrate was also considered to be a barrier for the distribution of ascidian species, since most species are also restricted to hard substrates (Moreno *et al.* 2014).

Substrate unavailability or the lack of suitable substrate are important geographic barriers for benthic hydroid species. For instance, the abundance, seasonality and reproductive periods of *Clytia gracilis* seem to modulate seasonal cycles of regression and growth ultimately related to environmental conditions (Jaubet & Genzano 2011). *Clytia gracilis*, a species with a wide distribution as a polyp, has a geographically restricted medusa stage (Cornelius 1995), which could be explained by its successful asexual reproductive strategy, and predominance of the polyp stage. Asexual reproduction seems to be the prime mechanism of maintenance of these populations, because their reproductive cycle also depends on adequate substrates for recruitment and growth of larvae (Jaubet & Genzano 2011). Similar patterns occur in other hydroids, in which the geographic range of the polyps does not coincide with that of the medusae, and the life stages have different environmental demands (*cf.* Mendoza-Becerril & Marques 2013).

Not all taxa respond similarly to different barriers, which also complicates interpretation. Piovesan *et al.* (2012), in reviewing the marine ostracod *Majungaella*, emphasized that the distribution of the genus followed the break of Western Gondwana and the opening of the Atlantic Ocean (*ca.* 115 Myr), which allowed the northward migration of marine taxa (Fairhead & Binks 1991; Jacobs *et al.* 2009). The emergence of the Atlantic Ocean affected climate, geography and oceanography (Jacobs *et al.* 2009), and established barriers for some taxa, while at the same time facilitating the dispersal of others. These barriers involve abiotic gradients (*e.g.*, temperature, salinity, oxygen concentration, nutrients), oceanographic regimes and geomorphological changes. Together or isolated, these changes may have restricted some taxa into one or more areas, or into areas of disjunction.

Dispersal across biogeographic barriers depends on special biological traits that allow a given lineage to explore new habitats and establish new populations (Luiz *et al.* 2012). Seasonality and population dynamics of hydroid species (*viz.*, Gili & Hughes 1995; Bavestrello *et al.* 2006; Rossi *et al.* 2012; Fernandez *et al.* 2014, 2015) are influenced by marine abiotic and biotic factors that, ultimately, may constitute geographic barriers for some species although not influencing the distribution of others. Temporal variation of species richness in assemblages of benthic hydroids has already been described, and two types of species in Hydrozoa have been recognized: species recruiting to new surfaces year-round, and species doing so sporadically and without strong seasonality (Migotto *et al.* 2001; Fernandez *et al.* 2014). Reasons for these different scenarios are not clear, but one could hypothesize that wide distributions of hydroid species may be due to the many different strategies of asexual and sexual reproduction in complex life cycles including polyp and/or medusa/medusoid stages (Gili & Hughes 1995), and their great capacity to colonize different substrates (*viz.*, Gili & Hughes 1995; Genzano & Rodriguez 1998; Migotto *et al.* 2001; Genzano 2002; Oliveira & Marques 2007, 2011). Cornelius (1992) discussed rafting on floating objects and resting stages of hydroids together with the medusa loss in hydrozoan lineages, emphasizing the wide distribution patterns presented by benthic stages without medusae in their life cycle. This pattern is considered a paradox since the medusa stage is classically interpreted as the main mechanism for successful dispersal in hydroids (Cornelius 1992). Another similar paradox frequently reported in biogeography concerns snails and slugs, which have wide patterns of geographic distribution, despite being slow, non-dynamic animals (Gittenberger 2012). However, these animals are transported mainly by birds, being capable to survive in their digestive tract, and therefore to spread along large areas (Gittenberger 2012).

Determining exactly how and which barriers affect marine organism distributions is not easy (Miranda & Marques 2011; Luiz *et al.* 2012). Knowledge of ecological, oceanographic and historical aspects, in addition to biological and genetic information of the organisms of interest is required (Luiz *et al.* 2012). We suggest that the areas of endemism outlined in this study may be viewed as initial models to stimulate further investigation.

## Conclusion

Studies in marine biogeography are still concentrated on characterizing patterns of geographical distribution and areas of endemism (Miranda & Marques 2011) – consequently, studies of marine historical patterns and applying specific historical methods in biogeography are few (*e.g.*, van Soest & Hajdu 1997; Fernandez *et al.* 2012). This is intrinsically related with the complex idiosyncrasies of the marine realm. First, there is no specific method in marine biogeography capable of dealing with the complexity and three-dimensionality of the marine realm as a whole (Miranda & Marques 2011). Depth data for example, that sometimes characterize pycnoclines, are rarely considered or available in biogeographic inferences. Therefore, the ocean volume is flattened into a two dimensional pattern, unreal for the actual distribution of marine taxa. For instance, two different water masses may be overlapping in two dimensions but their biota will never be really sympatric. Clearly, a similar problem may occur when dealing with distinct altitudes in the terrestrial realm. However, dispersal over long distances is more often universally accepted in the marine realm than in the terrestrial one (Heads 2005). Second, there are many marine habitats, such as poorly sampled deep-sea regions, for which faunal knowledge is insufficient to establish presence of endemic species (Costello *et al.* 2010). The lack of faunal knowledge in deeper marine areas makes it difficult to gather complete datasets with species records for continuous depth ranges (*i.e.*, from shallow waters to deep sea zones), mainly when dealing with large-scale areas. Associated with this issue is the taxonomic accuracy of the geographic records of species that are the basis for any sound biogeographic inference (Crisci *et al.* 2003; Miranda & Marques 2011). Therefore, taxonomic and sampling enhancements are still bottlenecks related to marine geographic distributions, endemism and biogeography.

The all-too-frequent use of dispersal as the potential explanation for many geographic distributions of marine organisms, and the difficulties in understanding vicariance and geographic barriers are pervasive in the marine biogeographic literature (Heads 2005). Biological factors (*e.g.*, different strategies of life cycles, epibiosis, fouling, rafting) are also poorly understood and thus difficult to use in marine biogeography (Miranda & Marques 2011). Thus, there are many obstacles to understanding biogeographic patterns “with our present incomplete knowledge of deep-ocean currents and habitat distribution” (Van Dover *et al.* 2002, p. 1257).

