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Blanca Figuerola, David K.A. Barnes, Paul Brickle, Paul E. Brewin



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1 **Bryozoan diversity around the Falkland and South Georgia Islands:**
2 **overcoming Antarctic barriers**

3 **Blanca Figuerola^{1*}, David K. A. Barnes², Paul Brickley^{3,4,5}, Paul E. Brewin^{4,6,7}**

4 ¹Biodiversity Research Institute (IRBio), Faculty of Biology, University of Barcelona, Av. Diagonal 643, 08028
5 Barcelona, Catalonia, Spain

6 ²British Antarctic Survey (BAS), Natural Environment Research Council, High Cross, Madingley Road,
7 Cambridge CB3 0ET, UK

8 ³South Atlantic Environmental Research Institute (SAERI), Box 609, Stanley, Falkland Islands, FIQQ 1ZZ,
9 South Atlantic

10 ⁴Shallow Marine Surveys Group (SMSG), 2 Philomel Pl, Stanley, Falkland Islands, FIQQ 1ZZ, South Atlantic

11 ⁵School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

12 ⁶Directorate of Natural Resources - Fisheries, Falklands Islands Government, PO Box 598, Stanley, Falkland
13 Islands, FIQQ 1ZZ, South Atlantic

14 ⁷Government of South Georgia & the South Sandwich Islands, Government House, Stanley, Falkland Islands,
15 FIQQ 1ZZ, South Atlantic

16 *Email: bfiguerola@gmail.com
17

18 **ABSTRACT:** There are a number of remote archipelagos distributed between 45-60°S.
19 The biota of these islands provide useful information to describe and understand
20 patterns in biodiversity and biogeography as well as potential impacts of climate change
21 on marine ecosystems. They are in key locations either side of the Polar Front but also
22 have limited influence from human activities. Here we investigate one taxon,
23 bryozoans, on South Atlantic shelf habitats of the Falkland (FI) and the sub-Antarctic
24 island of South Georgia (SG). We present new data on spatial distribution in these
25 islands, as well as an analysis of the bryozoological similarities between these and
26 neighbouring regions. A total of 85 species of cheilostome bryozoans (351 samples)
27 were found, belonging to 33 genera, including 18 potentially new genera and 23 new
28 species. Remarkably 68% and 41% of species were reported for the first time at FI and
29 SG, respectively. The highest and the lowest value of species richness and
30 species/genus ratio were found at East (EFI) and West Falkland (WFI), respectively,
31 likely showing a tendency for stronger intrageneric competition. New data from this
32 study were jointly analysed with data from the literature and existing databases,
33 revealing new bathymetric ranges in 32 species. The biogeographic affinities of the
34 bryozoans found give further evidence of the hypothesis of sequential separation of
35 Gondwana and support the changing concept that although the Polar Front acts as a
36 circumpolar biogeographic barrier it is not as impermeable as originally thought.
37 Potential dispersal mechanisms are also discussed.

38
39 **KEY WORDS:** Southern Ocean; Marine ecology; Benthos; Biodiversity;
40 Biogeography; Spatial patterns

44

INTRODUCTION

45 The Southern Ocean (SO) represents 8% of the world's ocean surface area. Its
46 northernmost limit is the Polar Front (PF), which is the strongest jet of the Antarctic
47 Circumpolar Current (ACC). The continental shelves of several archipelagos are
48 distributed around the SO, to the north and south and even across the PF. These island
49 biotas can inform about biodiversity, biogeography and potential impacts of climate
50 change on southern polar marine ecosystems, partly due to limited influence from
51 human activities (e.g. Hogg et al. 2011). However, there is a scarcity of biodiversity and
52 biogeographical baseline studies in the surrounding SO. These data are starting points
53 for monitoring and rapidly assessing changes associated with threats such as climate
54 change, the overexploitation of living resources and the establishment of invasive
55 marine species (Orensanz et al. 2002, Kaiser et al. 2013).

56

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

64

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

76

77 Bryozoans, a phylum of clonal and colonial invertebrates, are a poorly studied
78 member of SO benthos (Moyano 1982, López-Gappa 2000, Figuerola et al. 2012),
79 despite being abundant, speciose, ubiquitous and important members of many benthic
80 communities. Their colonies can form three-dimensional structures providing complex
81 habitats, nurseries and substrate for a wide range of marine organisms (Hayward 1995).
82 In particular, bryozoan-rich faunas of the shelf habitats of FI and SG remain
83 understudied (Hastings 1943, Hayward 1980, Bastida et al. 1992, Barnes 2000, Barnes
84 & Grave 2001) and new species continue to be described regularly (e.g. Wright et al.
85 2007, Hayward & Winston 2011).

86
87 The objectives of the current research are a) to present new data on species
88 occurrence and richness of cheilostome bryozoans from the poorly known FI and SG,
89 and, b) to understand the spatial relationships within these geographic regions. We
90 hypothesize that there will be differences in assemblage structure between these two
91 archipelagos separated by the PF, but there is also likely to be some genuine sharing of
92 species (along with those around Antarctica). This work will contribute to governmental
93 biodiversity and marine management initiatives of the Falkland Island Government and
94 the Government of South Georgia & the South Sandwich Islands.

95

96

MATERIALS AND METHODS

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

Species identification and literature data

109
110 The colonies of bryozoans were preserved in 96% ethanol for further taxonomic
111 identification. Samples collected were identified to the lowest taxonomic level possible
112 using binocular microscopy. Taxonomic identifications were made using existing
113 literature: d'Orbigny (1842), Busk (1884), Waters (1904), Hastings (1943), López
114 Gappa (1982), López Gappa & Lichtschein (1990), Hayward (1995), López de la
115 Cuadra & García-Gómez (2000), Branch & Hayward (2005) and Hayward & Winston
116 (2011).

117
118 Some literature data regarding bathymetric ranges and biogeographic
119 distribution of the studied species were obtained from Busk (1884), Hastings (1943),
120 López Gappa (1982, 2000), López Gappa & Lichtschein (1990), Branch & Hayward
121 (2005), Hayward & Winston (2011) and Figuerola et al. (2014), as well as from the
122 Antarctic Biodiversity Information Facility (ANTABIF; www.biodiversity.aq; Van de
123 Putte et al. 2016) and the Global Biodiversity Information Facility databases (GBIF;
124 www.gbif.org) (Table 2).

125

Statistics

126
127 Number of species was used to estimate biodiversity (S , species richness) and
128 species/genus ratios (S/G) were determined for EF and WF, shelf areas off FI (OFI) and
129 SG. These supported additional biogeographic comparisons in addition to just using
130 species composition and to infer levels of competitive interactions among species within
131 genera and/or diversification rates (Table 3). A low species/genus ratio may be
132 interpreted as a result of a strong intrageneric competition as congeneric species have
133 similar ecological requirements, thus limiting congeneric coexistence (Webb et al.
134 2002). Another hypothesis is that few genera could manage to survive and occupy the
135 highest latitude regions and diversify at higher rates there than they do in low latitudes
136 (high-latitude diversification hypothesis; Weir & Schluter 2007). Expected species
137 richness was estimated from species accumulation curves. Chao2 and Jackknife1 richness
138 estimators were used (Krebs 1999). Expected species richness of FI was also estimated
139 for the 6 dive surveys with similar sampling effort and depth by comparing the number
140 of species per locality. Bryozoan species discovery rates per effort for FI and SG were
141 also calculated (Table 4).

142

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

167

168

RESULTS

169 A total of 85 species of cheilostome bryozoans were found (in 351 samples;
170 including species of the genera *Austroflustra* and *Ogivalia*, not satisfactorily assigned to
171 existing families). The species recorded belonged to 29 families and 33 genera, and
172 were found at depths between 2 and 345 m within an area of the southwestern Atlantic
173 and Southern Ocean between 49° and 54° S, and between 35° and 63° W (Table 1 and 2;
174 Fig. 1). The list of the samples includes 18 potentially new genera and 23 new species.
175

176 The most diverse family was Microporellidae with 10 species (15.6% of total
 177 species found), followed by Smittinidae (9 species, 14.1%), Candidae and Hippothoidae
 178 (6 each, 9.4 %), Arachnopusiidae and Bugulidae (4 each, 6.2%), Exochellidae and
 179 Phidoloporidae (3 each, 4.7%), Celleporidae, Chaperiidae and Microporidae (2 each,
 180 3.1%) and Aeteidae, Aspidostomatidae, Cellariidae, Electridae, Escharinidae,
 181 Flustridae, Foveolariidae, Inversiulidae, Membraniporidae and Romancheinidae (1
 182 each, 1.6%). *Fenestrulina* and *Smittina*, both with 8 species, were the most abundant
 183 genera.

184

185 A total of 43 out of 66 species (65%) were reported for the first time around FI
 186 and ten out 24 (41%) for SG. Therefore, an expansion of their known geographical
 187 distribution is reported here (Table 2). One of the species (*Antarctothoa* cf. *dictyota*)
 188 had been previously reported to have only an Antarctic distribution, whilst four species
 189 found were endemic to Patagonian shelf and/or Chile (*Antarctothoa discreta*, *Electra*
 190 *longispina*, *Menipea patagonica*, *Romancheina labiosa*; Table 2).

191

192

Species richness

193 With regard to FI and SG, the highest values of species richness (S) and
 194 species/genus ratio (S/G) were found at EFI (Table 3; % S = 57.5; S/G = 1.87) with
 195 *Arachnopusia monoceros*, *Beania magellanica* and *Cellaria malvinensis* as the most
 196 abundant species. In contrast, the values of S and S/G ratio were lower at WFI (% S =
 197 21.25), with *Tricellaria aculeata* as the most abundant species in terms of station
 198 occurrences, and at SG (S/G = 1.09), respectively.

199

200 The expected species accumulation curves have still to reach the asymptote in
 201 the case of FI (Fig. 2-3). Species richness estimates (Chao2 and Jack1) indicated that
 202 the theoretical number of expected species would be between 82 and 88 (52 and 54 for
 203 the 6 dive surveys at about 8–12 m) in FI and 24 and 26 in SG, respectively.

204

205 With regard to the rates of bryozoan species being recorded for the first time,
 206 each new sample added 0.7 (3.5 for the 6 dive surveys) and 0.6 new species records to
 207 the fauna from FI and SG, respectively (Table 4).

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Bathymetric distribution

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Biogeographic distribution

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DISCUSSION

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New data from this study were jointly analysed with data from the literature and existing databases, revealing new bathymetric ranges in 32 species (37% of the species found in our study; Table 2). Thirty of eighty-five species (35%) found in our study were restricted to the continental shelf (128–200 m as the range of maximum depths defined by Portera et al. 2012).

