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Bryozoan diversity around the Falkland and South Georgia Islands: Overcoming Antarctic barriers



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Blanca Figuerola^{a,*}, David K.A. Barnes^b, Paul Brickle^{c, d, e}, Paul E. Brewin^{d, f, g}

^a Biodiversity Research Institute (IRBio), Faculty of Biology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Catalonia, Spain

^b British Antarctic Survey (BAS), Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

^c South Atlantic Environmental Research Institute (SAERI), Box 609, Stanley, FIQQ 1ZZ, South Atlantic, Falkland Islands

^d Shallow Marine Surveys Group (SMSG), 2 Philomel Pl, Stanley, FIQQ 1ZZ, South Atlantic, Falkland Islands

^e School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

^f Directorate of Natural Resources - Fisheries, Falklands Islands Government, PO Box 598, Stanley, South Atlantic, FIQQ 1ZZ, Falkland Islands

^g Government of South Georgia & the South Sandwich Islands, Government House, Stanley, FIQQ 12Z, South Atlantic, Falkland Islands

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ABSTRACT

There are a number of remote archipelagos distributed between 45 and 60 °S. The biota of these islands provide useful information to describe and understand patterns in biodiversity and biogeography as well as potential impacts of climate change on marine ecosystems. They are in key locations either side of the Polar Front but also have limited influence from human activities. Here we investigate one taxon, bryozoans, on South Atlantic shelf habitats of the Falkland (FI) and the sub-Antarctic island of South Georgia (SG). We present new data on spatial distribution in these islands, as well as an analysis of the bryozoological similarities between these and neighbouring regions. A total of 85 species of cheilostome bryozoans (351 samples) were found, belonging to 33 genera, including 18 potentially new genera and 23 new species. Remarkably 65% and 41% of species were reported for the first time at FI and SG, respectively. The highest and the lowest value of species richness and species/genus ratio were found at East (EFI) and West Falkland (WFI), respectively, likely showing a tendency for stronger intrageneric competition. New data from this study were jointly analysed with data from the literature and existing databases, revealing new bathymetric ranges in 32 species. The biogeographic affinities of the bryozoans found give further evidence of the hypothesis of sequential separation of Gondwana and support the changing concept that although the Polar Front acts as a circumpolar biogeographic barrier it is not as impermeable as originally thought. Potential dispersal mechanisms are also discussed.

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1. Introduction

The Southern Ocean (SO) represents 8% of the world's ocean surface area. Its northernmost limit is the Polar Front (PF), which is the strongest jet of the Antarctic Circumpolar Current (ACC). The continental shelves of several archipelagos are distributed around the SO, to the north and south and even across the PF. These island biotas can inform about biodiversity, biogeography and potential impacts of climate change on southern polar marine ecosystems, partly due to limited influence from human activities (e.g. Hogg et al., 2011). However, there is a scarcity of biodiversity and biogeographical baseline studies in the surrounding SO. These data

* Corresponding author.

E-mail address: bfiguerola@gmail.com (B. Figuerola).

are starting points for monitoring and rapidly assessing changes associated with threats such as climate change, the overexploitation of living resources and the establishment of invasive marine species (Orensanz et al., 2002; Kaiser et al., 2013).

Among these isolated land masses, the Falkland Islands (FI) are located on the eastern Patagonian shelf (500 km from the nearest continent), on the northern side of the PF. The archipelago consists of two main islands (East (EFI) and West Falkland (WFI)) and about 800 smaller islands. Their southeastern coasts are influenced by cold nutrient-rich waters from the northward flowing Falkland Current which originates from the ACC, and the northwestern coasts by temperate waters from the Argentine Drift, leading to differences on biodiversity between the two regions (Arkhipkin et al., 2013).

South of the PF, the island of South Georgia (SG) is located



1290 km south east of the FI and is part of the Scotia Arc (tips of a subsurface mountain chain linking the Andes and the Antarctic Peninsula). These archipelagos are thought to be a transitional region between South America and Antarctica, contrasting with the traditional view of Antarctica as an isolated area due to the ACC acting as a semi-porous barrier to southward transport (e.g. Arntz et al., 2005; Barnes, 2005). Considering its age, size and remoteness SG is considered a biodiversity hotspot in the SO, partly driven by its proximity to the ACC (rich in nutrients), its age, large shelf area and intersecting position between major faunas (Hogg et al., 2011). However, sea surface temperatures around this remote sub-Antarctic island are amongst the world's fastest warming waters (Whitehouse et al., 2008).

Bryozoans, a phylum of clonal and colonial invertebrates, are a poorly studied member of SO benthos (Moyano, 1982; López-Gappa, 2000; Figuerola et al., 2012), despite being abundant, speciose, ubiquitous and important members of many benthic communities. Their colonies can form three-dimensional structures providing complex habitats, nurseries and substrate for a wide range of marine organisms (Hayward, 1995). In particular, bryozoan-rich faunas of the shelf habitats of FI and SG remain understudied (Hastings, 1943; Hayward, 1980; Bastida et al., 1992; Barnes, 2000; Barnes and De Grave, 2001) and new species continue to be described regularly (e.g. Wright et al., 2007; Hayward and Winston, 2011).