Here, we have used a specific biogeographic method (for the first time with marine organisms) to infer and

discuss areas of endemism in the SWAO. Complementary methods (*e.g.*, PAE, three-item analysis) and different strategies to infer areas of endemism (*e.g.*, use of distinct spatial resolutions, contrast of inferred and assumed presences for the species) should be applied to improve understanding of marine biogeography. Also, we must develop new strategies that include the three-dimensionality of aquatic settings (*e.g.*, datasets with different depth ranges) to better examine these questions. We suggest that EA is a good first attempt to examine this problem because it considers both ecological and historical processes that are inseparable in the evolution of organisms. Finally, it is also important to consider the different and diverse life cycle strategies of marine species in marine biogeographic analyses and scenarios, since behavior and migratory capacity depend on oceanographic conditions and dispersal strategies of each stage of the life cycle.

## Acknowledgments

We would like to thank Alvaro Migotto for providing material and geographic data. Beatriz Mothes (Porifera collection of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul FZB-RS), Cristina Damborenea (Hydrozoa collection of the Museo de La Plata), and Eduardo Hajdu (Porifera collection of the Museu Nacional do Rio de Janeiro, MNRJ) provided access to study their collections. Adriana Morales helped in understanding some EA patterns and algorithms. We thank anonymous reviewers, Eduardo Hajdu and the editor Bastian Bentlage for their valuable comments and suggestions on earlier versions of this manuscript. This study was supported by grants from CAPES Proap-2008, Procad and Pró-Equipamentos 1887/2007, CNPq (Proc. 490348/2006-8, 304720/2009-7, 562143/2010-6, 563106/2010-7, 458555/2013-4), EXA 734/15 (UNMdP), FAPESP (Proc. 2004/09961-4, 2006/58226-0, 2010/52324-6, 2010/06927-0, 2011/50242-5, 2013/50484-4, 2014/24407-5) and PIP-CONICET 2012. This is a contribution of NP-BioMar, USP. James J. Roper revised the English in its entirety.

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Areas of endemism in the Southwestern Atlantic Ocean based on the distribution of benthic hydroids (Cnidaria: Hydrozoa). Zootaxa. Miranda, T.P., Genzano, G.N. & Marques, A.C.

Corresponding author: Thaís Pires Miranda, Departamento de Zoologia, Universidade de São Paulo, Caixa Postal 11461, 05422-970 São Paulo, SP, Brazil. E-mail: thaismir@ib.usp.br

Appendix I. List of species used in the endemism analysis (EA) with the corresponding numbers and the geographical coordinates of occurrence (-longitude -latitude). Highlighted species are endemic for the south Atlantic.

**1. *Acryptolaria conferta***: -37.588 -22.382; -48.666 -31.333; -49.525 -31.128; -59.550 -43.583; -50.510 -43.550; **2. *Aglaophenia acacia***: -53.083 -35.000; -53.100 -35.000; -57.218 -38.053; -58.533 -38.933; -53.250 -34.750; -54.750 -35.750; -54.750 -36.250; -55.750 -36.750; -54.750 -36.750; -56.250 -37.250; -56.750 -37.750; -57.250 -38.250; -57.500 -38.150; -58.580 -38.480; -60.250 -40.250; -61.750 -41.250; -64.000 -42.200; -64.750 -41.270; -65.000 -41.230; -64.000 -42.000; **3. *Aglaophenia latecarinata***: -41.947 -22.870; -44.339 -23.097; -44.409 -23.096; -44.816 -23.416; -44.833 -23.383; -45.150 -23.516; -45.290 -23.737; -45.303 -23.910; -45.348 -23.748; -45.349 -23.752; -45.349 -23.746; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -45.417 -23.823; -45.421 -23.828; -45.431 -23.864; -45.431 -23.831; -45.434 -23.869; -45.510 -23.836; -45.660 -23.766; -48.316 -25.572; -48.317 -25.574; -48.363 -25.735; -48.374 -27.162; -48.374 -27.199; -48.374 -28.013; -48.433 -27.143; -48.433 -27.228; -48.477 -27.141; -48.479 -27.134; -48.480 -27.153; -48.481 -27.147; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.522 -27.134; -48.522 -27.142; -48.522 -27.153; -48.522 -27.997; **4. *Aglaophenia rhynchocarpa***: -46.784 -26.767; **5. *Aglaophenia trifida***: -40.826 -22.335; -41.947 -22.870; -44.339 -23.097; -45.173 -23.768; -45.237 -23.813; **6. *Amphinema rugosum***: -45.421 -23.828; -45.422 -23.828; **7. *Amphisbetia operculata***: -48.522 -27.997; -57.300 -38.160; -61.650 -40.950; -55.750 -34.750; -55.250 -35.250; -54.750 -35.750; -54.750 -36.250; -55.750 -36.750; -54.750 -36.750; -56.250 -37.750; -57.500 -38.150; -57.750 -38.250; -57.250 -38.250; -58.580 -38.480; -61.150 -39.030; -61.500 -39.070; -61.750 -39.750; -61.250 -39.750; -64.500 -40.892; -61.750 -40.250; -60.750 -40.250; -62.300 -40.500; -61.750 -40.750; -61.250 -40.750; -62.250 -41.250; -61.750 -41.250; -61.250 -41.250; -64.000 -41.250; -62.250 -41.750; -64.000 -42.000; -58.600 -42.470; -63.283 -42.468; -69.310 -51.520; -63.116 -42.589; -62.821 -42.786; -62.732 -42.841; **8. *Antennella secundaria***: -48.522 -27.134; **9. *Asyncoryne ryniensis***: -45.412 -23.827; **10. *Bimeria vestita***: -44.623 -23.057; -45.397 -23.728; -45.398 -23.728; -45.405 -23.819; -45.421 -23.828; -45.431 -23.831; -46.370 -23.977; -46.788 -24.188; -47.000 -24.400; -48.311 -25.573; -48.322 -25.584; -48.473 -25.702; -48.510 -27.216; -48.522 -27.134; -48.522 -27.997; -48.530 -25.842; -48.563 -25.893; -48.616 -26.117; -57.250 -37.750; -57.750 -38.240; -64.010 -42.030; **11. *Bougainvillia muscus***: -42.018 -22.971; -43.906 -22.936; -44.888 -23.365; -45.032 -23.458; -45.231 -23.780; -47.910 -25.065; -47.912 -25.058; -47.916 -25.059; -48.434 -27.145; -48.473 -25.702; -48.480 -27.153; -48.481 -27.147; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.522 -27.132; -48.522 -27.153; -48.522 -27.216; -48.561 -25.889; -48.571 -25.958; -48.589 -26.997; -48.601 -26.775; -48.613 -26.774; -48.786 -28.563; -48.786 -28.773; -48.800 -26.028; -48.815 -28.773; -49.730 -29.350; -53.083 -35.000; -53.100 -35.000; -56.750 -36.250; -60.380 -38.911; -62.260 -38.700; -64.350 -42.500; **12. *Bougainvillia rugosa***: -45.423 -23.828; -48.613 -26.774; **13. *Campanularia agas***: -57.152 -38.078; -57.285 -38.100; -57.300 -38.160; -57.390 -38.020; -56.250 -37.250; -55.750 -37.250; -57.750 -38.250; -57.250 -38.250; -56.750 -38.250; -61.750 -39.750; -60.750 -39.750; -61.750 -40.250; -60.250 -40.250; -62.250 -41.250; -62.250 -41.750; **14. *Campanularia hincksii***: -45.153 -23.806; -48.522 -27.134; **15. *Campanularia subantarctica***: -62.250 -41.750; **16. *Cladocoryne floccosa***: -45.349 -23.746; -45.398 -23.728; -45.405 -23.819; -45.417 -23.823; -45.421 -23.828; -45.422 -23.828; -45.431 -23.831; -45.699 -24.099; -48.479 -27.134; -48.481 -27.147; **17. *Cladonema radiatum***: -45.397 -23.728; -45.421 -23.828; **18. *Clytia gracilis***: -39.921 -22.407; -41.839 -22.772; -41.868 -22.746; -42.018 -22.971; -43.159 -22.943; -43.200 -23.020; -43.201 -23.036; -43.906 -22.936; -44.168 -23.132; -44.409 -23.096; -44.606 -23.252; -44.623 -23.057; -44.816 -23.416; -44.833 -23.383; -44.839 -23.379; -44.888 -23.365; -45.020 -23.734; -45.032 -23.458; -45.100 -23.500; -45.133 -23.500; -45.150 -23.516; -45.216 -23.533; -45.216 -23.900; -45.233 -23.883; -45.303 -23.910; -45.311 -23.582; -45.349 -23.746; -45.383 -23.783; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.400 -23.733; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -45.412 -23.827; -45.416 -23.816; -45.417 -23.823; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; -45.431 -23.831; -45.433 -23.816; -45.434 -23.869; -45.443 -23.831; -45.699 -24.099; -46.369 -23.979; -47.910 -25.065; -47.912 -25.058; -47.916 -25.049; -47.924 -25.068; -48.316 -25.571; -48.322 -25.584; -48.363 -25.735; -48.374 -27.139; -48.374 -27.199; -48.374 -28.013; -48.433 -27.228; -48.477 -27.141; -48.479 -27.134; -48.480 -27.153; -48.481 -27.147; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.522 -27.132; -48.522 -27.153; -48.522 -27.216; -48.522 -27.997; -48.535 -25.578; -48.560 -25.862; -