The database compiled from biogeographic regions contained records for 90 genera and 196 species, which included 43 families (Appendix A). The highest values of species/genus ratio (S/G) were found at Falkland Islands (FI; S/G = 1.89), followed by Tierra del Fuego (TF; S/G = 1.78), Southern Argentina (SA; S/G = 1.77), Antarctica (AN; S/G = 1.69), Southern Chile (SC; S/G = 1.42), New Zealand (NZ and PE; S/G = 1.28), South Georgia and Prince Edwards (SG; S/G = 1.25), Tasmania (T; S/G = 1.2), Antipodes (A; S/G = 1.21), Bouvet Island (B; S/G = 1.12), and Kerguelen (K; S/G = 1).

Single-linkage clustering analysis shows that the first group (1) was represented by the South American Region, the Antarctic region and the South Georgia Province. The Southern Chile Province showed lower affinity to other provinces of the same group in our results (Fig. 4). New Zealand–Australian Region (A, NZ, PE and T) were clustered together (2). Finally, the isolated Bouvet (3) and Kerguelen islands (4) were strong outliers, characterized by a lower number of species. The ANOSIM tests showed that these groupings were statistically strong (ANOSIM Global R = 0.793, p = 0.001).

A decade ago Clarke et al. (2007) asked how well we knew the southern polar fauna. It is also the key first requirement of implementing the Convention on Biological Diversity. Clarke et al.'s (2007) question has since grown in importance, with West Antarctica becoming a hotspot of physical climate change and biological responses (Constable et al. 2015). Bryozoans have proved to be an important indicator taxon of biological responses to physical change (Barnes 2015), yet the current study shows some regions are still poorly characterised for some faunas. In particular, more of the 24% of the samples analysed (351) in our study belonged to different species,

244 including several potentially new genera and species. This suggests a more intensive
245 sampling would lead to find a greater diversity.

246

247 **Bryozoan diversity from the Falkland and South Georgia Islands**

248 The species/genus ratios (S/G) were found to range between 1 and 2, similar to
249 the values determined by Krug et al. (2008), who found S/G ratios to level off at
250 approximately 1.7 S/G in marine bivalves above 40° latitude. Considering the data
251 found here for FI and SG, the highest and the lowest value of species richness (S) and
252 S/G ratio were found at EFI (% S = 57.5; S/G = 1.87) and at WFI (% S = 21.25; S/G =
253 1.09), respectively, likely showing a tendency for stronger intrageneric competition
254 and/or the existence of genera containing species with lower speciation potential at WFI
255 (Webb et al. 2002). However, it is known confamilial competition is more frequent than
256 congeneric in bryozoans (Barnes & Neutel 2016).

257

258 Remarkably, 65% (43 of 66 species) and 41% (10 of 24) of species analysed in
259 the current study were reported for the first time in FI and SG, respectively. This
260 demonstrates that this region, despite having a long and considerable political and
261 scientific footprint, has been poorly explored so far with respect to bryozoans and
262 probably many other taxa (Hastings 1943, López-Gappa & Lichtschein 1990, López-
263 Gappa 2000, Moyano 2005, Hogg et al. 2011). In fact, the expected species-
264 accumulation curves did not approach and asymptote in the case of the FI. Thirty-eight
265 species for the 6 dive surveys at similar depths (8–12 m depth) and sixty-six species in
266 total (including bottom-sampling trawl and dive surveys) were found but the species
267 richness statistics (Chao2 and Jack1) predict that between 52 and 54 and 82 and 88
268 species will be found, respectively, as more samples are collected. In contrast, the
269 expected species-accumulation curve seems close to asymptote in the case of SG at
270 depths between 5 and 19 m with twenty-four species reported and fewer samples
271 required (between 24 and 26). Bryozoan species discovery rates by FI and SG were
272 similar to values previously reported for South Sandwich and South Orkney Islands by
273 Barnes & Kuklinksi (2010). Moreover, the same value for SG was reported in this
274 study. However, a more than threefold increase in rate value (3.5) was found for the six
275 dive surveys at similar depths. This suggests that more shallowsurveys are needed,
276 focusing on collecting bryozoans, in order to obtain a meaningful inventory of coastal
277 biota in one of the world's largest and key Marine Protected Areas. Overall, the

278 interpretation of these results must be treated with some caution due to the different
279 sampling effort and methodologies between studies. However, the number of the
280 sampled stations of each region was approximately equal and most samples were
281 collected by diving.

282

283

Bathymetric distribution

284 Most bryozoan species found in our study exhibit an unusually high range of
285 eurybathy. New bathymetric ranges were found in 32 species (35% of the studied
286 species), expanding their known geographic distributions. Of these, 35 bryozoan species
287 occurred deeper than 200 m, the most eurybathic species being *Chaperiopsis galeata*,
288 with a depth range of 0–4700 m. The bathymetric ranges determined by our study
289 support previous work showing wide depth ranges for many Antarctic and sub-Antarctic
290 cheilostome bryozoans (Barnes & Kuklinski 2010, Figuerola et al. 2012, 2014). This
291 fits a wider pattern of eurybathy in southern polar species across taxa (Brey et al. 1996),
292 thought to be driven by advance and retreat of grounded ice across continental shelves
293 during glacial cycles. However, this pattern is not peculiar to polar seas as some
294 bryozoan species from New Zealand are also highly eurybathic (Taylor et al. 2004).
295 Therefore, other factors are likely influencing in this distribution (e.g. colonies being
296 transported to greater depths by bottom currents).

297

298

Biogeographic distribution

299 The S/G ratios did not decline from lower to higher latitudes as found in marine
300 bivalves by Krug et al. (2008). In fact, Southern Chile (SC; S/G = 1.42), New Zealand
301 (NZ and PE; S/G = 1.28), South Georgia and Prince Edwards (SG; S/G = 1.25),
302 Tasmania (T; S/G = 1.2), Antipodes (A; S/G = 1.21), Bouvet Island (B; S/G = 1.12),
303 and Kerguelen (K; S/G = 1) showed lower values than Antarctica (AN; S/G = 1.69).
304 Thus, the trend of more species per genus in the polar zone than in some regions at
305 lower latitudes could be due to relatively higher net rates of speciation as few lineages
306 might manage to reach the poles and to diversify (high-latitude diversification
307 hypothesis). However, molecular data is needed to clarify the monophyly of the genera
308 involved in this study.

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A substantial proportion of species (28 and 19 species in FI and SG,
respectively; 79 and 42%) also had an Antarctic distribution. Similarly, previous studies

312 revealed a low percentage of endemic bryozoan species (56%, Barnes & Griffiths 2008,
313 55%, Figuerola et al. 2012). These studies confirm bryozoans are able to live in a broad
314 range of conditions (e.g. salinity and temperature; Barnes & Griffiths 2008).

315

316 Our cluster analyses of bryozoan species composition are consistent with the
317 theory of a sequential separation of Gondwana during the Tertiary. The Antarctic and
318 cold-temperate South American Regions and the SG Province were clustered together,
319 suggesting closer faunal affinities, supporting the results in several studies,
320 documenting several shared marine species between Antarctica and South America (e.g.
321 Moyano 1982, 1999, 2005, Barnes & Grave 2001, Arntz et al. 2005, Ramos-Esplá et al.
322 2005, Barnes & Griffiths 2008, Figuerola et al. 2012, 2014). Griffiths et al. (2009) also
323 suggested a strong similarity in composition between Antarctica and South America for
324 bryozoans as these regions were the last fragments drifting apart during the break-up of
325 Gondwana (Upchurch 2008). The New Zealand–Australian Region was clustered
326 separately in the current study, which is in agreement with the hypothesis that this
327 region broke up long before the Antarctic-South American separation. Although the
328 New Zealand–Australian Region formed the same cluster as PE in our results, the last
329 one showed lower affinity to other regions. In addition, the B and K represented the
330 most separated groups. The isolation of the three sub-Antarctic islands, their long period
331 of separation and the undersampling could explain their lower similarity values found in
332 our study.

333

334 Apart from these geological events in Gondwana history, differences in spatial
335 patterns of biodiversity suggest that different factors including dispersal factors
336 contribute to present distributional patterns. In particular, most species found here can
337 be regarded as eurybathic and consequently, having the capacity to colonize new
338 regions, freely migrating in and out of the SO via the deep abyssal plains as suggested
339 by other authors (deep-sea faunal exchange; e.g. Brandt et al. 2007). Therefore, the
340 relevant proportion of Antarctic bryozoan species found in sub-antarctic regions in our
341 study could be attributed to this dispersal pathway. In fact, migrations of taxa from AN
342 to South America through the deep-sea basins during glacial maxima have been
343 suggested by several authors (Thatje et al. 2005, Brandt et al. 2007, Clarke 2008).
344 Motile marine animals such as isopods and pycnogonids can also increase the bryozoan

345 connection between regions, transporting bryozoan colonies that are attached to them.
346 Some authors reported several Antarctic pycnogonid species and the common Antarctic
347 marine isopod *Glyptonotus antarcticus* fouled by Antarctic cheilostome bryozoans such
348 as the species *Smittina rogickae* found in our study (Key & Barnes 1999). However, this
349 biotic vector only allows the transport across short distances.

350

351 In addition, bryozoan species from shallow and deep waters also have
352 opportunities to colonize South American regions via the Scotia Arc (tips of a
353 subsurface mountain chain linking the Andes and the Antarctic Peninsula) that could act
354 as stepping stones (Arntz et al. 2005). In particular, this potential dispersal pathway may
355 be responsible for the closer faunistic relation found in our study between South
356 America and Subantarctic SG and the Sandwich Islands as part of the Scotia Arc, as
357 suggested by other authors for different taxa (Arntz et al. 2005, Barnes 2005, Ramos-
358 Esplá et al. 2005, Primo & Vázquez 2007).

359

360 A considerable proportion of bryozoan species in our study also incorporate an
361 Antarctic distribution, which indicates that the Polar Front (PF), which acts as a
362 circumpolar biogeographic barrier, is not as impermeable as some authors originally
363 considered (Clarke et al. 2005, Brandt et al. 2007). The distribution of water masses in
364 the world ocean has been suggested as a main agent of dispersal of marine species.
365 Moreover, the influence of subantarctic Falkland Current in lower latitudes favors the
366 establishment of cold-water organisms in the Argentine coast. Figuerola et al. (2014)
367 showed a high percentage of bryozoan species from the Patagonian region with an
368 Antarctic distribution. Most cheilostomes possess seemingly low larval-dispersal
369 potential (benthic, lecithotrophic larvae). However, currents could distribute
370 lecithotrophic larvae a substantial distance and consequently, increase their potential for
371 rate of geographic range growth, as the longevity of this phase in Antarctic bryozoans is
372 poorly known, as suggested by Downey et al. (2012) for Antarctic sponges.

