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Multivariate analyses of Antarctic and sub-Antarctic seaweed distribution patterns: An evaluation of the role of the Antarctic Circumpolar Current

Paola Franzan Sanches [a,*], Franciane Pellizzari [b], Paulo Antunes Horta [c]

[a] Universidade de São Paulo, Laboratório de Manejo, Ecologia e Conservação Marinha, Instituto Oceanográfico, Praça do Oceanográfico, 191, CEP. 05508-120 São Paulo-SP, Brazil
[b] Universidade Estadual do Paraná, Campus Paranaguá, Laboratório de Ficologia e Qualidade de água do Mar, Rua Comendador Correia Júnior, 117, CEP. 83203-280 Paranaguá-PR, Brazil
[c] Programa de Pós Graduação em Ecologia, Centro de Ciências Biológias Universidade Federal de Santa Catarina, CEP. 88040-970 Florianópolis-SC, Brazil

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ABSTRACT

Biogeographic barriers and ecological corridors are fundamental in defining macroecological and evolutionary processes. Ocean circulation, considering present and past patterns of continental drift, can isolate or connect many groups of marine organisms, including seaweeds. These benthic organisms present spores and propagules as planktonic stages that drift with currents and or tides, and have been a sensible indicator of changes to biogeographical distribution patterns. Phycological studies have been exhaustive in the sub-Antarctic and Antarctic seaweed communities. However, the role of the Antarctic Circumpolar Current (ACC) in shaping marine phytogeographic diversity has been poorly investigated. The ACC connects the major world oceans and redistributes oceanic properties, such as heat, salt, and nutrients, consisting of three major circumpolar fronts (in order of north to southward): the Sub-Antarctic Front (SAF), the Antarctic Polar Front (PF), and the Southern Antarctic Circumpolar Front (SACF). This paper's aim is to understand the role of the ACC fronts as a constraint on seaweed distribution patterns in different taxonomic levels, in relation to the southern Sub-Tropical areas, as well as to compare sections connected with South America (1: north), influenced by the Ross Sea Gyre (2: Western Antarctica Peninsula) and by the Weddell Sea Gyre (3: Eastern Antarctica Peninsula). nMDS showed differences in the distributional patterns of species and genera in relation to the zones and sections. The predicted latitudinal gradient of species richness was observed, and by comparing biogeographic zones, two main clusters were observed: Sub-tropical and Sub-Antarctica; and Polar Front (Antarctic Peninsula) and SACF (areas surrounding continental Antarctica), suggesting, for this sort of macroscale analysis, that ACC still has a role of “watershed barrier”. However, a lower dissimilarity (higher similarity) was observed between the 2nd (Eastern Antarctica Peninsula – EAP – or under influence of the Weddell Sea Gyre, and some sub-Antarctic islands as South Orcadas, South Georgia and Crozet Archipelago) and the 1st sectors (Chilean and Argentinean Patagonia and surrounding islands, Falklands, South Shetlands and including Antarctic Peninsula). When considering recently reported changes in diversity patterns of these locations, this result could demonstrate the existence of a clear species distributional flux, despite evidence of the ACC being a limit to dispersal. Therefore, this contribution has used previously published data to provide a tool for monitoring future biogeographical changes to the flora and fauna of this region of the Antarctic and sub-Antarctic areas due to changes in biogeographical distribution, resulting either from natural dispersion due to global meteoceanographic changes, and or biological invasions related to anthropogenic activities. We could be witness to a period of changes in Antarctic diversity, suggesting that Antarctica may not be as isolated as was once thought.

1. Introduction

For many decades, species distribution patterns have been guiding scientists toward an understanding of the planet's history, climate and geological changes. In marine environments, the role of currents is still being discussed (Myers, 1997) as biogeographical barriers in terms of limiting dispersal, acting as physical barriers, or serving as ecological filters based on specific oceanographic properties of the temperature, salinity, density, pH, or sea surface height. Conversely, they can also function as ecological corridors, providing a connection between many geographic areas and distinct ecosystems (Treml et al., 2008) by transporting larvae, spores, and propagules of different groups of organisms (Barber et al., 2000), including seaweeds.