48.561 -25.889; -48.563 -25.893; -48.589 -26.997; -48.601 -26.775; -48.603 -26.777; -48.616 -26.117; -48.767 -25.931; -48.786 -28.786; -48.815 -28.773; -49.730 -29.350; -49.732 -29.358; -53.083 -35.000; -53.100 -35.100; -53.366 -35.716; -54.883 -35.033; -55.234 -34.903; -53.366 -36.083; -57.616 -38.283; -55.750 -36.750; -57.250 -37.750; -56.250 -37.750; -57.750 -38.250; -57.250 -38.250; -61.750 -39.750; -61.750 -41.250; -61.250 -41.250; -61.690 -41.290; -64.000 -42.200; -60.750 -40.250; **19. Clytia hummelincki**: -45.421 -23.828; -45.431 -23.831; -48.536 -25.851; **20. Clytia linearis**: -44.283 -23.117; -44.409 -23.096; -44.839 -23.379; -45.032 -23.458; -45.237 -23.813; -45.349 -23.746; -45.366 -23.833; -45.397 -23.728; -45.400 -23.633; -45.405 -23.819; -45.412 -23.827; -45.417 -23.859; -45.421 -23.828; -45.422 -23.828; -45.431 -23.831; -45.443 -23.831; -45.471 -23.823; -45.510 -23.836; -45.699 -24.099; -47.910 -25.065; -48.322 -25.584; -48.514 -27.131; -48.561 -25.899; -48.589 -26.997; -48.603 -26.777; **21. Clytia noliformis**: -45.303 -23.910; -45.349 -23.746; -45.397 -23.728; -48.481 -27.147; -48.538 -25.844; -48.601 -26.775; -48.603 -26.777; **22. Corydendrum parasiticum**: -45.422 -23.828; **23. Cormorpha januarii**: -43.216 -22.883; -45.091 -23.533; -48.566 -27.433; -48.533 -27.446; -48.551 -27.559; -48.583 -27.600; -61.833 -39.116; -65.025 -42.616; -61.500 -39.070; -64.320 -42.520; -64.710 -42.640; **24. Coryne eximia**: -48.786 -28.563; -48.815 -28.773; -57.152 -38.078; -57.250 -37.750; -57.750 -38.240; -57.250 -38.250; -59.250 -38.750; **25. Coryne producta**: -45.421 -23.828; -45.422 -23.828; **26. Cryptolarella abyssicola**: -39.921 -22.407; **27. Dentitheca bidentata**: -45.425 -23.828; -45.466 -23.883; -48.363 -25.735; -48.589 -26.997; **28. Diphasia digitalis**: -44.346 -23.136; -44.399 -23.097; **29. Diphasia tropica**: -44.346 -23.136; -44.409 -23.096; -45.405 -23.819; -45.398 -23.728; -45.417 -23.823; -48.522 -27.142; **30. Dipurena reesi**: -45.422 -23.828; -64.950 -40.740; **31. Dynamena crisioides**: -44.882 -23.351; -45.100 -23.500; -45.150 -23.516; -45.348 -23.748; -45.349 -23.752; -45.398 -23.728; -45.400 -23.633; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -45.417 -23.823; -45.421 -23.828; -45.422 -23.828; -46.388 -23.975; -46.750 -24.166; -47.000 -24.383; -47.910 -25.065; -48.311 -25.573; -48.492 -27.129; -48.514 -27.131; -48.522 -27.196; -48.536 -25.851; -48.591 -25.978; **32. Dynamena dalmasi**: -37.588 -22.382; -40.826 -22.335; -41.947 -22.870; -44.346 -23.136; -44.339 -23.097; -44.409 -23.096; -45.461 -23.888; -48.433 -27.143; -48.433 -27.228; -48.522 -27.132; -48.522 -27.134; -48.522 -27.216; -48.522 -27.997; **33. Dynamena disticha**: -37.588 -22.382; -43.200 -23.020; -44.409 -23.096; -44.461 -23.229; -44.783 -23.366; -44.816 -23.416; -44.839 -23.379; -45.216 -23.533; -45.303 -23.910; -45.349 -23.752; -45.349 -23.746; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -45.417 -23.823; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; -45.431 -23.831; -45.443 -23.831; -45.471 -23.823; -45.510 -23.836; -45.666 -23.766; -46.116 -23.850; -48.311 -25.573; -48.363 -25.735; -48.374 -27.162; -48.374 -28.013; -48.433 -27.143; -48.433 -27.228; -48.434 -27.145; -48.434 -27.199; -48.464 -27.139; -48.464 -27.140; -48.464 -27.190; -48.464 -27.223; -48.477 -27.141; -48.479 -27.134; -48.481 -27.147; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.522 -27.132; -48.522 -27.134; -48.522 -27.153; -48.522 -27.216; -48.522 -27.997; -48.589 -26.997; -48.601 -26.775; -48.603 -26.777; -48.613 -26.774; -57.390 -38.020; -57.450 -38.080; -57.750 -38.250; **34. Dynamena quadridentata**: -44.409 -23.096; -44.816 -23.416; -45.349 -23.746; -45.400 -23.633; -45.408 -23.760; -45.409 -23.819; -45.417 -23.823; -45.421 -23.828; -45.510 -23.836; -45.666 -23.766; -48.363 -25.735; -48.479 -27.134; -48.510 -27.216; -48.522 -27.997; **35. Ectopleura crocea**: -43.150 -22.934; -46.369 -23.979; -46.388 -23.975; -46.750 -24.166; -46.783 -24.183; -46.788 -24.188; -46.966 -24.316; -47.000 -24.383; -47.000 -24.400; -47.116 -24.466; -47.900 -25.033; -47.916 -25.049; -47.950 -25.000; -48.311 -25.573; -48.473 -25.702; -48.508 -25.520; -48.510 -27.216; -48.514 -27.131; -48.532 -25.607; -48.538 -25.844; -48.560 -25.862; -48.561 -25.889; -48.571 -25.958; -48.613 -26.774; -48.616 -26.117; -48.767 -25.931; -48.786 -28.563; -48.786 -28.773; -48.815 -28.773; -49.730 -29.350; -49.734 -29.358; -55.750 -34.750; -57.250 -37.750; -57.750 -38.250; -59.250 -38.750; -67.680 -52.280; -68.720 -50.220; **90. Plumularia floridana**: -43.200 -23.020; -45.422 -23.828; -47.900 -25.033; **36. Ectopleura dumortieri**: -45.421 -23.828; -45.422 -23.828; **37. Ectopleura obypa**: -45.349 -23.746; **38. Eudendrium capillare**: -45.397 -23.728; -45.400 -23.750; -45.666 -23.766; **39. Eudendrium caraiuru**: -43.150 -22.934; -44.283 -23.117; -44.346 -23.136; -44.888 -23.365; -45.133 -23.500; -45.216 -23.533; -45.383 -23.783; -45.397 -23.728; -45.400 -23.633; -45.400 -23.816; -45.418 -23.824; -45.422 -23.827; -45.430 -23.833; -47.900 -25.033; -47.910 -25.065; -48.322 -25.584; -57.285 -38.100; -57.390 -38.020; **40. Eudendrium carneum**: -41.991 -23.006; -44.167 -23.134; -44.300 -23.016; -44.409 -23.096; -44.833 -23.383; -45.100 -23.500; -45.133 -23.500; -45.150 -23.516; -45.303 -23.910; -45.383 -23.783; -45.397 -23.728; -45.400 -23.633; -45.407 -23.812; -45.418 -23.824; -46.116 -23.850; -46.369 -23.979; -46.388 -23.975; -47.000 -24.383; -48.311 -25.573; -48.322 -25.584; -48.367 -27.450; -48.374 -27.162; -48.374 -27.199; -48.467 -27.400; -48.473 -25.702; -48.477 -27.141; -48.480 -27.153; -48.481 -27.147; -48.487 -25.517; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.522 -27.134; -48.522 -27.142; -48.522 -27.216; -48.530 -25.842; -48.538 -27.492; -48.550 -27.133; -48.560 -25.862; -48.561 -25.889; -45.561 -25.890; -48.563 -25.893; -48.567 -27.417; -48.567 -27.600; -48.589 -26.997; -48.786 -28.563; -48.786 -28.131; -48.786 -28.195; **41. Eudendrium merulum**: -48.500 -27.733; **42. Eudendrium pocaruquarum**:

-44.882 -23.351; -45.050 -23.416; -45.397 -23.728; -45.400 -23.750; **43. *Eudendrium ramosum***: -41.839 -22.772; -41.868 -22.746; -44.833 -23.383; -45.400 -23.816; -45.418 -23.824; -53.083 -35.000; -54.250 -34.750; -56.250 -37.750; -56.750 -37.750; -57.250 -38.250; -57.750 -38.250; -54.750 -38.750; -62.250 -41.250; **44. *Eutima sapinhoa***: -45.412 -23.627; -45.426 -23.654; -45.431 -23.682; **45. *Filellum contortum***: -56.440 -37.480; **46. *Gonothyraea loveni***: -57.450 -38.100; -57.750 -38.250; -58.580 -38.480; **47. *Grammaria abietina***: -54.250 -36.750; -56.250 -38.250; -55.250 -38.750; **48. *Gymnangium allmani***: -41.947 -22.870; **49. *Halecium beanii***: -57.285 -38.100; -57.390 -38.020; -53.750 -35.750; -53.250 -35.750; -55.750 -36.250; -55.250 -36.250; -53.750 -36.250; -55.250 -36.750; -54.750 -36.750; -56.250 -37.250; -55.750 -37.250; -56.750 -37.750; -56.250 -37.750; -55.750 -37.750; -57.750 -38.250; -57.250 -38.250; -56.750 -38.250; -56.250 -38.250; -59.250 -38.750; -57.750 -38.750; -55.750 -38.750; -55.250 -38.750; -54.750 -38.750; -58.580 -38.480; -61.750 -39.250; -60.250 -39.250; -57.250 -39.250; -60.250 -39.750; -59.750 -39.750; -57.250 -38.250; -62.732 -42.841; **50. *Halecium bermudense***: -40.826 -22.335; -45.423 -23.828; -48.433 -27.143; **51. *Halecium delicatulum***: -44.409 -23.096; -45.081 -23.520; -45.421 -23.828; -45.422 -23.828; -45.426 -23.829; -57.152 -38.078; -54.180 -36.660; -57.750 -38.250; -68.286 -54.866; **52. *Halecium dichotomum***: -45.081 -23.520; -45.422 -23.828; -45.408 -23.760; -48.374 -27.162; -52.766 -35.166; **53. *Halecium dyssymetrum***: -44.409 -23.096; -45.150 -23.516; -45.397 -23.728; -45.398 -23.728; -45.408 -23.760; -45.422 -23.828; -45.699 -24.099; -48.433 -27.228; -48.464 -27.140; -48.464 -27.190; -48.464 -27.223; -48.479 -27.134; -48.481 -27.147; -48.510 -27.216; -48.522 -27.132; -48.522 -27.134; -48.522 -27.153; -48.522 -27.216; -48.522 -27.997; **54. *Halecium lightbourni***: -43.200 -23.020; -48.374 -27.162; **55. *Halecium tenellum***: -45.303 -23.910; -45.405 -23.819; -45.409 -23.819; -45.412 -23.827; -45.421 -23.828; -45.422 -23.828; -45.431 -23.831; -48.480 -27.153; -48.510 -27.216; **56. *Halopteris carinata***: -46.784 -26.767; **57. *Halopteris constricta***: -45.398 -23.728; -45.421 -23.828; -45.423 -23.828; -64.010 -41.130; -64.010 -42.030; **58. *Halopteris diaphana***: -43.201 -23.036; -44.623 -23.057; -44.632 -23.233; -45.216 -23.533; -45.348 -23.748; -45.349 -23.746; -45.349 -23.752; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -45.422 -23.828; -45.431 -23.831; -45.666 -23.766; -46.116 -23.850; -48.589 -26.997; -48.601 -26.775; **59. *Halopteris polymorpha***: -41.947 -22.870; -44.346 -23.136; -44.409 -23.096; -45.081 -23.520; -45.412 -23.827; -45.417 -23.859; -45.421 -23.828; -45.422 -23.828; -45.431 -23.864; -45.471 -23.823; -48.363 -25.735; -48.433 -27.228; -48.433 -27.143; -48.522 -27.134; **60. *Hartlaubella gelatinosa***: -60.250 -39.250; -61.750 -40.250; -60.750 -40.250; -61.750 -40.750; -61.750 -41.250; -61.250 -41.250; **61. *Hebella scandens***: -44.399 -23.097; -44.409 -23.096; -45.348 -23.748; -45.398 -23.728; -45.405 -23.819; -45.408 -23.760; -45.417 -23.823; -45.434 -23.869; -46.248 -23.993; -48.477 -27.417; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.616 -26.117; -57.450 -38.080; -57.750 -38.250; **62. *Hincksella cylindrica***: -37.588 -22.746; -41.868 -22.746; -48.522 -27.134; -48.522 -27.196; -48.522 -27.997; **63. *Hydractinia uniformis***: -45.412 -23.851; **64. *Idiellana pristis***: -45.081 -23.520; -45.409 -23.819; -45.421 -23.828; -45.422 -23.828; -45.699 -24.099; -47.900 -25.033; -48.322 -25.584; -48.359 -25.547; -48.363 -25.735; **65. *Lafoea coalescens***: -37.588 -22.382; **66. *Lafoea dumosa***: -49.400 -31.083; -53.366 -36.083; -55.616 -38.366; -55.816 -39.083; -56.516 -51.316; -53.750 -35.750; -54.750 -36.750; -54.250 -36.750; -57.250 -38.250; -56.250 -38.250; -55.750 -38.750; -55.250 -38.750; -54.750 -38.750; -68.286 -54.866; **67. *Lafoeina amirantensis***: -41.868 -22.746; -43.906 -22.936; -44.816 -23.416; -45.412 -23.827; -45.666 -23.766; -45.699 -24.099; -48.374 -27.199; -48.510 -27.216; -48.589 -26.997; **68. *Leuckartiara octona***: -45.421 -23.828; **69. *Lovenella gracilis***: -48.514 -27.131; **70. *Lytocarpia canepa***: -57.075 -38.133; -54.750 -38.750; -55.750 -39.250; -55.500 -39.460; -55.750 -40.250; -57.250 -41.250; -54.100 -41.200; **71. *Lytocarpia tridentata***: -43.151 -22.895; -44.816 -23.416; -45.081 -23.520; -45.303 -23.910; -45.392 -23.829; -45.398 -23.728; -45.405 -23.819; -45.421 -23.828; -45.422 -23.828; -45.431 -23.864; -45.471 -23.823; -45.510 -23.836; -46.369 -23.979; -48.374 -28.013; -48.374 -27.199; **72. *Macrorhynchia grandis***: -41.947 -22.870; **73. *Macrorhynchia philippina***: -44.140 -23.139; -44.290 -23.020; -44.401 -22.977; -45.366 -23.833; -45.392 -23.829; -45.397 -23.728; -45.421 -23.828; -45.422 -23.828; -45.426 -23.829; -45.431 -23.864; -45.443 -23.831; -45.510 -23.836; -48.322 -25.584; -48.359 -25.547; -48.363 -25.735; -48.374 -27.199; -48.374 -27.232; -48.477 -27.141; -48.488 -26.180; -48.510 -27.216; -48.589 -26.997; **74. *Monostaechas quadridens***: -37.588 -22.382; -40.826 -22.335; -41.839 -22.772; -43.200 -23.020; -44.399 -23.097; -44.409 -23.096; -45.422 -23.828; -45.461 -23.888; -48.374 -27.199; -48.522 -27.216; -48.522 -27.997; -57.250 -38.250; **75. *Monothecha margareta***: -44.409 -23.096; -45.303 -23.910; -45.349 -23.746; -45.397 -23.728; -45.405 -23.813; -45.408 -23.760; -45.417 -23.823; -45.421 -23.828; -45.431 -23.831; -45.434 -23.869; -45.471 -23.823; -45.666 -23.766; -45.699 -24.099; -48.316 -25.572; -48.374 -27.162; -48.433 -27.143; -48.433 -27.228; -48.464 -27.139; -48.464 -27.223; -48.479 -27.134; -48.480 -27.153; -48.481 -27.147; -48.492 -27.129; -48.510 -27.216; -48.522 -27.142; -48.522 -27.216; -48.522 -27.997; -48.536 -25.851; -48.561 -25.889; -48.601 -26.775; -48.603 -26.777; **76. *Monothecha pulchella***: -57.152 -38.078; -57.285 -38.100; -57.250 -38.250; -64.000 -42.200; **77. *Nemalecium lighti***: -41.868 -22.746; -44.853 -23.414; -44.888 -23.365; -45.032 -23.458; -45.349 -23.752; -45.392 -23.829; -