373

374 Oceanic rafting, mainly using macroalgae, has probably played an important role
375 in the biogeography of diverse marine invertebrate species (Fraser et al. 2011). In
376 particular, bryozoans are effective colonizers of surfaces and one of the most important
377 components of biofouling travelling via floating items such as macroalgae and
378 driftwood (Watts et al. 1998, Barnes 2002). For example, Barnes & Fraser (2003)

379 reported five bryozoan species attached to a piece of plastic that was collected on
380 Adelaide Island (Antarctic Peninsula). This item of debris had been in the water for at
381 least 1 yr and most colonies were reproductively active and therefore had the possibility
382 of releasing larvae during their transport on that debris. This dispersal pathway of
383 organisms can be facilitated by the existence of eddies of ACC (Clarke et al. 2005) or
384 human dispersal mechanisms, which allows very rapid dispersion worldwide (e.g.
385 ballast water, vessel hulls and marine debris of anthropogenic origin such as floating
386 plastic; Barnes 2002). On the other hand, long-distance dispersal of some bryozoan
387 species attached to drifting natural substrates can be attributed to the eastwards flow of
388 the ACC (Barnes 2002). This has been confirmed by the presence a mixture of Tierra
389 del Fuego and Antarctic bryozoan species in other remote Subantarctic regions of the
390 Indian Ocean influenced by the ACC (e.g. Prince Edward, Crozet and Kerguelen;
391 Moyano 1999). The rapid increase in the number of ships sailing around AN over the
392 last few decades and climate change will most likely facilitate the introduction and
393 establishment of non-native species in AN, by reduction of oceanographic barriers
394 (Aronson et al 2007). However, more studies are need to know the influence of drifting
395 processes on bryozoan composition as the strong similarity found in this study could be
396 also related with the poor knowledge about bryozoan composition in some areas.

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CONCLUSIONS

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Our results demonstrate that these sub-Antarctic islands and surrounding regions have been poorly explored so far and essential baseline surveys are still lacking for even some of the better studied taxa, such as bryozoans. Bryozoans are likely to represent one of the better taxa to detect future changes (such as caused by anthropogenic perturbations) so distributional studies should be valuable. In particular, further surveys should mainly focus on slope and deep-water bryozoan faunas of South America and Antarctica. Our study supports the high-latitude diversification hypothesis since a trend of more species per genus in the polar zone than in some regions at lower latitudes was found. Moreover, bryozoological affinities found in the current study gave further evidence of the hypothesis of sequential separation of Gondwana during the Tertiary, with less taxonomically diverse species assemblages in the last fragments drifting apart, and support the changing concept that although the Polar Front (PF) acts as a circumpolar biogeographic barrier it is not as impermeable as originally thought.

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REFERENCES

- 423 Arkhipkin A, Brickle P, Laptikhovskiy V (2013) Links between marine fauna and
 424 oceanic fronts on the Patagonian Shelf and Slope. *Life Mar Sci* 30:19–37
- 425 Aronson RB, Thatje S, Clarke A, Peck LS, Blake DB et al (2007) Climate change and
 426 invasibility of the Antarctic benthos. *Ann Rev Ecol Evol Syst* 38:129–154
- 427 Arntz WE, Thatje S, Gerdes D, Gili J, Gutt J, Jacob UTE, Montiel A, Orejas C, Teixidó
 428 N (2005) The Antarctic-Magellan connection: macrobenthos ecology on the shelf
 429 and upper slope, a progress report. *Sci Mar* 69:237–269
- 430 Barnes DKA (2000) Diversity, recruitment and competition on island shores at south-
 431 polar localities compared with lower latitudes: encrusting community examples.
 432 *Hydrobiologia* 440:37–44
- 433 Barnes DKA (2002) Invasions by marine life on plastic debris. *Nature* 416:808–809
- 434 Barnes DKA (2005) Changing chain: past, present and future of the Scotia Arc's and
 435 Antarctica's shallow benthic communities. *Sci Mar* 69:65–89
- 436 Barnes DKA (2015) Antarctic sea ice losses drive gains in benthic carbon drawdown.
 437 *Curr Biol* 25:R789–R790
- 438 Barnes DKA, Fraser KPP (2003) Rafting by five phyla on man-made flotsam in the
 439 Southern Ocean *Mar Ecol Prog Ser* 262:289–291
- 440 Barnes DKA, De Grave S (2001) Ecological biogeography of southern polar encrusting
 441 faunas. *J Biogeogr* 28:359–365
- 442 Barnes DKA, Lehane C (2001) Competition, mortality and diversity in South Atlantic
 443 coastal boulder communities. *Polar Biol* 24:200–208
- 444 Barnes DKA, Griffiths HJ (2008) Biodiversity and biogeography of southern temperate
 445 and polar bryozoans. *Glob Ecol Biogeogr* 17:84–99

- 446 Barnes DKA, Kuklinski P (2010) Bryozoans of the Weddell Sea continental shelf, slope
447 and abyss: did marine life colonize the Antarctic shelf from deep water, outlying
448 islands or in situ refugia following glaciations? *J Biogeogr* 37:1648–1656
- 449 Barnes DKA, Neutel AM (2016) Severity of seabed spatial competition decreases
450 towards the poles. *Curr Biol* 26: R307–R318
- 451 Bastida R, Roux A, Martínez DE (1992) Benthic communities of the Argentine
452 continental shelf. *Oceanol Acta* 15:687–698
- 453 Branch ML, Hayward PJ (2005) New species of cheilostomatous Bryozoa from
454 subantarctic Marion and Prince Edward Islands. *J Nat Hist* 39:2671–2704
- 455 Brandt A, Broyer C De, Mesel I De, Ellingsen KE, Gooday AJ, Hilbig B, Linse K,
456 Thomson MRA, Tyler PA (2007) The biodiversity of the deep Southern Ocean
457 benthos The biodiversity of the deep Southern Ocean benthos. *Philos T Roy S*
458 362:39–66
- 459 Brewin PE, Brickle P (2011) Expedition report: Subtidal and intertidal survey of the
460 north coast of South Georgia. Shallow Marine Surveys Group Cruise report, 10pp
- 461 Brey T, Dahm C, Gorny M, Klages M, Stiller M, Arntz WE (1996) Do Antarctic
462 benthic invertebrates show an extended level of eurybathy? *Antarct Sci* 8:3–6
- 463 Briggs JC, Bowen BW (2012) A realignment of marine biogeographic provinces with
464 particular reference to fish distributions. *J Biogeogr* 39:12–30
- 465 Busk G (1884) Report on the Polyzoa collected by H.M.S. Challenger during the years
466 1873-1876. Part 1. The Cheilostomata. Report on the Scientific Results of the
467 Voyage of HMS Challenger. *Zoology* 10:1–216
- 468 Clarke A (2008) Antarctic marine benthic diversity: patterns and processes. *J Exp Mar*
469 *Bio Ecol* 366:48–55
- 470 Clarke A, Barnes DK, Hodgson DA (2005) How isolated is Antarctica? *Trends Ecol*
471 *Evol* 20:1–3
- 472 Clarke A, Griffiths HJ, Linse K, Barnes DKA, Crame JA (2007) How well do we know
473 the Antarctic marine fauna? A preliminary study of macroecological and
474 biogeographical patterns in Southern Ocean gastropod and bivalve molluscs.
475 *Divers Distrib* 13:620–632
- 476 Clarke KR, Green RH (1988) Statistical design and analysis for a ‘biological effects’
477 study. *Mar Ecol Prog Ser* 46:213–226
- 478 Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for
479 ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–

- 480 Curtis coefficient for denuded assemblages. *J Exp Mar Bio Ecol* 330:55–80
- 481 Constable AJ, Melbourne-Thomas J, Corney SP, Arrigo KR, Barbraud C, Barnes DKA,
482 Bindoff NL, Boyd PW, Brandt A, Costa DP, Davidson AT, Ducklow HW,
483 Emmerson L, Fukuchi M, Gutt J, Hindell MA, Hofmann EE, Hosie GW, Iida T,
484 Jacob S, Johnston NM, Kawaguchi S, Kokubun N, Koubbi P, Lea M-A, Makhado
485 A, Massom RA, Meiners K, Meredith MP, Murphy EJ, Nicol S, Reid K, Richerson
486 K, Riddle MJ, Rintoul SR, Smith WO, Southwell C, Stark JS, Sumner M,
487 Swadling KM, Takahashi K T, Trathan PN, Welsford DC, Weimerskirch H,
488 Westwood KJ, Wienecke BC, Wolf-Gladrow D, Wright SW, Xavier JC, Ziegler P
489 (2014) Climate change and Southern Ocean ecosystems I: how changes in physical
490 habitats directly affect marine biota. *Glob Change Biol* 20:3004–3025
- 491 d’Orbigny AD (1841-1847) *Voyage dans l’Amérique méridionale* 5, pt. 4: Zoophytes, 7-
492 28 (1847), Pl. 1,3,5 (1841), 2,4,6-3 (1842). Paris and Strasbourg.
- 493 Downey RV, Griffiths HJ, Linse K, Janussen D (2012) Diversity and distribution
494 patterns in high Southern latitude sponges. *PLoS ONE* 7(7): e41672
- 495 Figuerola B, Ballesteros M, Monleón-Getino T, Avila C (2012) Spatial patterns and
496 diversity of bryozoan communities from the Southern Ocean: South Shetland
497 Islands, Bouvet Island and Eastern Weddell Sea. *Syst Biodivers* 10:109–123
- 498 Figuerola B, Gordon DP, Polonio V, Cristobo J, Avila C (2014) Cheilostome bryozoan
499 diversity from the southwest Atlantic region: Is Antarctica really isolated? *J Sea*
500 *Res* 85:1–17
- 501 Fraser CI, Nikula R, Waters JM (2011) Oceanic rafting by a coastal community. *Proc R*
502 *Soc B Biol Sci* 278:649–55
- 503 Hastings A (1943) Polyzoa (Bryozoa). I. Scrupocellariidae, Epistomiidae,
504 Farciminariidae, Bicellariellidae, Aeteidae, Scrupariidae. *Discov Reports* 32:301–
505 510
- 506 Hayward PJD (1980) Cheilostomata (Bryozoa) from the South Atlantic. *J Nat Hist*
507 14:701–721
- 508 Hayward PJ (1995) *Antarctic Cheilostomatous Bryozoa*. Oxford: Oxford University
509 Press
- 510 Hayward PJ, Winston JE (2011) Bryozoa collected by the United States Antarctic
511 Research Program: new taxa and new records. *J Nat Hist* 45:2259–2338
- 512 Hogg OT, Barnes DKA, Griffiths HJ (2011) Highly Diverse, Poorly Studied and
513 Uniquely Threatened by Climate Change: An Assessment of Marine Biodiversity

