

Climate Change, Glacier Retreat and a New Ice-Free Island Offer New Insights on Antarctic Benthic Responses

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Abstract:

The Antarctic Peninsula is among the places on Earth that registered major warming in the last 60 years. Massive ice losses, represented by glacier retreat, ice-shelf collapses and sea-ice reduction are among the main impacts of this regional warming. The loss of sea-bed ice coverage, on the one hand has been affecting benthic assemblages, but on the other it is opening up new areas for benthic colonisation. Potter Cove (South Shetland Islands) offered the opportunity of assessing both processes. We recently reported a sudden shift of benthic assemblages related to increased sedimentation rates caused by glacier retreat. This glacier retreat also uncovered a new island that presents a natural experiment to study Antarctic benthic colonisation and succession. We sampled the new island by photo-transects taken up to 30 m depth. Here, we report an unexpected benthic assemblage characterised by high species richness, diversity and structural complexity with a well-developed three-dimensional structure and epibiotic relationships. Filter feeders comprised the largest trophic group at all depths, mainly ascidians, sponges and bryozoans. Densities were also surprising, recording only six ascidian species with a mean of ~ 310 ind/m². These values are at least an order of magnitude higher than previous Antarctic reports on early colonisation. This finding challenges the extended idea of a slow and continuous recruitment in Antarctica. However, it also opens the question of whether these complex assemblages could have been present under the glacier in ice-free refuges that are now exposed to open sea conditions. Under the current scenario of climate change, these results acquire high relevance as they suggest a two-fold effect of the Antarctic Peninsula warming: the environmental shifts that threaten coastal ecosystems, and also the opening up of new areas for colonisation that may occur at a previously unimagined speed.

Keywords: Antarctica, new ice-free areas, benthos

Introduction

The Antarctic Peninsula and large parts of West Antarctica have warmed significantly over recent decades and are considered among the fastest warming regions on Earth (Steig et al. 2009, Turner et al. 2009, Abram et al. 2013, Bromwich et al. 2013). This warming has profound influences on the cryosphere, including ice-shelf collapses, a decrease in the extent and seasonality of sea-ice and an intensification in the ice scour frequency (Scambos et al. 2000, Stammerjohn et al. 2012, Ducklow et al. 2013, Barnes 2016). Furthermore, the majority of glaciers over the West Antarctic Peninsula (WAP) have retreated during the last 60 years (Cook et al. 2014). The 25 de Mayo/King George Island, one of the South Shetland Islands where Potter Cove is located, is not an exception: ice caps registered a loss of about 20.5 km² in area between 2000 and 2008 (Rückamp et al. 2011). The Fourcade Glacier surrounding Potter Cove shows an accelerated retreat, affecting the hydrographical characteristics of the cove and driving significant changes in established benthic communities (Monien et al. 2011, Rückamp et al. 2011, Schloss et al. 2012, Bers et al. 2013, Quartino et al. 2013, Deregibus et al. 2015, Pasotti et al. 2015, Sahade et al. 2015). This glacier retreat is also opening new ice-free areas, providing an excellent opportunity to study colonisation and succession processes in Antarctic ecosystems. The first study carried out in these newly areas of Potter Cove showed that macroalgae are colonising the newly available substrate, with an almost complete absence of macro- and megafaunal sessile groups (Quartino et al. 2013).

The relative constancy of environmental variables prevailing in Antarctic benthic ecosystems, together with the slow growth rates and population turnover registered in the vast majority of benthic invertebrates, has led to an image of a certain stability in structural patterns and a low speed in ecological processes in the Antarctic benthos

(Arntz et al. 1994, Barnes and Conlan 2007, Smale and Barnes 2008). Despite recent reports of fast colonisation and growth rates of some species following catastrophic environmental changes or in some artificial substrates (Rauschert, 1991, Raes et al. 2010, Gutt et al. 2011, Barnes 2013, Dayton et al. 2013, Fillinger et al. 2013; Quartino et al. 2013, Dayton et al. 2016), the experimental works carried out on colonisation and early succession showed a general pattern of very slow recruitment and development (Dayton, 1979, Pearse and Pearse 1991, Barnes 1996, Stanwell-Smith and Barnes 1997, Bowden 2005, Bowden et al. 2006). These reports suggest that, although there can be fast development in species or in higher taxa such as macroalgae and some sponges, at the community or assemblage level the general idea of slow processes can be maintained. Nevertheless, studies on colonisation and succession are still scarce, pointing to the necessity of further investigation of these processes that will play a key role in the responses of Antarctic benthos to the current climatic change.