45.398 -23.728; -45.405 -23.819; -45.408 -23.760; -45.412 -23.827; -45.417 -23.859; -45.418 -23.824; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; **78. ?*Nemertesia ciliata***: -45.052 -23.427; **79. *Nemertesia ramosa***: -46.784 -26.767; -55.560 -40.020; -63.116 -42.589; **80. *Obelia bidentata***: -43.906 -22.936; -45.349 -23.746; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -47.910 -25.065; -47.912 -25.058; -47.916 -25.049; -47.922 -25.017; -47.924 -25.068; -48.535 -25.578; -48.571 -25.958; -48.575 -25.929; -48.603 -26.777; -48.624 -25.559; -57.450 -38.100; -57.750 -38.250; -61.250 -39.250; -62.620 -41.150; -64.000 -41.400; -64.000 -42.000; -69.310 -51.520; **81. *Obelia dichotoma***: -41.838 -22.772; -41.867 -22.746; -42.018 -22.971; -43.158 -22.943; -43.200 -23.020; -43.906 -22.936; -44.283 -23.117; -44.346 -23.136; -44.399 -23.097; -44.409 -23.096; -44.816 -23.416; -44.865 -23.356; -44.888 -23.365; -45.032 -23.458; -45.052 -23.427; -45.100 -23.500; -45.237 -23.813; -45.303 -23.910; -45.348 -23.748; -45.349 -23.752; -45.349 -23.746; -45.366 -23.633; -45.392 -23.829; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.405 -23.813; -45.405 -23.819; -45.409 -23.819; -45.412 -23.827; -45.417 -23.823; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; -45.426 -23.829; -45.431 -23.831; -45.510 -23.836; -45.555 -23.795; -46.376 -23.969; -46.378 -23.969; -46.750 -24.166; -46.966 -24.316; -47.900 -25.033; -47.910 -25.065; -47.912 -25.058; -47.916 -25.049; -47.924 -25.068; -48.311 -25.573; -48.316 -25.571; -48.317 -25.574; -48.322 -25.582; -48.363 -25.735; -48.374 -27.162; -48.374 -27.199; -48.479 -27.134; -48.480 -27.153; -48.481 -27.147; -48.499 -27.749; -48.510 -27.216; -48.514 -27.131; -48.522 -27.216; -48.522 -27.134; -48.532 -25.607; -48.534 -27.571; -48.535 -25.578; -48.560 -25.862; -48.561 -25.889; -48.589 -26.997; -48.601 -26.775; -48.603 -26.777; -48.624 -25.559; -48.767 -25.931; -48.786 -28.563; -48.786 -28.773; -48.800 -26.028; -48.815 -28.773; -49.730 -29.350; -49.732 -29.358; -53.083 -35.000; -53.100 -35.000; -57.152 -38.078; -57.254 -38.105; -57.390 -38.020; -57.450 -38.100; -60.286 -38.919; -55.750 -36.250; -55.250 -36.250; -54.750 -36.250; -54.750 -36.750; -57.750 -38.250; -57.250 -38.250; -56.750 -38.250; -61.150 -39.030; -59.250 -38.750; -57.750 -38.750; -61.250 -39.250; -60.750 -39.250; -61.750 -39.750; -61.250 -39.750; -60.750 -39.750; -61.750 -40.250; -64.000 -42.000; **82. *Obelia geniculata***: -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -48.311 -25.573; -48.479 -27.134; -48.481 -27.147; -48.510 -27.216; -48.514 -27.131; -48.538 -25.844; -48.561 -25.889; -48.601 -26.775; -48.603 -26.777; -48.616 -26.117; -48.815 -28.773; -65.000 -42.660; -68.720 -50.220; -67.680 -52.280; **83. *Orthopyxis caliculata***: -44.839 -23.379; -45.366 -23.633; -45.400 -23.633; -48.479 -27.134; -48.480 -27.153; -48.492 -27.129; -48.514 -27.131; -48.561 -25.889; -48.589 -26.997; -48.601 -26.775; -48.603 -26.777; -48.616 -26.117; **84. *Orthopyxis sargassicola***: -44.283 -23.117; -44.409 -23.096; -44.816 -23.416; -45.349 -23.746; -45.397 -23.728; -45.398 -23.728; -45.405 -23.819; -45.408 -23.760; -45.417 -23.823; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; -45.431 -23.831; -45.471 -23.823; -45.555 -23.795; -46.783 -24.183; -48.374 -27.162; -48.374 -27.199; -48.433 -27.143; -48.464 -27.139; -48.464 -27.190; -48.464 -27.223; -48.479 -27.134; -48.481 -27.147; -48.492 -27.129; -48.514 -27.131; -48.601 -26.775; -48.603 -26.777; -48.613 -26.774; -48.616 -26.117; -48.815 -28.773; -53.100 -35.000; **85. *Parascyphus repens***: -64.010 -42.030; **86. *Parawrightia robusta***: -48.616 -26.117; -49.730 -29.350; **87. *Pennaria disticha***: -44.283 -23.117; -44.300 -23.016; -44.839 -23.379; -44.859 -23.416; -45.116 -23.723; -45.133 -23.500; -45.386 -23.803; -45.398 -23.728; -45.417 -23.823; -45.418 -23.824; -45.421 -23.828; -45.422 -23.828; -45.433 -23.831; -45.510 -23.836; -45.666 -23.766; -46.116 -23.850; -46.369 -23.979; -47.000 -24.383; -47.000 -24.400; -47.900 -25.033; -48.311 -25.573; -48.363 -25.735; -48.473 -25.702; -48.561 -25.889; -48.562 -27.123; -48.591 -25.978; -48.603 -26.777; -48.613 -26.774; **88. *Phialella belgicae***: -53.983 -34.600; -57.450 -38.100; -57.750 -38.250; -60.250 -39.250; -60.250 -39.750; **89. *Phialella chilensis***: -56.967 -35.167; -56.750 -35.250; -56.750 -35.750; -53.750 -35.750; -56.250 -38.250; **90. *Plumularia insignis***: -55.250 -35.250; -55.750 -35.750; -54.750 -38.750; -50.510 -43.550; -54.100 -41.200; **91. *Plumularia setacea***: -43.200 -23.020; -47.950 -29.381; -48.510 -27.216; -48.522 -27.132; -48.522 -27.997; -51.700 -33.216; -52.766 -35.166; -54.883 -35.033; -55.234 -34.903; -57.254 -38.105; -57.285 -38.100; -57.370 -38.170; -57.370 -38.283; -57.450 -38.100; -64.479 -42.950; -55.750 -34.750; -52.750 -35.250; -53.750 -35.750; -53.250 -35.750; -55.000 -36.450; -55.750 -36.250; -55.250 -36.250; -57.000 -37.000; -56.250 -37.250; -55.250 -37.250; -57.250 -37.750; -56.750 -37.750; -56.250 -37.750; -57.500 -38.150; -57.750 -38.250; -57.250 -38.250; -56.750 -38.250; -59.250 -38.750; -57.750 -38.750; -61.150 -39.030; -61.750 -39.250; -61.250 -39.250; -60.250 -39.250; -61.750 -39.750; -60.750 -39.750; -62.600 -41.100; -64.000 -41.500; -64.000 -42.200; -68.720 -50.220; -62.732 -42.841; **92. *Plumularia strictocarpa***: -44.285 -23.025; -44.888 -23.365; -45.303 -23.910; -45.392 -23.829; -45.412 -23.827; -45.421 -23.828; -45.422 -23.828; -45.431 -23.831; -47.910 -25.065; -48.481 -27.147; -48.601 -26.775; -53.100 -35.000; -65.517 -46.784; **93. *Pycnotheca mirabilis***: -45.303 -23.910; -48.374 -27.162; -48.374 -27.199; -48.374 -28.013; -48.479 -27.134; -48.481 -27.147; -48.510 -27.216; -48.601 -26.775; **94. *Ralpharia sactisebastiani***: -45.466 -23.883; **95. *Rhizogeton nudus***: -57.750 -38.240; **96. *Salacia desmoides***: -48.433 -27.143; -48.433 -27.228; -48.464 -27.140; -48.464 -27.190; -48.522 -27.132; -48.522 -27.134; -48.522 -27.142; -48.522 -27.153; -48.522 -27.216; -48.522 -27.997; **97. *Scandia mutabilis***: -44.888 -23.365; -45.434 -23.869; -45.417 -23.823; -48.311 -25.573; -48.514 -27.131;