- 514 on South Georgia's Continental Shelf. PLoS One 6:e19795
- 515 ICON (1996) The first shallow marine survey around the Falkland Islands. Prepared by
516 IC Consultants Ltd and Brown and Root Environmental, for the Falkland Islands
517 Government, July 1996. 46pp
- 518 Kaiser S, Branda SN, Ingels J, Leese F, Schiaparelli S, Arango CP, Badhe R, Bax N,
519 Ridder C De, Dubois P, Ellingsen KE, Glover AG, Griffiths HJ, Gutt J, Halanich
520 KM, Havermans C, Held C, Janussen D, Lo A, Wilson NG, Yasuhara M (2013)
521 Patterns, processes and vulnerability of Southern Ocean benthos: a decadal leap in
522 knowledge and understanding. Mar Biol 160:2295–2317
- 523 Key MM, Barnes DK (1999) Bryozoan colonization of the marine isopod *Glyptonotus*
524 *antarcticus* at Signy Island, Antarctica. Polar Biol 21:48–55
- 525 Key MM, Knauff JB, Barnes DKA (2013) Epizoic bryozoans on predatory pycnogonids
526 from the South Orkney Islands, Antarctica: "If you can't beat them, join them". In:
527 Bryozoan Studies 2010, Eds. Ernst A, Schäfer P, Scholz J, 137–153. Springer,
528 Heidelberg.
- 529 Krebs CJ (1999) Ecological Methodology. 2nd edition. Benjamin Cummings, Menlo
530 Park, California.
- 531 Krug AZ, Jablonski D, Valentine JW (2008) Species-genus ratios reflect a global
532 history of diversification and range expansion in marine bivalves. Proc Roy Soc
533 London B 275:1117–1123
- 534 Kuklinski P, Barnes DKA (2009) A new genus and three new species of Antarctic
535 cheilostome Bryozoa. Polar Biol 32:1251–1259
- 536 López de la Cuadra C, García-Gómez J (2000) The cheilostomate Bryozoa (Bryozoa:
537 Cheilostatida) collected by the Spanish "Antártida 8611" expedition to the
538 Scotia Arc and South Shetland Islands. J Nat Hist 34:755–772
- 539 López-Gappa J (2000) Species richness of marine Bryozoa in the continental shelf and
540 slope off Argentina (south-west Atlantic). Divers Distrib 6:15–27
- 541 López-Gappa J, Lichtschein V (1990) Los briozoos colectados por el B/I Shinkai Maru
542 en la plataforma Continental Argentina. 1 República Argentina Serv Hidrogr Nav
543 32
- 544 Moyano HI (1982) Magellanic Bryozoa: Some Ecological and Zoogeographical
545 Aspects. Mar Biol 96:81–96
- 546 Moyano HIG (1999) Magellan Bryozoa: a review of the diversity and of the
547 Subantarctic and Antarctic zoogeographical links. Sci Mar 63:219–226

- 548 Moyano HIG (2005) Scotia Arc bryozoans: a narrow bridge between two different
549 faunas. *Sci Mar* 69:103–112
- 550 Orensanz JM, Schwindt E, Pastorino G, Juan JL, Bortolus A, Casas G, Darrigran G, El
551 R, Piriz L, Obenat S, Pascual M, Penchaszadeh P, Scarabino F, Spivak ED,
552 Vallarino EA (2002) No longer the pristine confines of the world ocean: a survey
553 of exotic marine species in the southwestern Atlantic. *Biol Invasions* 4:115–143
- 554 Portela J, Acosta J, Cristobo J, Muñoz A, Parra S et al (2012) Management strategies to
555 limit the impact of bottom trawling on VMEs in the high seas of the SW Atlantic.
556 In: Cruzado A (Ed.), *Marine Ecosystems*, pp. 199–228 (InTech 978-953-51-0176-
557 5, chapter, 9).
- 558 Primo C, Vázquez E (2007) Zoogeography of the Antarctic ascidian fauna in relation
559 to the sub-Antarctic and South America. *Antarct Sci* 19:321
- 560 R Core Team (2014). R: A language and environment for statistical computing. R
561 Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org)
562 [project.org](http://www.R-project.org)
- 563 Ramos-Esplá AA, Cárcel JA, Varela M (2005) Zoogeographical relationships of the
564 littoral ascidiofauna around the Antarctic Peninsula, in the Scotia Arc and in the
565 Magellan region. *Sci Mar* 69:215–223
- 566 Taylor PD, Gordon DP, Batson PB (2004) Bathymetric distributions of modern
567 populations of some common Cenozoic Bryozoa from New Zealand, and
568 paleodepth estimation. *New Zeal J Geol Geop* 47:57–69
- 569 Thatje S, Hillenbrand C-D, Larter R (2005) On the origin of Antarctic marine benthic
570 community structure. *Trends Ecol Evol* 20:534–40
- 571 Upchurch P (2008) Gondwanan break-up: legacies of a lost world? *Trends Ecol Evol*
572 23:229–236
- 573 Waters AW (1904) Bryozoa. Résultats du Voyage du S.V. 'Belgica', Zoologie.
574 Expedition Antarctique Belge 4:1–114
- 575 Watts PC, Thorpe JP, Taylor PD (1998) Natural and anthropogenic dispersal
576 mechanisms in the marine environment: a study using cheilostome Bryozoa. *Philos*
577 *Trans R Soc B Biol Sci* 353:453–464
- 578 Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and
579 community ecology. *Annu Rev Ecol Syst* 33:475–505
- 580 Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction
581 rates of birds and mammals. *Science* 315:1574–1576

582 Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008) Rapid
583 warming of the ocean around South Georgia, Southern Ocean, during the 20th
584 century: Forcings, characteristics and implications for lower trophic levels. Deep
585 Sea Res Part I Oceanogr Res Pap 55:1218–1228

586 Wright PJ, Hayward PJ, Hughes RN (2007) New species of *Antarctothoa*
587 (*Cheilostomata*: *Hippothoidae*) from the Falkland Isles, South Shetland Isles and
588 the Magellan Strait. *J Mar Biol Assoc United Kingdom* 87:1133–1140

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Figures and Tables

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620 **Table 1.** Depth and coordinates of the sampling stations from the Falkland Islands and
 621 the South Georgia. Samples were obtained by SCUBA diving and bottom trawling from
 622 vessels (FI shelf samples).

Site	Location	Latitude (S)	Longitude (W)	Depth (m)
OFI	Shelf	51° 22.3'	63° 20.4'	162
OFI	Shelf	50° 32.7'	62° 49.6'	149
OFI	Shelf	50° 6.5'	62° 28.5'	148
OFI	Shelf	49° 54.1'	62° 13'	144
OFI	Shelf	49° 51.8'	61° 7.5'	162
OFI	Shelf	50° 6.9'	61° 51.7'	157
OFI	Shelf	50° 22'	61° 42.6'	161
OFI	Shelf	51° 1.1'	61° 37.5'	146
OFI	Shelf	50° 35.9'	61° 32.8'	162
OFI	Shelf	50° 41.4'	61° 24.4'	143
OFI	Grand Jason Island	51° 03.05'	61° 04.03'	0-4.7
OFI	Shelf	50° 8.2'	60° 53.2'	159
OFI	Shelf	50° 20.5'	60° 49.6'	154
OFI	Shelf	52° 35.42'	60° 20.21'	160-190
OFI	Shelf	50° 53.1'	60° 14.9'	132
OFI	Beauchene Island	52° 54.07'	59° 10.35'	8.5-23.6
OFI	Beuchene Island	52° 54.4'	59° 10.2'	8-24
OFI	Shelf	49° 44.7'	58° 21.8'	345
OFI	Shelf	52° 16.22'	58° 05.10'	160-190
OFI	Shelf	52° 24.18'	57° 54.35'	300-320
WFI	New Island	51° 41.56'	61° 19.67'	12-17.5
WFI	New Island	51° 43.60'	61° 18.44'	12-17.5
WFI	New Island	51° 42.23'	61° 13.50'	12-17.5
WFI	Staerts Island	51° 53.31'	61° 11.31'	2-20
WFI	Grand Jason Island	51° 02.10'	61° 05.28'	24-32.9
WFI	Grand Jason Island	51° 04.77'	61° 03.98'	3-21.2
WFI	Grand Jason Island	51° 04.77'	61° 03.98'	3-21.2
WFI	Grand Jason Island	51° 04.46'	61° 03.58'	3-21.2
WFI	Port Stephens	52° 11.37'	60° 46.90'	0.8-11.4
WFI	Port Stephens	52° 11.00v	60° 44.90'	3.6-18
WFI	Port Stephens	52° 11.00'	60° 44.90'	3.6-18
WFI	Port Stephens	52° 11.51'	60° 44.61'	3.6-18
WFI	Port Stephens	52° 11.23'	60° 44.15	0.7-21.7
WFI	Cape terrible, West Point Island	51°19.36'	60° 43.49'	7-20

WFI	West Point isalnd	51° 20.60'	60° 43.42'	7-20
WFI	West Point Island	51° 21.63'	60° 42.60'	7-20
WFI	Off Cape Meredith Falklands	52° 16.12'	60° 39.7'	100
WFI	Pebble Island	51° 17.40'	59° 32.90'	3-4.8
WFI	Pebble Island	51° 16.60'	59° 32.55'	3.6-11.6
EFI	Ruggles Bay	51° 56.7'	59° 40.73'	2
EFI	Ruggles Bay	51° 56.7'	59° 40.73'	10
EFI	Ruggles Bay	51° 59.91'	59° 37.68'	9
EFI	Ruggles Bay	51° 59.91'	59° 37.68'	9
EFI	Fanning Head	51° 27.63'	59° 08.41'	11-15.2
EFI	Fanning Head	51° 27.97'	59° 08.20'	11.2-14.5
EFI	Fanning Head	51° 28.28'	59° 07.87'	2-21
EFI	Fanning Head	51° 28.55'	59° 07.07'	8.3-13
EFI	Fanning Head	51° 28.55'	59° 07.07'	8.3-13
EFI	Sea Lion Island	52° 25.77'	59° 03.03'	7- 9.5
EFI	Mare Harbour	51° 53.82'	58° 30.11'	6.7-7.5
EFI	Stanley harbour	51° 41.31'	57° 49.19'	8-18
EFI	Gypsy Cove	51° 40.43'	57° 48.38'	9
EFI	Kelly Rocks	51° 40.23'	57° 45.24'	10
EFI	Tussock Island	51° 40.2'	57° 44.60'	12
EFI	Lighthouses of Staleny	51° 40.53'	57° 44.23'	8
EFI	Cristina Bay	51° 41.15'	57° 44. 03'	2
SG	-	54° 16.37	38° 12.28	8-18
SG	Bird Island	54° 1.9'	38° 1.2'	16
SG	Bird Island	54° 2.4'	38° 0.13'	8
SG	Bird Island	54° 2.4'	38° 0.13'	18
SG	Jagged Point	54° 4.3'	37° 7.11'	12
SG	Right Whale Bay	54° 0.1'	37° 40.52'	7
SG	Stromness Bay	54° 9.26'	37° 26.3'	18
SG	Stromness Bay	54° 9.26'	37° 26.3'	14
SG	Rossita Harbour	54° 0.41'	37° 26.3'	5-15
SG	Prion Island	54° 1.51'	37° 15.3'	12
SG	Prion Island	54° 1.51'	37° 15.3'	19
SG	Prion Island	54° 1.51'	37° 15.3'	10
SG	Stromness Bay	54° 9.21'	36° 40.7'	16
SG	Husvik	54° 10.17'	36° 40.24'	8
SG	Husvik	54° 10.9'	36° 39.18'	12
SG	Cooper Bay	54° 47.6'	35° 50.33'	15
SG	Cooper Bay	54° 47.4'	35° 48.29'	12
SG	Cooper Bay	54° 47.4'	35° 48.29'	14

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Table 2. Bathymetric ranges and biogeographic distributions in the cold-temperate and polar southern hemisphere of the species studied from the shallow waters (average depths of about 200 m) using data from the present study, the literature, and the GBIF and ANTABIF (Van de Putte et al. 2016). *New bathymetric range described in this study, **First record for Falkland and/or South Georgia Islands. Cold-temperate South American Region (Provinces: AN = Antarctica; FI = Falkland Islands, SA = Southern Argentina; SC = Southern Chile, and TF = Tierra del Fuego), New Zealand–Australian Region (cold-temperate provinces: A = Antipodes, NZ = New Zealand, and T= Tasmania) and Antarctic and Sub-Antarctic regions (SG = South Georgia, B = Bouvet Island, PE = Prince Edward Islands, and K= Kerguelen).