The retreat experienced by the Fourcade Glacier surrounding Potter Cove has left not only the newly ice-free areas previously mentioned, but also uncovered a rocky island in the inner part of the cove since 2003 (Quartino et al. 2013). This new island, reaching ~30 m depth, offers an excellent opportunity to study colonisation and primary succession in polar coastal areas. Therefore, our main aim was to investigate the current status of benthic communities on this new island. On the basis of previous reports and experimental studies in Antarctic benthos, we hypothesised that shallow depths on the island will be dominated by macroalgae, and deeper zones by a few animal pioneer species like the ascidian *Molgula pedunculata*, with very low species richness and coverage. We expected to provide some important insights into the possible responses of Antarctic benthos to the current warming, especially as experienced by the Antarctic Peninsula.

Materials and methods

Area of investigation and sampling design

25 de Mayo/King George Island is the largest island in the South Shetland Archipelago, located ~100 km off the tip of the Antarctic Peninsula. Potter Cove (62°14' S, 58°38' W), where the Argentine Antarctic Station Carlini (formerly Jubany) and the Argentine-German Dallmann Laboratory are located, is a small fjord-like inlet that opens into Maxwell Bay (Fig. 1a,b). A shallow sill (<30 m) separates the inner and outer cove sections. The inner cove is characterized by soft sediments and shallower depth (<50 m) than the outer cove, where the bottom is mainly rocky and depths are >100 m. A comprehensive description of the coastal ecosystem of Potter Cove can be found in Wiencke et al. (2008), and the hydrographical characteristics and environmental conditions of the last two decades have been recently reported by Schloss et al. (2012).

Fourcade Glacier shows a remarkable retreat of several hundred metres that, in 2003, uncovered a new island (62°13'23.6" S, 58°38'41.0" W, Fig. 1c) in the NE coast of the cove (Rückamp et al. 2011). The accelerated melting of this glacier in recent years has been so fast that currently the island is ~200 m away from the glacier front. The visible surface of the island is relatively small (<80 m long, see Supplementary material Appendix 1, Fig. A1), but the size of the island below the sea surface is considerably larger. The walls of the island are of hard rocky substrate with steep slopes, even with vertical cliffs, and reach a maximum depth of 30 m. The island topography is irregular, with occasional step-like terraces, numerous overhangs, small caves and crevices, and it is surrounded by soft bottoms. Sediment accumulation rates at this location are relatively high (Pasotti et al. 2015).

Photographic surveys of the island walls at 10, 15, 20, 25 and 30 m depths were undertaken during the austral summer from December 2009 to March 2010 by SCUBA diving. A high definition SONY SR-12 digital camera housed in an Amphibico case and fitted with 2 led lights was used to take the pictures. An aluminum frame (40 x 30 cm) was attached to the housing and used to quantify the sampled area. At each depth profile, photographs were taken every ca. 2 metres along the fixed transect. A total of 50 replicates were taken at each depth, resulting in a sampled area of $\sim 30 \text{ m}^2$. The resolution of images was sufficiently fine to detect and identify organisms as small as $\sim 10 \text{ mm}$ in diameter. High definition video transects along the island were also recorded as supplementary material in support of the photographs, including a video transect taken at 5 m depth that was not taken into account for analyses and was just used as an observational approach to the assemblage features.

As a local control and to further compare with the assemblages present in the island, a series of artificial panels and cleaned natural areas were established by SCUBA diving in the island in December 2009. Eleven experimental round PVC panels (grey, 33 cm diameter, 1.5 cm thick) were installed in an approximately horizontal line along a 30-m-section of the wall at 15 m depth. The distance between the panels varied from 2 to 3 m depending on the relief of the rock wall. The panels were sanded to increase rugosity and their circular shape minimised edge effects per surface unit. Then, to test and avoid material effects, five natural areas of 40 x 30 cm at 15 m depth were cleaned, all the flora and fauna were removed, and they were brushed until bare rock was observed. Photographs were taken annually to follow colonisation and succession under both treatments.