* Corresponding author.
E-mail addresses: paolafsanches@gmail.com, pfranzan@usp.br (P.F. Sanches), francianep@yahoo.com, franciane.pellizzari@unespar.edu.br (F. Pellizzari), pahorta@ccb.ufsc.br (P.A. Horta).

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Biogeographic studies of macroalgae started with Lamouroux in 1826, who correlated diversity and latitudinal changes in species composition (Garbary, 1987). Descriptive taxonomy and species lists comparing similarities among areas were the basis of primary techniques and assessments (Camus, 2001). Theoretical experimentation introduced tests of limiting factors for distribution, including physiological tolerance (Garbary, 1987; Zacher et al., 2007; Wiencke and Dieck, 1990). Biomolecular approaches allowed the establishment of phylogenetic relationships, which improved our understanding of algal evolutionary relationships (Macaya and Zuccarello, 2010; Teske et al., 2011).

Due to historical and practical limitations (i.e., problems related to sampling effort and lack of feasible alternatives in methodology), the diversity of Antarctic seaweeds has been underestimated (Clayton, 1994; Oliveira et al., 2009). Most seaweeds of this particular region have no specific keys, and as a result, some taxa have been misidentified. Even so, as well as physiology and chemistry (Wiencke, 1988; Gómez, 2001; Amsler et al., 2005a, 2005b), diversity studies are broad (Lamb and Zimmerman, 1977; Neushul, 1964; Zielinski, 1981; Ramirez and Villouta, 1984; Cormaci et al., 1992; Papenfuss, 1964; Pedrini, 1992; Westermeier et al., 1992; Chung et al., 2000; Wiencke and Clayton, 2002; Quartino et al., 2005; Oliveira et al., 2009; Pellizzari et al., in press). By now, Antarctica has about 130 species of macroalgae (Wincke and Clayton, 2002), including 75 species of Rhodophyta, 25 Phaeophyceae and 15 Chlorophyta (Skottsberg, 1960), with ca. 30% of these taxa being endemic. The endemism is highest among Phaeophyceae, (Ascoseirales) and some genera such as *Gainia*, *Antarcticothamnion*, *Notophycus*, *Himantothallus*, *Cystophaera*, *Phaeurus*, *Lambia* and *Lola* (Rakusa-Suszczewski and Zieliński, 1993; Clayton, 1994; Wiencke and Clayton, 2002).

However, biogeographic approaches related to seaweed distributional patterns observed in high latitudes in the Southern Hemisphere are scarce (Hommersand et al., 2009). Thus, previous studies attempting to address the biogeography of this group have been conducted in different regions, at various scales, and have used different sources of data (van den Hoek, 1975, 1984; Santelices, 1980; Bolton and Stegenga, 1987, 1990; Stegenga et al., 1997; Bolton et al., 2004; Kerswell, 2006).

As traditionally discussed since Knox (1960), oceanic circulation patterns, in most cases, represent one of main drivers of biogeographical boundaries. Although much is known about the role of marine currents distributing seaweeds and generating biogeographic patterns in middle southern latitudes (Bolton, 1994), few studies have been conducted in the Antarctic and sub-Antarctic regions.

The Polar Front (called the Antarctic Convergence in the older literature) is the strongest of a series of eastward-flowing jets of the Antarctic Circumpolar Current (ACC). The ACC consists of three major circumpolar fronts, which are, from north to south, the sub-Antarctic Front (SAF), the Antarctic Polar Front (PF), and the Southern Antarctic Circumpolar Current Front (SACCF). The fronts separate distinct surface water masses and are associated with strong currents and strong lateral gradients in temperature, salinity, and biological productivity (Moore and Abbott, 2000, 2002). The PF is also a strong barrier to free north–south exchange of water, and thus represents a potential distinctive biogeographical discontinuity. Associated with this is a high degree of species-level endemism in the Antarctic marine invertebrate and fish faunas and seaweeds, which is indicative of a long period of evolution in relative isolation. The only exceptions to this are the faunas of the midwater and the deep-sea, in which the Polar Front appears to not have been a barrier. However, the traditional view of Antarctica and the surrounding Southern Ocean as an isolated system is now being challenged by the recent discovery of adult North Atlantic spider crabs and larvae of subpolar marine invertebrates at the Antarctic Peninsula (Clarke et al., 2005). These observations question whether the well-described biogeographical similarities between the benthic fauna of the Antarctic Peninsula and the Magellan region of South America result from history (i.e., the two regions were once contiguous), or from a previously unrecognized low level of faunal exchange. Clarke et al. (2005), suggest that such exchange might be influenced by regional climate change, and also could be exacerbated by changes in human impact. Regarding seaweeds, Pellizzari et al. (in press) also suggest that the higher number of taxa recorded in the South Shetland Islands compared to previous studies in Antarctica could not be only associated with past sampling failure, but also with possible changes in connectivity patterns of the Southern Ocean and Antarctica, natural or otherwise.