Species	Bathymetric range (m)	Biogeographic distribution	References
<i>Aetea</i> sp.		FI**	This study
<i>Amastigia benemunita</i> (Busk, 1884)	10*–586.33 (previously 50)	FI, SA, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Amastigia</i> cf. <i>vibraculifera</i> Hastings, 1943	52.13–79	FI, SA	López Gappa (2000) and GBIF database
<i>Amastigia gaussi</i> (Kluge, 1914)	5–1586	AN, FI, SA, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Andreella</i> cf. <i>uncifera</i> (Busk, 1884)	10.3*–183 (previously 25)	AN, FI, SA, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Antarctothoa</i> cf. <i>bougainvillei</i> (d'Orbigny, 1842)	0–379.5	AN, B, FI, PE, SA, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Antarctothoa</i> cf. <i>dictyota</i> (Hayward, 1993)	1–150	AN, FI	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Antarctothoa discreta</i> (Busk, 1854)	8*–247 (previously 60)	FI**, SA, SC, TF	López Gappa (2000) and GBIF database
<i>Arachnopusia</i> cf. <i>columnaris</i> Hayward and Thorpe, 1988	46–621	AN, FI**	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Arachnopusia monoceros</i> (Busk, 1854)	0–410	AN, FI, NZ, SA, SC, SG, T, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Arachnopusia</i> sp. 1	345*	FI**	This study
<i>Arachnopusia</i> sp. 2	15.7*	SG**	This study
<i>Aspidostoma giganteum</i> (Busk, 1854)	4–1893	AN, FI, SA, SC, SG, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Austroflustra</i> cf. <i>australis</i> López-Gappa, 1982	100*–1241.67 (previously 272)	FI, SA, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases

<i>Austroflustra gerlachi</i> López Gappa, 1982	272–1897.67	FI, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Beania costata</i> (Busk, 1876)	8–169	AN, FI, PE, SA, T, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Beania inermis</i> (Busk, 1852)	0–140	AN, FI, NZ, SA, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Beania magellanica</i> (Busk, 1852)	0–272	FI, K, NZ, PE, SA, T, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Caberea darwinii</i> Busk, 1884	5–1513	AN, B, FI, NZ, PE, SA, SG, T, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Camptoplites tricornis</i> (Waters, 1904)	5–2000	AN, FI**, SG	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Carbasea ovoidea</i> Busk, 1852	5–641	AN, FI, K, PE, SA, SC, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Cellaria malvinensis</i> (Busk, 1852)	0–846.03	AN, FI, NZ, PE, SA, SC, SG, TF	Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Celleporella</i> cf. <i>alia</i> Hayward, 1993	10*–650 (previously 22.5)	AN, B, FI, PE, SC, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Celleporella</i> sp. Gray, 1848	9.1*	FI**	This study
<i>Chaperiopsis galeata</i> (Busk, 1854)	0–4700	AN, FI, NZ, SA, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Chaperiopsis patulosa</i> (Waters, 1904)	2*–1000 (previously 25.5)	AN, FI, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Electra</i> cf. <i>longispina</i> (Calvet, 1904)	11.5*–35 (previously 35)	FI**, TF	López Gappa (2000); GBIF database
<i>Escharoides</i> cf. <i>tridens</i> (Calvet, 1909)	2–585	AN, FI**, SG	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Exochella longirostris</i> Jullien, 1888	0–286	AN, FI, SA, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Exochella</i> sp. Jullien, 1888	9.1*	FI**	This study
<i>Fenestulina</i> cf. <i>exigua</i> (Waters, 1904)	8–522	AN, SG	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Fenestulina crystallina</i> Hayward and Ryland, 1990	93–1620	AN, FI**, SA	Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Fenestulina majuscula</i> Hayward, 1980	0–66	FI, PE, SA, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Fenestulina malusii</i> Audouin, 1826	0–219	A, AN, FI, NZ, SG, T, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Fenestulina</i> sp. 1 Jullien, 1888	8.4*	SG**	This study
<i>Fenestulina</i> sp. 2 Jullien, 1888	9.1*–10.3*	FI**	This study
<i>Fenestulina</i> sp. 3 Jullien, 1888	9*	FI**	This study
<i>Fenestulina</i> sp. 4 Jullien, 1888	17.5*	SG**	This study

<i>Foveolaria terrifica</i> (Hincks, 1881)	145–1629	FI, SA, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Hippothoa</i> cf. <i>flagellum</i> Manzoni, 1870	1–3501	AN, FI, NZ, PE, SA, SG, T, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Inversiula</i> cf. <i>nutrix</i> Jullien, 1888	0–410	AN, B, FI**, SA, SG, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Membranipora</i> cf. <i>membranacea</i> (Linnaeus, 1767)	0–80	FI, NZ, T	López Gappa (2000) and GBIF database
<i>Menipea patagonica</i> Busk, 1852	7.1*–350 (previously 30)	FI, TF	López Gappa (2000); GBIF and biodiversity.aq databases
<i>Micropora</i> cf. <i>notialis</i> Hayward and Ryland, 1993	7–953	AN, FI, NZ, SA, SC, SG	Barnes and Lehane (2001); López Gappa (2000); GBIF and biodiversity.aq databases
<i>Microporella crustula</i> Hayward and Winston, 2011	8*–825.17 (previously 825.17)	AN, FI**, SA	Hayward and Winston (2011); Figuerola et al. (2014)
<i>Microporella hyadesi</i> (Jullien, 1888)	49–903 (previously 104)	A, FI, NZ, SA, SC, SG, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Ogivalia</i> sp. Jullien, 1882	157*–162*	FI**	This study
<i>Osthimosia</i> cf. <i>curtioscula</i> Hayward, 1992	5*–1150	AN, FI**, SG	GBIF and biodiversity.aq databases
<i>Osthimosia</i> cf. <i>multifaria</i> Hayward and Winston, 2011	10.3*–115 (previously 115)	FI**, TF	Hayward and Winston (2011)
<i>Osthimosia</i> sp. 1 Jullien, 1888	9*–12*	FI**	This study
<i>Osthimosia</i> sp. 2 Jullien, 1888	10*–12*	FI**	This study
<i>Osthimosia</i> sp. 3 Jullien, 1888	13.8*	FI**	This study
<i>Reteporella magellensis</i> (Busk, 1884)	30–1393.33	FI, SA, SC, TF	Hayward and Winston (2011); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Reteporella</i> sp. 1 Busk, 1884	148*	FI**	This study
<i>Reteporella</i> sp. 2 Busk, 1884	143*–159*	FI**	This study
<i>Romancheina labiosa</i> (Busk, 1854)	6–31	FI**, SA, SC, TF	López Gappa (2000); Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Smittina antarctica</i> (Waters, 1904)	5–1150	AN, FI**, SG	GBIF and biodiversity.aq databases
<i>Smittina</i> cf. <i>rogickae</i> Hayward and Taylor, 1984	0–1635.33	AN, FI**, SA	Figuerola et al. (2014); GBIF and biodiversity.aq databases
<i>Smittina</i> sp. 1 Norman, 1903	149*	FI**	This study

<i>Smittina</i> sp. 2 Norman, 1903	10.3*–149*	FI**	This study
<i>Smittina</i> sp. 3 Norman, 1903	10.3*	FI**	This study
<i>Smittina</i> sp. 4 Norman, 1903	10.3*	FI**	This study
<i>Smittina</i> sp. 5 Norman, 1903	9*	FI**	This study
<i>Smittina</i> sp. 6 Norman, 1903	9*	FI**	This study
<i>Smittoidea</i> sp. Osburn, 1952	–	FI**	This study
<i>Toretocheilum</i> sp. Rogick, 1960	12.3*	SG**	This study
<i>Tricellaria aculeata</i> (d'Orbigny, 1847)	0–341	A, AN, FI, K, NZ, PE, SA, SC, TF	López Gappa (2000); GBIF and biodiversity.aq databases
Unknown_1	24–32.9	FI**	This study
Unknown_2	8.5-23.6	FI**	This study
Unknown_3	345	FI**	This study
Unknown_4	8–12	SG*	This study
Unknown_5	8–18	SG*	This study
Unknown_6	345	FI**	This study
Unknown_7	-	FI**	This study
Unknown_8	345	FI**	This study
Unknown_9	12	SG*	This study
Unknown_10	05–18	SG*	This study
Unknown_11	143	FI**	This study
Unknown_12	9	FI**	This study
Unknown_13	12.3	SG*	This study
Unknown_14	8.4–9	SG*	This study
Unknown_15	-	FI**	This study
Unknown_16	144–162	FI**	This study
Unknown_17	11.5	SG*	This study
Unknown_18	12.3	SG*	This study

Table 3. Species distribution along the Falkland and South Georgia Islands. Regions: East (EFI) and West Falkland Islands (WFI), shelf areas off Falkland Islands (OFI) and South Georgia (SG). For each site: number of sampling stations, number of species found (n sps), percentage of relative species richness (% S), species/genus (S/G) ratio and the most abundant species found in the sample.

Site	no. stations	n sps	%S	S/G ratio	Most abundant species
EFI	17	46	57.5	1.84	<i>Arachnopusia monoceros</i> , <i>Beania magellanica</i> , <i>Cellaria malvinensis</i>
OFI	20	27	33.75	1.17	<i>Aspidostoma giganteum</i>
SG	19	24	30	1.09	<i>Antarctothoa</i> cf. <i>bougainvillei</i> , <i>Inversiula</i> cf. <i>nutrix</i> , <i>Menipea patagonica</i>
WFI	19	17	21.25	1.21	<i>Tricellaria aculeata</i>

Table 4. Bryozoan species discovery rate by locality and bryozoan species richness for the South Atlantic and Southern Ocean. Table modified from Barnes & Kuklinski (2010). Data are from current study (bold), López de la Cuadra & García Gómez (2000), Barnes & Kuklinski (2010) and Hayward & Winston (2011). * Value calculated for the 6 dive surveys.