Data analysis

Photographs were projected onto grids of 100 points and those underlying each organism were counted to estimate percentage cover and bare substratum per square metre. Densities and percent cover were analysed from the photographs with ImageJ (Schneider et al. 2012). All solitary animals in each photograph were counted and the total number divided by the area sampled to estimate densities. All discernible fauna were identified to the lowest possible taxonomic level, which was generally species (although bryozoans and some sponges could not always be identified to this level). Some components of the biota were excluded from the analysis: encrusting taxa (some smaller bryozoans and terebellid polychaetes) could not be accurately identified and quantified. Faunal components were classified into two groups: mobile and sessile animals.

Diversity across different depths was compared using the Shannon-Wiener index H' , Pielou's evenness J' and cumulative k-dominance curves. To test for significant differences among depths, a jackknife procedure was used to obtain pseudovalues that allowed the estimation of mean and variance and the use of ANOVA (Magurran 2004). The Levene test was used to check for variance homogeneity and a Student-Newman-Keuls *post hoc* procedure to detect depths that significantly differed. All abundance values in the text are given ± 1 SE. To assess structural patterns of the assemblages and to analyse vertical and horizontal spatial variations, a series of multivariate analyses were performed. A similarity matrix using Bray-Curtis distance was constructed after a square-root transformation (in order to reduce dominance weight) of percentage cover of the species. The similarity matrix obtained was used to perform descriptive classification and ordination analyses. A cluster analysis using the unweighted pair group method average (UPGMA) to construct the dendrogram was used as a classification analysis, and a non-metric multidimensional scaling (nMDS) was used as

an ordination technique. To facilitate visualisation and interpretation of cluster and nMDS analyses, the original 50 samples per depth were pooled (10 consecutive images) resulting in 5 replicates. The analyses were also performed with the original samples to test for possible bias caused by pooled data, and the output is included in Supplementary material (Appendix 2, Fig. A2a and A2b). Then, to test for significant differences among *a priori* defined assemblages (defined by depths), the same similarity matrix was used to perform a one-way Analysis of Similarities (ANOSIM), and a Similarities of Percentages (SIMPER) analysis was performed to investigate which species were responsible for the observed dissimilarities (Clarke and Gorley 2006). A cut-off point of 75% of total dissimilarity between groups was used. All analyses were performed using the software PAST 2.1 (Hamer et al. 2001), except the diversity indices, which were performed with Infostat (Di Rienzo et al. 2015).

Results

The overall species richness of the island was $S' = 32$. A total of 27 faunal taxa, representing 8 phyla, together with 5 algal species, were recorded (Table 1). Zoobenthos prevailed over macroalgae at all depths sampled (Fig. 2a). However, a video-transect taken at 5 m depth (not included in the analysis) showed a higher cover of macroalgae and a poor faunal community represented by few starfishes and ascidian patches, especially the species *Cnemidocarpa verrucosa*, and by a large number of the limpet *Nacella concinna*. The macroalgae coverage was very low and decreased markedly with depth, reaching a value close to zero at 25–30 m depth ($0.03 \pm 0.02\%$ and $0.02 \pm 0.02\%$ respectively). The maximum macroalgae cover was $7.29 \pm 1.62\%$ at 10 m, and approximately 83% of the total macroalgae cover at this depth was due to a single species, *Plocamium cartilagineum*. Four other algae species were recorded in the study

area but were present at very low percentages (for a detailed description of macroalgal assemblages see Quartino et al. 2013, Deregibus et al. 2015). On the other hand, faunal percentage cover did not show a bathymetric pattern, with the highest, $64.37 \pm 1.99\%$, and the lowest, $35.28 \pm 3.02\%$, registered at 25 and 30 m depth respectively.

Sessile fauna showed much higher coverage and density than mobile fauna, representing 99% of the total cover at 25 m depth (Fig. 2b). Mobile fauna, represented by 12 species dominated numerically by the limpet *N. concinna* and the seastar *Odonstaster validus*, showed a peak of abundance at 10 m, with 3.34% of total fauna abundance, and then decreased constantly with depth, reaching values close to zero at 25–30 m.

Ascidians were represented by only six species, five solitary and one colonial. They were the most abundant group, in terms both of coverage and of density at all depths. Solitary species were the major contributors, with $47.09 \pm 1.67\%$ of coverage and a density of 308.63 ± 51.02 individuals m^{-2} . *Cnemidocarpa verrucosa* was the most abundant species with a density of 125.82 ± 5.71 individuals m^{-2} , followed by *Molgula pedunculata* with 91.91 ± 4.92 individuals m^{-2} (Fig. 3). The other ascidian species were *Corella antarctica*, *Ascidia challengerii*, *Pyura bouvetensis* and the colonial *Sycozoa gaimardi*, just represented by 4 epibiont colonies on bryozoans. The first two species, *C. antarctica* and *A. challengerii*, showed an interesting and contrasting bathymetric distribution pattern. While the density of the former increased with depth (with the exception of 30 m, where its density was low), *A. challengerii* showed the highest density at 10 m depth and decreased with increasing depth.