**98. *Sertularella areyi***: -44.346 -23.136; -44.399 -23.097; -48.522 -27.132; -48.522 -27.134; -48.433 -27.143; -48.522 -27.153; -48.522 -27.216; -48.522 -27.997; **99. *Sertularella conica***: -41.947 -22.870; -45.153 -23.806; -45.405 -23.819; -48.479 -27.134; -48.510 -27.216; -57.750 -38.250; -57.250 -38.250; -56.250 -38.250; **100. *Sertularella cylindritheca***: -45.471 -23.823; **101. *Sertularella gaudichaudi***: -54.040 -36.200; -57.616 -38.283; -66.616 -51.316; -53.750 -35.750; -57.750 -38.250; -57.250 -38.250; -56.250 -38.250; -55.750 -38.750; -55.250 -38.750; -62.250 -41.750; **102. *Sertularella leiocarpa***: -47.950 -29.388; **103. *Sertularella ?polyzonias***: -40.826 -22.335; -53.366 -35.716; **104. *Sertularella tenella***: -37.588 -22.382; -44.409 -23.096; -48.433 -27.228; -48.434 -27.145; -48.464 -27.140; -48.522 -27.216; -48.522 -27.997; -48.522 -27.132; -48.666 -31.333; -49.525 -31.128; -53.100 -35.000; -53.366 -36.083; -54.883 -35.033; -55.234 -34.903; -55.616 -38.366; -57.152 -38.078; -57.218 -38.053; -57.254 -38.105; -57.390 -38.020; -57.750 -38.133; -53.750 -35.750; -55.750 -36.250; -55.250 -36.250; -53.750 -36.250; -55.750 -36.750; -55.250 -36.750; -56.250 -37.250; -57.750 -38.250; -57.250 -38.250; -56.250 -38.250; -57.750 -38.750; -62.250 -41.250; -61.750 -41.250; -62.250 -41.750; -63.116 -42.589; **105. *Sertularia distans***: -37.588 -22.382; -45.032 -23.458; -45.216 -23.533; -45.303 -23.910; -45.349 -23.746; -45.397 -23.728; -45.405 -23.819; -45.408 -23.760; -45.414 -23.853; -45.417 -23.823; -45.431 -23.831; -45.555 -23.795; -46.370 -23.997; -46.388 -23.975; -46.966 -24.316; -47.000 -24.383; -47.922 -25.017; -48.311 -25.573; -48.477 -27.417; -48.479 -27.134; -48.481 -27.147; -48.510 -27.216; -48.522 -27.132; -48.522 -27.134; -48.522 -27.153; -48.522 -27.216; -48.522 -27.997; -48.538 -25.844; -48.601 -26.775; -48.616 -26.117; **106. *Sertularia loculosa***: -44.409 -23.096; -44.816 -23.416; -45.349 -23.746; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.408 -23.760; -45.417 -23.823; -45.417 -23.859; -45.422 -23.828; -45.426 -23.829; -45.431 -23.831; -45.471 -23.823; -45.510 -23.836; -45.666 -23.766; -48.311 -25.573; -48.522 -27.134; -48.522 -27.997; **107. *Sertularia marginata***: -43.200 -23.020; -44.399 -23.097; -44.409 -23.096; -44.623 -23.057; -44.816 -23.416; -44.833 -23.383; -44.839 -23.379; -44.865 -23.350; -44.865 -23.356; -44.882 -23.351; -45.032 -23.458; -45.100 -23.500; -45.216 -23.533; -45.290 -23.737; -45.303 -23.910; -45.348 -23.748; -45.397 -23.728; -45.397 -23.746; -45.398 -23.728; -45.405 -23.819; -45.408 -23.760; -45.417 -23.823; -45.417 -23.859; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; -45.434 -23.869; -45.471 -23.823; -45.510 -23.836; -45.555 -23.795; -45.666 -23.766; -46.369 -23.979; -46.388 -23.975; -46.783 -24.183; -46.966 -24.316; -47.000 -24.383; -47.000 -24.400; -47.116 -24.466; -48.311 -25.573; -48.322 -25.584; -48.363 -25.735; -48.464 -27.190; -48.473 -25.702; -48.777 -27.141; -48.480 -27.153; -48.481 -27.147; -48.492 -27.129; -48.510 -27.216; -48.514 -27.131; -48.536 -25.851; -48.561 -25.889; -48.589 -26.997; -48.603 -26.777; -48.616 -26.117; **108. *Sertularia notabilis***: -45.417 -23.823; -46.248 -23.993; **109. *Sertularia rugosissima***: -45.666 -23.766; -45.408 -23.760; -46.370 -23.977; -48.311 -25.573; -48.601 -26.775; **110. *Sertularia tumida***: -48.363 -25.735; -48.510 -27.216; **111. *Sertularia turbinata***: -44.283 -23.117; -44.346 -23.136; -44.399 -23.097; -44.409 -23.096; -44.641 -23.229; -44.816 -23.416; -44.839 -23.379; -45.100 -23.500; -45.348 -23.748; -45.349 -23.746; -45.349 -23.752; -45.397 -23.728; -45.398 -23.728; -45.400 -23.633; -45.405 -23.819; -45.412 -23.827; -45.417 -23.823; -45.423 -23.828; -45.431 -23.831; -45.434 -23.869; -45.443 -23.831; -45.471 -23.823; -45.508 -23.860; -45.510 -23.836; -45.516 -23.833; -45.666 -23.766; -48.363 -25.735; -48.477 -27.141; -48.479 -27.134; -48.480 -27.153; -48.481 -27.147; -48.492 -27.129; -48.514 -27.131; -48.522 -27.196; -48.589 -26.997; -48.601 -26.775; **112. *Sphaerocoryne* sp.**: -48.510 -27.216; **113. *Stegopoma irregularis***: -57.152 -38.078; -55.750 -40.250; **114. *Stylactaria hooperi***: -45.375 -23.819; -45.422 -23.828; -45.421 -23.828; -45.405 -23.813; -45.422 -23.828; **115. *Symplectoscyphus flexilis***: -62.250 -41.750; **116. *Symplectoscyphus magellanicus***: -53.366 -36.083; **117. *Symplectoscyphus milneanus***: -64.010 -41.130; -64.010 -42.030; **118. *Symplectoscyphus subdichotomus***: -47.950 -29.381; -55.900 -37.567; -56.116 -38.066; -53.750 -35.750; -53.250 -35.750; -52.750 -35.750; -53.750 -36.250; -54.750 -36.750; -54.250 -36.750; -56.000 -37.550; -55.750 -37.750; -57.750 -38.250; -57.250 -38.250; -56.750 -38.250; -56.250 -38.250; -55.750 -38.750; -55.250 -38.750; -54.750 -38.750; -60.750 -40.250; -58.700 -42.700; -68.720 -50.220; -63.116 -42.589; -62.821 -42.786; **119. *Synthecium protectum***: -55.750 -35.750; -53.750 -36.250; -54.750 -36.750; -54.250 -36.750; -55.750 -37.750; -57.750 -38.250; -57.250 -38.250; -56.750 -38.250; -56.250 -38.250; -55.750 -38.750; -54.750 -38.750; -63.283 -42.468; -63.116 -42.589; -62.732 -42.841; -62.443 -43.035; **120. *Synthecium tubithecum***: -37.588 -22.382; -45.409 -23.819; **121. *Thyroscyphus marginatus***: -44.409 -23.096; -44.399 -23.097; **122. *Thyroscyphus ramosus***: -44.888 -23.365; -45.081 -23.520; -45.100 -23.500; -45.122 -23.525; -45.133 -23.500; -45.366 -23.833; -45.392 -23.829; -45.407 -23.812; -45.417 -23.823; -45.422 -23.828; -45.433 -23.616; **123. *Tulpa tulipifera***: -59.550 -43.583; -50.510 -43.550; -54.100 -41.200; **124. *Turritopsis nutricula***: -42.018 -22.971; -43.200 -23.020; -43.906 -22.936; -44.623 -23.057; -44.888 -23.365; -45.032 -23.458; -45.349 -23.746; -45.412 -23.827; -45.421 -23.828; -45.422 -23.828; -45.423 -23.828; -45.431 -23.831; -45.443 -23.831; -45.510 -23.836; -45.533 -23.823; -47.000 -24.400; -47.900 -25.033; -47.912 -25.058; -48.514 -27.131; -48.589 -26.997; -48.601 -26.775; -48.603 -26.777; **125. *Ventromma halecioides***: -43.159 -22.943; -44.401 -22.977; -44.606 -23.252; -45.349 -23.746; -45.397 -23.728; -45.405 -23.813; -45.405 -23.819; -45.408 -23.760; -45.412 -23.827; -45.421 -

23.828; -45.422 -23.828; -47.900 -25.033; -47.950 -25.000; -48.374 -27.162; -48.433 -27.143; -48.481 -27.147; -48.499 -27.749; -48.514 -27.131; -48.535 -25.578; -48.601 -26.775; -48.603 -26.777; **126.**  
**Zanlea costata:** -45.417 -23.823; **127. Zygophylax infundibulum:** -39.921 -22.407; **128. Zygophylax sibogae:** -40.000 -22.500; -40,500 -22.750; **129. Zyzzyzus warreni:** -45.386 -23.803; -45.412 -23.827; -45.421 -23.823; -45.421 -23.828; -45.426 -23.837; -45.433 -23.827; -45.440 -23.827; -45.521 -23.831; -48.510 -27.216.