	Falkland Islands	South Georgia Islands	South Sandwich Islands	South Georgia Islands	Bouvet Island	Weddell Sea
New species per sample	0.7, 3.5*	0.6	0.5	0.7	3.5	0.39
Total species known	120	146	65	110	34	201

Appendix A. Biogeographic distributions of the species studied from shallow waters in the South American Region. Pulled data from the present study, the literature and the GBIF and SCAR databases. **First record for Falkland and/or South Georgia Islands. Cold-temperate South American Region (Provinces: AN = Antarctica; FI = Falkland Islands, SA = Southern Argentina; SC = Southern Chile, and TF = Tierra del Fuego), New Zealand–Australian Region (cold-temperate provinces: A = Antipodes, NZ = New Zealand, and T= Tasmania)) and Antarctic and Sub-Antarctic regions (SG = South Georgia, B = Bouvet Island, PE = Prince Edward Islands, and K= Kerguelen).

Species	Geographic distr. (Provinces)
<i>Adelascopora secunda</i> Hayward and Thorpe, 1988	AN, FI, SA, SG, TF
<i>Adeonella fuegensis</i> (Busk, 1852)	SC, TF
<i>Adeonella patagonica</i> Hayward, 1988	AN, FI, SA
<i>Aetea anguina</i> (Linnaeus, 1758)	A, AN, FI, NZ, SA, T, TF
<i>Aetea australis</i> Jullien, 1888	A, NZ, SA, SC, TF
<i>Aetea curta</i> Jullien, 1888	FI, TF
<i>Aetea ligulata</i> Busk, 1852	FI, NZ, SA, TF
<i>Aimulosia australis</i> Jullien, 1888	AN, SA, SG, TF
<i>Amastigia benemunita</i> (Busk, 1884)	FI, SA, SG, TF
<i>Amastigia gaussi</i> (Kluge, 1914)	AN, FI, SA, SG, TF
<i>Amastigia nuda</i> Busk, 1852	FI, NZ, SA, T, TF
<i>Amastigia vibraculifera</i> Hastings, 1943	FI, SA
<i>Amphiblestrum familiaris</i> Hayward and Thorpe, 1989	SA
<i>Amphiblestrum novella</i> Hayward and Thorpe, 1989	FI, TF
<i>Apiophragma hyalina</i> (Waters, 1904)	AN, SA
<i>Andreella patagonica</i> López Gappa, 1981	SA, TF
<i>Andreella uncifera</i> (Busk, 1884)	AN, FI, SA, SG, TF
<i>Antarctothoa bougainvillei</i> (d'Orbigny, 1842)	AN, B, FI, PE, SA, SG, TF
<i>Antarctothoa dictyota</i> (Hayward, 1993)	AN, FI
<i>Antarctothoa discreta</i> (Busk, 1854)	FI**, SA, SC, TF
<i>Arachnopusia admiranda</i> Moyano, 1982	SA
<i>Arachnopusia columnaris</i> Hayward and Thorpe, 1988	AN, FI**

<i>Arachnopusia discors</i> Hayward & Thorpe, 1988	TF
<i>Arachnopusia globosa</i> Hayward and Thorpe, 1988	FI, SA, SG
<i>Arachnopusia monoceros</i> (Busk, 1854)	AN, FI, NZ, SA, SC, SG, T, TF
<i>Arachnopusia velligera</i> Hayward and Thorpe, 1988	A, NZ, SA
<i>Aspericreta favulosa</i> Hayward and Thorpe, 1989	AN, SA
<i>Aspidostoma giganteum</i> (Busk, 1854)	AN, FI, SA, SC, SG, TF
<i>Austroflustra australis</i> López-Gappa, 1982	FI, SA, TF
<i>Austroflustra gerlachi</i> López Gappa, 1982	FI, TF
<i>Austrothoa yagana</i> (Moyano and Gordon, 1980)	SA, SC
<i>Beania costata</i> (Busk, 1876)	AN, FI, PE, SA, T, TF
<i>Beania fragilis</i> Ridley, 1881	FI, SA, SC, TF
<i>Beania inermis</i> (Busk, 1852)	AN, FI, NZ, SA, TF
<i>Beania magellanica</i> (Busk, 1852)	FI, K, NZ, PE, SA, T, TF
<i>Beania maxilla</i> (Jullien, 1888)	FI, SA, SC, TF
<i>Beania unicornis</i> Hastings, 1943	FI, SA
<i>Bracebridgia subsulcata</i> (Smitt, 1873)	SA
<i>Buffonellodes glabra</i> Hayward, 1991	FI, SA, SC, TF
<i>Buffonellodes rimosa</i> Jullien, 1888	A, AN, FI, NZ, SA, SC, TF
<i>Caberea darwinii</i> Busk, 1884	AN, B, FI, NZ, PE, SA, SG, T, TF
<i>Caberea darwinii guntheri</i> Hastings, 1943	TF
<i>Callopora deseadensis</i> López Gappa, 1981	SA, SC, TF
<i>Calloporina patagonica</i> Hayward and Ryland, 1990	SA, TF
<i>Camptolites atlanticus</i> Hastings, 1943	FI, SA
<i>Camptolites bicornis</i> (Busk, 1884)	A, AN, B, NZ, PE, SA
<i>Camptolites bicornis</i> var. <i>quadriangularis</i> Hastings, 1943	TF
<i>Camptolites tricornis</i> (Waters, 1904)	AN, FI**, SG
<i>Carbasea elegans</i> Busk, 1852	AN, SA
<i>Carbasea ovoidea</i> Busk, 1852	AN, FI, K, PE, SA, SC, SG, TF
<i>Catadysis immersum</i> (Busk, 1884)	FI, SA, TF
<i>Catadysis pygmaeum</i> Moyano, 1985	SC
<i>Cellaria clavata</i> (Busk, 1884)	AN, FI, PE, SA, SG, TF
<i>Cellaria coronata</i> (Rogick, 1956)	AN, SC

<i>Cellaria malvinensis</i> (Busk, 1852)	AN, FI, NZ, PE, SA, SC, SG, TF
<i>Cellaria scoresbyi</i> Hastings, 1946	A, FI, NZ, PE, SA, SC, TF
<i>Cellaria variabilis</i> (Busk, 1884)	FI, SA, SC, TF
<i>Cellarinella dubia</i> Waters, 1904	AN, FI, SA, TF
<i>Celleporella alia</i> Hayward, 1993	AN, B, FI, PE, SC, SG, TF
<i>Celleporella discreta</i> (Busk, 1854)	SA, SC
<i>Celleporella hyalina</i> Linnaeus, 1767	AN, B, NZ, SA, SC, SG, T, TF
<i>Celleporella patagonica</i> Busk, 1852	SA, TF
<i>Celleporella tehuelcha</i> López Gappa, 1985	TF
<i>Celleporina bicostata</i> Hayward, 1980	FI, SA, TF
<i>Celleporina lacrimula</i> Hayward, 1992	TF
<i>Chaperia acanthina</i> (Lamouroux, 1825)	A, AN, FI, NZ, SA
<i>Chaperiopsis cervicornis</i> (Busk, 1854)	AN, B, NZ, PE, T, TF
<i>Chaperiopsis galeata</i> (Busk, 1854)	AN, FI, NZ, SA, SG, TF
<i>Chaperiopsis indefensa</i> Hayward and Thorpe, 1988	SA
<i>Chaperiopsis orbiculata</i> Hayward and Thorpe, 1988	AN, FI, SG, TF
<i>Chaperiopsis patulosa</i> (Waters, 1904)	AN, FI, TF
<i>Chaperiopsis propinqua</i> Hayward and Thorpe, 1988	AN, FI, TF
<i>Chartella notialis</i> Hayward and Winston, 1994	AN, TF
<i>Chondriovelum angustilobata</i> (Moyano, 1974)	SA, SC, TF
<i>Chorizopora brongniartii</i> (Audouin, 1826)	NZ, SA, T
<i>Cornucopina ovalis versa</i> Hastings, 1943	FI, TF
<i>Cornucopina pectogemma</i> (Goldstein, 1882)	AN, NZ, PE, SA, SG
<i>Crisularia hyadesi</i> (Jullien, 1888)	SA
<i>Electra longispina</i> (Calvet, 1904)	FI**, TF
<i>Electra monostachys</i> (Busk, 1854)	SA, TF
<i>Ellisina antarctica</i> Hastings, 1945	A, AN, FI, NZ, SA, TF
<i>Ellisina incrustans</i> (Waters, 1898)	AN, FI, SA, TF
<i>Escharoides tridens</i> (Calvet, 1909)	AN, FI**, SG
<i>Exochella discors</i> Hayward, 1991	SA
<i>Exochella hymanae</i> (Rogick, 1956)	AN, SA, SG
<i>Exochella longirostris</i> Jullien, 1888	AN, FI, SA, TF

<i>Fenestulina antarctica</i> Hayward and Thorpe, 1990	AN, SA
<i>Fenestulina crystallina</i> Hayward and Ryland, 1990	AN, FI**, SA
<i>Fenestulina dupla</i> Hayward and Ryland, 1990	SA, TF
<i>Fenestulina exigua</i> (Waters, 1904)	AN, SG
<i>Fenestulina fritilla</i> Hayward and Ryland, 1990	AN, FI, SA, SG, TF
<i>Fenestulina horrida</i> Moyano, 1985	SA, TF
<i>Fenestulina incusa</i> Hayward and Ryland, 1990	SA, TF
<i>Fenestulina majuscula</i> Hayward, 1980	FI, PE, SA, TF
<i>Fenestulina malusii</i> Audouin, 1826	A, AN, FI, NZ, SG, T, TF
<i>Flustrapora magellanica</i> Moyano, 1970	AN, FI, SA, TF
<i>Foveolaria terrifica</i> (Hincks, 1881)	FI, SA, TF
<i>Galeopsis bullatus</i> Hayward, 1993	AN, SA, SG
<i>Galeopsis patagonicus</i> Hayward, 1993	FI, SA
<i>Galeopsis pentagonus</i> (d'Orbigny, 1847)	FI, NZ, SA, TF
<i>Gigantopora spathula</i> Hayward and Winston, 2011	AN, SA
<i>Gregarinidra variabilis</i> (Moyano, 1974)	FI, SA
<i>Himantozoum obtusum</i> Hastings, 1943	AN, FI, SA, TF
<i>Hippadenella falklandensis</i> Hayward, 1991	FI
<i>Hippadenella margaritifera</i> (Quoy and Gaimard, 1824)	FI, SA, TF
<i>Hippadenella rouzaudi</i> (Calvet, 1904)	FI, SA, SC
<i>Hippomonavella ramosae</i> López de la Cuadra and García Gómez, 2000	SA, SG
<i>Hippoporina aulacomyae</i> López Gappa, 1981	SA
<i>Hippothoa divaricata</i> Lamouroux, 1821	NZ, T, TF
<i>Hippothoa flagellum</i> Manzoni, 1870	AN, FI, NZ, PE, SA, SG, T, TF
<i>Ichthyaria oculata</i> Busk, 1884	FI, PE, SA, TF
<i>Inversiula nutrix</i> Jullien, 1888	AN, B, FI**, SA, SG, TF
<i>Inversiula patagonica</i> Hayward and Ryland, 1991	SA, TF
<i>Lacerna eatoni</i> (Busk, 1876)	AN, K, SA, SC, TF
<i>Lacerna hosteensis</i> Jullien, 1888	AN, FI, SA, SG, TF
<i>Lageneschara peristomata</i> Hayward and Winston, 2011	AN, FI, SA
<i>Melicerita atlantica</i> Busk, 1884	SA
<i>Melicerita blancoae</i> López Gappa, 1981	AN, FI, SA, TF