The objectives of the current research are a) to present new data on species occurrence and richness of cheilostome bryozoans from the poorly known FI and SG, and, b) to understand the spatial relationships within these geographic regions. We hypothesize that there will be differences in assemblage structure between these two archipelagos separated by the PF, but there is also likely to be some genuine sharing of species (along with those around Antarctica). This work will contribute to governmental biodiversity and marine managment initiatives of the Falkland Island Government and the Government of South Georgia & the South Sandwich Islands.

2. Materials and methods

New samples were collected during six SCUBA diving surveys carried out in the FI at about 8–12 m depth (November–December 2014). Collections were made by hand. Additional inshore shallow samples from the FI were collected during a Falkland Island Government (FIG) commissioned survey in 1996 (ICON, 1996) SCUBA diver survey. Other FI inshore samples were collected haphazardly at various times by the Shallow Marine Surveys Group (SMSG) during routine ecological diver surveys. FI shelf samples were obtained from the FIG Fisheries Department specimen collection, collected by scientific observers on commercial fishing bottom trawling vessels around the FI shelf (2008–2010). Samples from SG were collected by hand during a SCUBA diver survey in November 2010, by the SMSG (Brewin and Brickle, 2011). All sampling sites were georeferenced by GPS and depth was registered at each station (Fig. 1; Table 1).

2.1. Species identification and literature data

The colonies of bryozoans were preserved in 96% ethanol for further taxonomic identification. Samples collected were identified to the lowest taxonomic level possible using binocular microscopy. Taxonomic identifications were made using existing literature: d'Orbigny (1842), Busk (1884), Waters (1904), Hastings (1943), López-Gappa (1982), López-Gappa and Lichtschein (1990), Hayward (1995), López de la Cuadra and García-Gómez (2000), Branch and Hayward (2005) and Hayward and Winston (2011). Some literature data regarding bathymetric ranges and biogeographic distribution of the studied species were obtained from Busk (1884), Hastings (1943), López-Gappa (1982), López-Gappa (2000), López-Gappa and Lichtschein (1990), Branch and Hayward (2005), Hayward and Winston (2011) and Figuerola et al. (2014), as well as from the Antarctic Biodiversity Information Facility (ANTABIF; www.biodiversity.aq; Van de Putte et al., 2016) and the Global Biodiversity Information Facility databases (GBIF; www.gbif.org) (Table 2).

2.2. Statistics

Number of species was used to estimate biodiversity (S, species richness) and species/genus ratios (S/G) were determined for EF and WF, shelf areas off FI (OFI) and SG. These supported additional biogeographic comparisons in addition to just using species composition and to infer levels of competitive interactions among species within genera and/or diversification rates (Table 3). A low species/genus ratio may be interpreted as a result of a strong intrageneric competition as congeneric species have similar ecological requirements, thus limiting congeneric coexistence (Webb et al., 2002). Another hypothesis is that few genera could manage to survive and occupy the highest latitude regions and diversify at higher rates there than they do in low latitudes (highlatitude diversification hypothesis; Weir and Schluter, 2007). Expected species richness was estimated from species accumulation curves. Chao2 and Jacknife1 richness estimators were used (Krebs, 1999). Expected species richness of FI was also estimated for the 6 dive surveys with similar sampling effort and depth by comparing the number of species per locality. Bryozoan species discovery rates per effort for FI and SG were also calculated (Table 4).

Data presented here from FI and SG were analysed together with previous data from Southern Argentina and compared to other provinces (Southern Chile and Tierra del Fuego) and regions. Previously considered boundaries in the South American Region are: northern - Valdez Peninsula on the east coast and Taitao Peninsula on the west coast. Other cold-temperate regions analysed were: the Sub-Antarctic region (Provinces: South Georgia, Bouvet, Prince Edward and Kerguelen), the Antarctic Region and the New Zealand-Australian Region (Provinces: Tasmania, New Zealand and Antipodes) (see Briggs and Bowen, 2012). Data considered were those from shallow waters (average depths of about 200 m). Species were checked for name changes prior to analyses. Species/genus ratios (S/G) were determined for biogeographic regions. Similarity between regions was calculated on presence/absence data using Bray-Curtis similarity index. Bray-Curtis index was chosen, as one of the most widely employed indices, being equivalent to the Sörensen index for presence-absence matrices (Clarke et al., 2006). Singlelinkage clustering was used to graphically display Bray-Curtis similarity matrices. Biogeographic regions for each species found in the current study and species from the Southern Argentina are detailed in Appendix A. In order to verify that the defined groups were statistically supported, we performed an analysis of similarity (ANOSIM), which does not require normal distributional data. The ANOSIM randomization test compares within- and between-group similarity of elements measured by the Bray-Curtis index and calculates a global R statitistic. The resulting *R*-value ranges between 0 and 1, with high values indicating a large degree of discrimination among groups (Clarke and Green, 1988). All statistical analyses were performed using Vegan software (R version 3.1.2; R Core Team, 2014).

3. Results

A total of 85 species of cheilostome bryozoans were found (in

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