The complex system of fronts of the northern boundaries of the Southern Ocean is defined by the interaction of the ACC with northern oceanic systems (Atlantic, Indian and Pacific oceans). The onset of the ACC is related to the break-up of Gondwana and, in particular, to the separation of Australia from Antarctica, and of South America from the Antarctic Peninsula. The precise dates for these events are still debated, but are generally considered to be ca. 25 million years before present. This event was crucial in determining the thermal properties, sea surface height and consequently the biogeographical isolation of the Southern Ocean. Until the past decade, no evidence was found for the north–south exchange of macroalgae species in this area. However, distributional influences of the ACC were demonstrated for marine invertebrates and crustaceans (Clarke et al., 2005). Pierrat et al. (2013) also showed that this barrier was insufficient in preventing the dispersal of bivalves. On the other hand, Barnes et al. (2006) showed that the PF virtually guarantees endemism with no establishment of exotic species in these high latitudes.

Ivar do Sul et al. (2011) reported that fishing operations in the Southern Ocean were identified as the major source of marine debris. Depending on the type of debris, plastics from lower latitudes may easily cross the PF, providing a possible link for plastic marine debris or alien species between Antarctica and South America (the closest intercontinental connection). Following Barnes et al. (2006) ice shelf and icebergs forced the evolution of a distinct biota adapted to conditions imposed by the ACC, or by isolation. These two papers show that connectivity exists, but also the barrier does. Thus, morphological, reproductive, and physiological characteristics, which determine species tolerances to environmental conditions, were susceptible to evolutionary pressure and were, ultimately, reflected in the phylogenetic relationships among them (Verbrugen et al., 2009). In mobile marine taxa (spores, or propagules, in the case of seaweeds), at all stages of their life cycle, there is evidence of mechanisms that drive diversification serving more as filters to evolution than barriers (Boehm et al., 2013). Thus, relationships among ocean circulation, marine barriers, dispersal potential, and tolerances to environmental conditions combined with selective pressures are possibly leading to species diversification patterns (Floeter et al., 2008).

In this context, Verbrugen et al. (2009) questioned whether "species distribution is restricted to an ocean by local environmental limits, or by a species intrinsic distribution limit." It is well known that latitudinal gradients determine richness in both marine and terrestrial environments. However, according to Kerswell (2006), seaweeds do not always respond to this pattern. Moreover, polar organisms are more tolerant to adverse and extreme environmental conditions than tropical organisms (Peck, 2005). It is worthy to note that some studies using molecular markers (Hommersand et al., 2009; Medeiros, 2013) are revealing that cryptic taxa previously listed in both Maritime Antarctica and South America, attributed to the genera *Plocamium*, *Ulothrix* and even *Iridaea*, are in fact cryptic species representing distinct taxonomic entities (Pellizzari et al., in press).

Therefore, this contribution aims to discuss if the ACC would constitute a true barrier to present-day seaweed dispersion, and whether there might be differences in species compositions among the three major ACC circumpolar fronts (SAF, PF and SACCF). Finally, we aim to verify the putative influence of ACC fronts on the species, genera, family and order composition of the Rhodophyta, Phaeophyceae and Chlorophyta, based on previous checklists of benthic Antarctic and