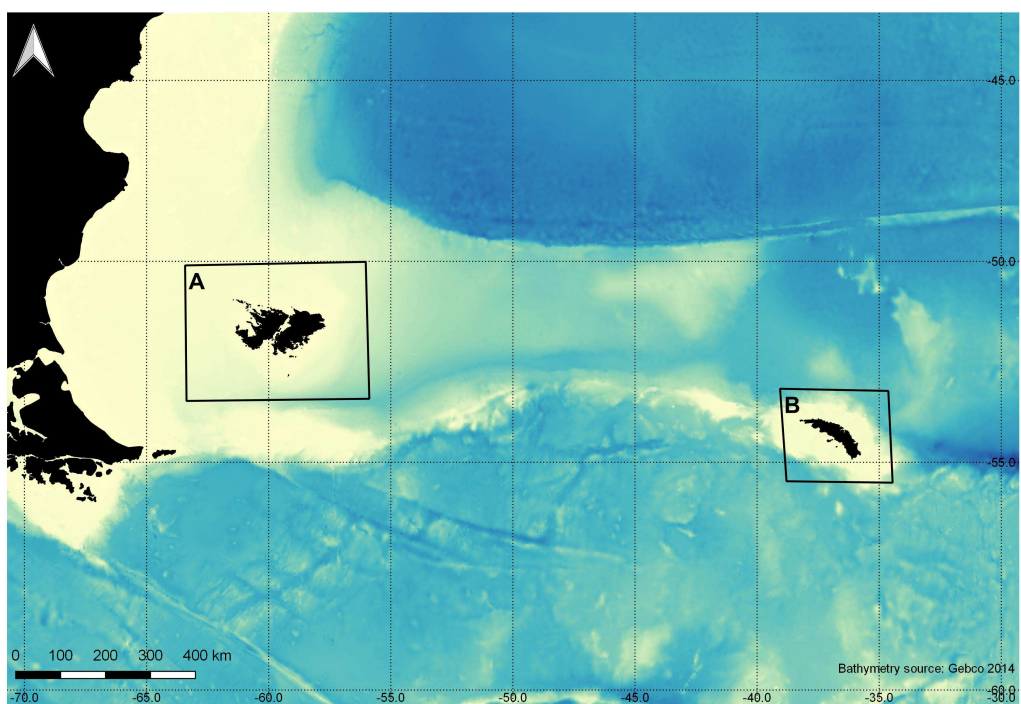
<i>Melicerita temaukeli</i> Moyano, 1997	TF
<i>Membranicellaria dubia</i> (Busk, 1884)	SA
<i>Membranipora membranacea</i> (Linnaeus, 1767)	FI, NZ, T
<i>Menipea flagellifera</i> Busk, 1884	AN, FI, K, PE, SA, TF
<i>Menipea patagonica</i> Busk, 1852	FI, TF
<i>Metroperiella galeata</i> (Busk, 1854)	SA, TF
<i>Micropora brevissima</i> Waters, 1904	AN, FI, SA, SG, TF
<i>Micropora notialis</i> Hayward and Ryland, 1993	AN, FI**, NZ, SA, SC, SG
<i>Microporella crustula</i> Hayward and Winston, 2011	AN, FI**, SA
<i>Microporella diademata</i> (Lamouroux, 1825)	FI, NZ, SA, T, TF
<i>Microporella hyadesi</i> (Jullien, 1888)	A, FI, NZ, SA, SC, SG, TF
<i>Microporella personata</i> (Busk, 1854)	B, FI, SA, T, TF
<i>Neoflustra dimorphica</i> López Gappa, 1982	TF
<i>Neothoa chiloensis</i> (Moyano, 1982)	SA, SC
<i>Notoplites antarcticus</i> (Waters, 1904)	AN, SA
<i>Notoplites elongatus</i> (Busk, 1884)	AN, FI, PE, SA, SG, TF
<i>Odontoporella adpressa</i> (Busk, 1854)	A, FI, NZ, SA, TF
<i>Ogivalia elegans</i> (d'Orbigny, 1847)	FI, PE, SA, SC, SG, TF
<i>Orthoporidra brachyrhyncha</i> Moyano, 1985	AN, TF
<i>Orthoporidra compacta</i> (Waters, 1904)	A, AN, NZ, SG, T
<i>Orthoporidra petiolata</i> (Waters, 1905)	AN, SC, TF
<i>Orthoporidra stenorhyncha</i> Moyano, 1985	AN, SA
<i>Orthoporidroides erectus</i> (Waters, 1888)	FI, SC, SG, TF
<i>Osthimosia bicornis</i> (Busk, 1881)	A, AN, B, FI, NZ, PE, SA, SG, TF
<i>Osthimosia curtioscula</i> Hayward, 1992	AN, FI**, SG
<i>Osthimosia eatonensis</i> (Busk, 1881)	A, AN, FI, K, NZ, PE, SA, SG, TF
<i>Osthimosia malingae</i> Hayward, 1992	AN, SA
<i>Osthimosia magna</i> Moyano, 1974	FI, SA, TF
<i>Osthimosia multifaria</i> Hayward and Winston, 2011	FI**, TF
<i>Osthimosia signata</i> (Busk, 1881)	AN, SC
<i>Paracellaria cellarioides</i> Hayward and Thorpe, 1989	FI, SA, SG, TF
<i>Paracellaria elephantina</i> Hayward and Thorpe, 1989	AN, SA

<i>Parafigularia magellanica</i> (Calvet, 1904)	SA, TF
<i>Parasmittina dubitata</i> Hayward, 1980	FI, SA, TF
<i>Platychelyna planulata</i> Hayward, 1980	FI, TF
<i>Plesiothoa australis</i> Moyano and Gordon, 1980	NZ, SA
<i>Porella hyadesi</i> Jullien, 1888	AN, TF
<i>Reteporella antennata</i> Ramalho et al., 2011	SA
<i>Reteporella magellensis</i> (Busk, 1884)	FI, SA, SC, TF
<i>Reteporella longichila</i> Hayward, 1993	AN, SA
<i>Reteporella sulcula</i> Hayward and Winston, 2011	AN, SA
<i>Reteporella tortuosa</i> Hayward and Winston, 2011	AN, SA
<i>Romancheina labiosa</i> (Busk, 1854)	FI**, SA, SC, TF
<i>Sclerodomus denticulatus</i> Busk, 1884	SA
<i>Scruparia ambigua</i> (d'Orbigny, 1847)	AN, NZ, SA, T, TF
<i>Scrupocaberea ornithorhyncus</i> (Wyville Thomson, 1858)	NZ, T, TF
<i>Scrupocellaria puelcha</i> (d'Orbigny, 1847)	SA
<i>Securiflustra bifoliata</i> d'Hondt, 1981	FI
<i>Smittina anecdota</i> Hayward and Thorpe, 1990	AN, SA
<i>Smittina antarctica</i> (Waters, 1904)	AN, FI**, SG
<i>Smittina insulata</i> Hayward and Thorpe, 1990	FI, TF
<i>Smittina jacobensis</i> (Busk, 1884)	FI, PE, SA, TF
<i>Smittina jullieni</i> Moyano, 1983	FI, SA, SG, TF
<i>Smittina lebruni</i> (Waters, 1905)	SA, SC, TF
<i>Smittina leptodentata</i> Hayward and Thorpe, 1990	FI, TF
<i>Smittina marionensis</i> (Busk, 1854)	AN, FI, PE, TF
<i>Smittina monacha</i> Jullien, 1888	FI, SA, SC, TF
<i>Smittina pliofistulata</i> Hayward and Thorpe, 1990	FI
<i>Smittina portiuscula</i> Hayward and Thorpe, 1990	SA
<i>Smittina rogickae</i> Hayward and Taylor, 1984	AN, FI**, SA
<i>Smittina smittiana</i> (Busk, 1884)	AN, FI, SA, SC, TF
<i>Smittina stigmatophora</i> (Busk, 1884)	FI, SA
<i>Smittina undulimargo</i> Moyano, 1983	SC
<i>Smittoidea bulbosa</i> Hayward & Thorpe, 1990	TF

<i>Smittoidea cribrooecia</i> Hayward and Thorpe, 1990	FI
<i>Smittoidea malleata</i> Hayward and Thorpe, 1989	AN, SA
<i>Smittoidea pachydermata</i> Hayward and Thorpe, 1990	FI, SA, SG, TF
<i>Smittoidea rhynchota</i> Hayward and Thorpe, 1990	AN, SG, TF
<i>Smittoidea sigillata</i> (Jullien, 1888)	AN, FI, SA, TF
<i>Stephanollona longispinata</i> (Busk, 1884)	A, NZ, SA
<i>Stomhypselosaria watersi</i> Hayward and Thorpe, 1989	AN, FI, SA, SG, TF
<i>Talivittaticella frigida</i> (Waters, 1904)	AN, PE, SA, TF
<i>Tricellaria aculeata</i> (d'Orbigny, 1847)	A, AN, FI, K, NZ, PE, SA, SC, TF
<i>Turbicellepora patagonica</i> Hayward, 1992	SA
<i>Turritigera cribrata</i> Hayward, 1993	AN, SA, SG
<i>Turritigera stellata</i> Busk, 1884	AN, PE, SA, TF
<i>Umbonula alvarezziana</i> (d'Orbigny, 1847)	SA, TF
<i>Xylochotridens rangifer</i> Hayward & Thorpe, 1989	AN, TF

Fig. 1. Map of the sampling stations from the Falkland and the South Georgia Islands.

A) Falkland Islands; B: South Georgia.



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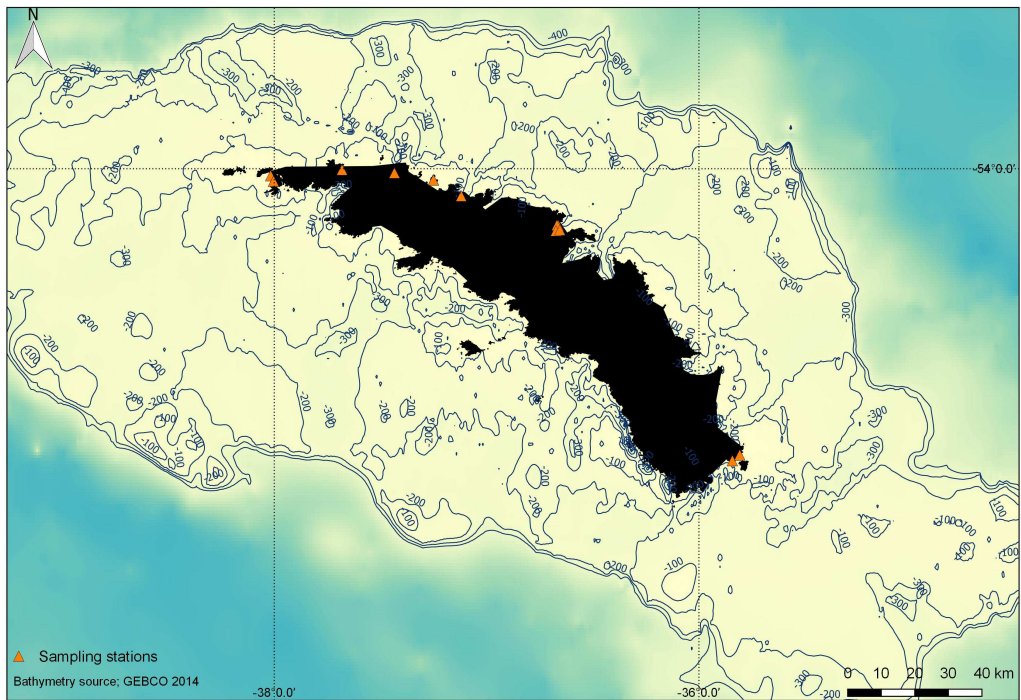
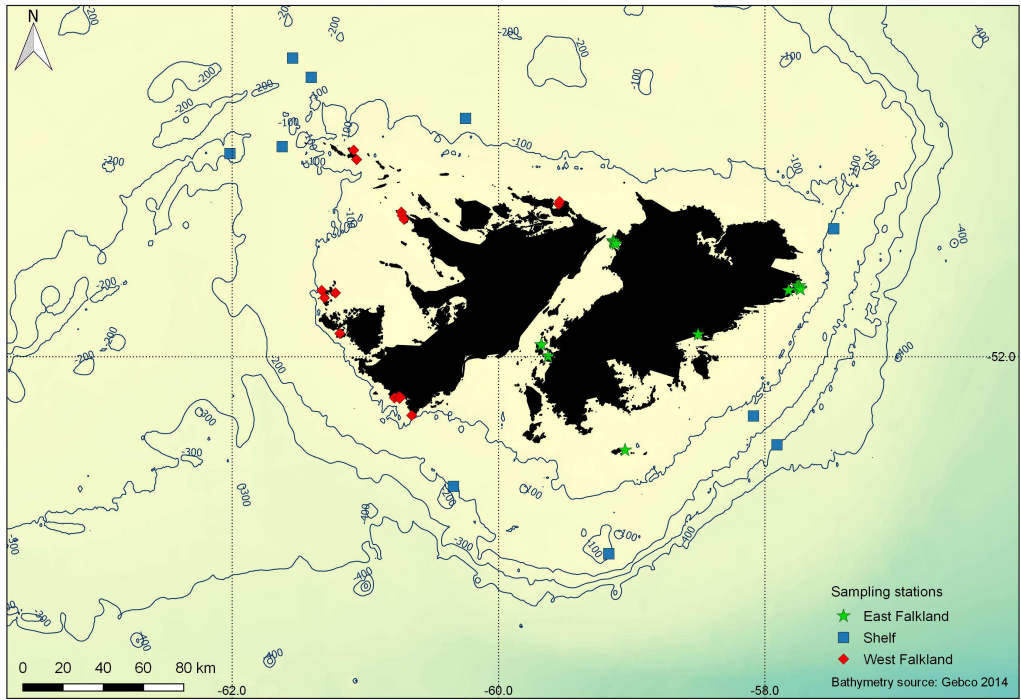
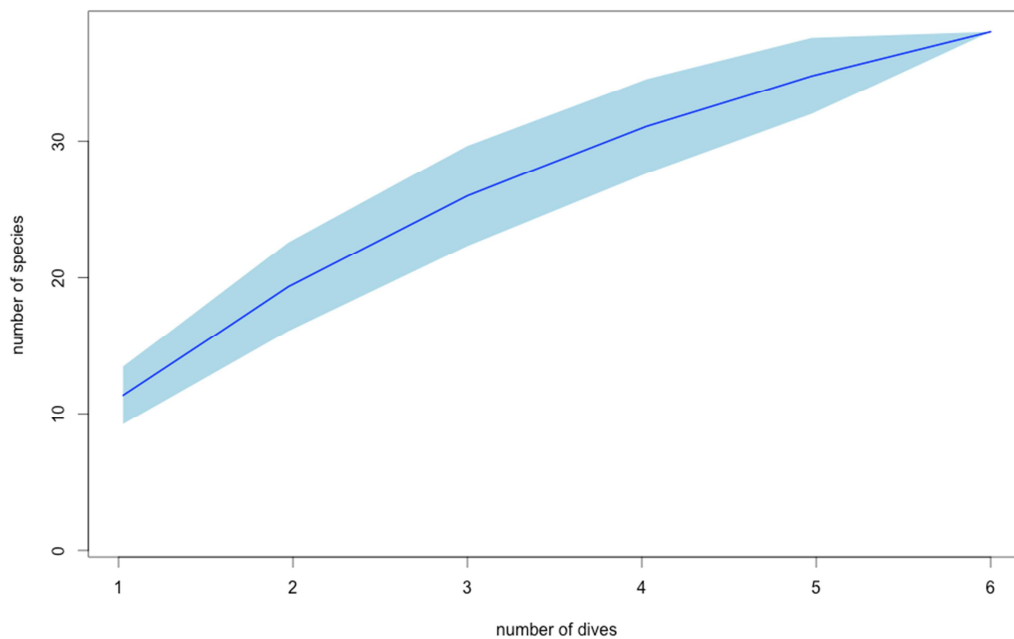


Fig. 2. Expected species accumulation curve (blue) with 95% confidence interval (shaded band) based on data from 6 dive surveys for bryozoans from the Falkland Islands.



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Fig. 3. Expected species accumulation curves for the Falkland (blue) and South Georgia Islands (orange) with 95% confidence interval (shaded bands) based on data from the current study.

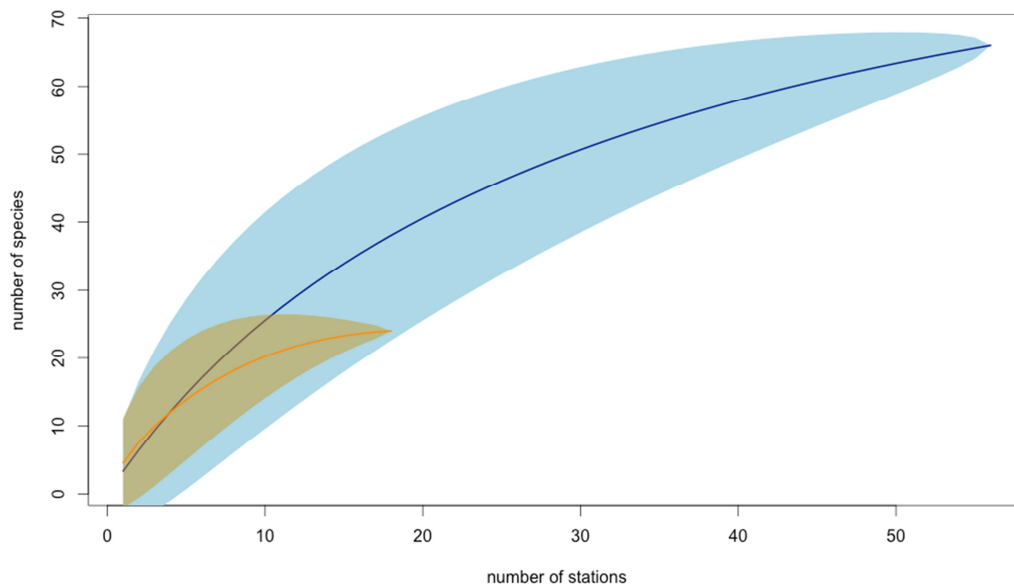
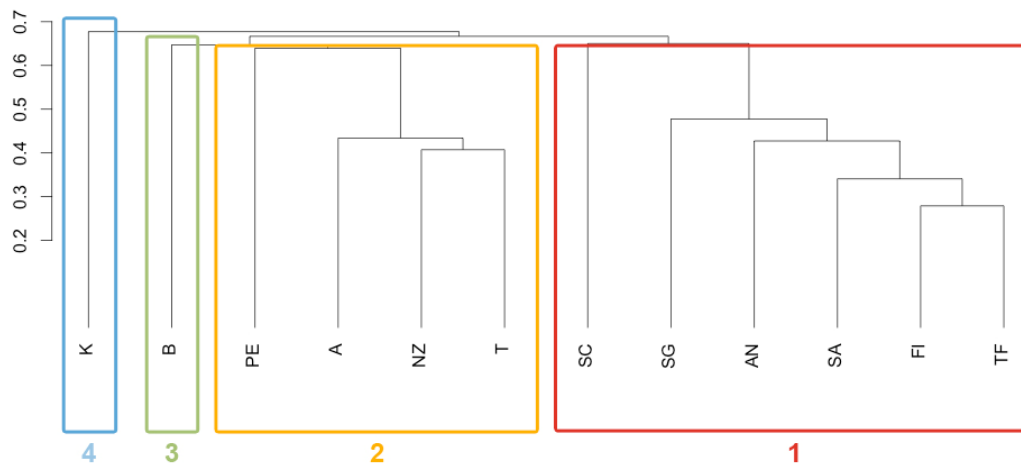


Fig. 4. Dendrogram of the hierarchical clustering (single linkage) of the bryozoan fauna using Bray-Curtis distance. Additional data have been obtained from the literature and from GBIF and ANTABIF databases. Cold-temperate South American Region (provinces: AN = Antarctica; FI = Falkland Islands, SA = Southern Argentina; SC = Southern Chile, and TF = Tierra del Fuego), New Zealand–Australian Region (cold-temperate provinces: A = Antipodes, NZ = New Zealand, and T= Tasmania) and Antarctic and Sub-Antarctic regions (SG = South Georgia, B = Bouvet Island, PE = Prince Edward Islands, and K= Kerguelen).



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A total of 18 unknown bryozoan genera and 23 species were found.

The study reveals new bathymetric ranges in 32 species.

The study gave evidence of the hypothesis of sequential separation of Gondwana.

The study supports the changing concept that the Polar Front is not as impermeable.

Potential dispersal mechanisms are also discussed.

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