Sponges followed ascidians in percentage cover with a mean of $3.03 \pm 0.32\%$ (Fig. 4). Total abundance of sponges decreased markedly across the bathymetric gradient, with the lowest percentage cover ($0.9 \pm 0.31\%$) recorded at 30 m depth. One

undetermined species (*Haliclona* sp.2) was the most abundant, representing between 25 and 70% of total sponge coverage, with large colonies reaching more than 50 cm in length. The most diverse phylum within mobile fauna, Echinodermata, were represented by six species of asteroids. *Odontaster validus* was the most abundant asteroid with a mean density of 7.7 ± 0.75 individuals m^{-2} . Other taxa were also present, but their distribution was sparser and coverage was very low (<2%). These were bryozoans, anthozoans, the ctenophore *Lyrocteis flavopallidus*, the nemertean *Parborlasia corrugatus*, the sea slug *Doris kerguelenensis* and the lamellarian gastropod *Marseniopsis mollis*.

Species composition was similar at all depths but estimated indexes: species richness (S'), diversity Shannon: H' (log base 10) and evenness, Pielou: (J'), showed significant differences among depths (ANOVA, $F = 4457.39$, $p < 0.0001$, Supplementary material Appendix 3, Table A1). However, these differences did not show a bathymetric pattern. This is also confirmed by k-dominance curves that showed a higher evenness at 10 m depth but also a higher dominance of the first abundant taxa (*C. verrucosa*) than at other depths such as 20 and 25 m (Supplementary material Appendix 3, Fig. A3).

In spite of the lack of a clear and well-defined bathymetric pattern in diversity, multivariate analyses were able to detect a subtle bathymetric pattern in assemblage structure. The classification analyses clustered samples by depth, where groups were separated at high similarities, indicating that assemblages from different depths were quite homogeneous. But similarities were still higher within than between depths and there was also a gradient with higher similarities between contiguous depths (Fig. 5). This was confirmed by nMDS analysis, which showed samples in a single large group, but with a continuous but clear bathymetric pattern along the main axis (Fig. 6).

ANOSIM also showed a slight but general significant difference between depths (Global ANOSIM $R = 0.19$, $p = 0.01$, 999 permutations). Pairwise comparisons also showed significant differences, especially between interspersed depths, while contiguous depths showed higher similarities as indicated by R values (Supplementary material Appendix 3, Table A2). SIMPER analysis also confirmed slight differences between contiguous depths, and larger differences between alternating depths, e.g. similarity between 10 and 15 m and between 10 and 30 m. The analysis also indicated that the species responsible for the dissimilarities between different depths were the macroalgae *P. cartilagineum* and the ascidian *C. verrucosa* (between 10 m and the rest of the depths), while ascidians explained the differences at all deeper zones (Supplementary material Appendix 3, Table A3).

The succession panels and cleaned natural areas established as controls for the natural experiment represented by the appearance of the island did not show any megafaunal development, which was very different from the assemblages recorded on the island with similar exposure times (Fig. 7).

Discussion

The uncovering of a new island in Potter Cove by glacier retreat is an excellent natural experiment to assess colonisation and succession processes in coastal Antarctic benthic ecosystems. The rich assemblages discovered were a striking and completely unexpected finding that led to the rejection of our initial hypothesis and posed the question as to whether these complex assemblages could develop in such a short time, or if they were already established under the glacier in ice-free refuges. Either of these options presents alternatives that had not been previously reported in Antarctica. To our knowledge, habitats under marine-terminating glaciers (tidewater glaciers) have not

been explored for benthic ecosystems. Moreover, habitats under floating glaciers could be expected to present extreme environmental conditions, for example low, if any, food supply and large salinity changes due to under-ice melt water discharge (Pritchard et al. 2012). On the other hand, if the assemblages observed developed in six years, then colonisation and initial succession can be much faster, even at the multi-species level, than previously thought, which is a challenging idea for the widely held image of low speed processes in Antarctic benthos.

Our results showed rich assemblages, in terms of species richness and diversity, together with high percentage cover and densities (Fig. 8). The high number of taxa present in the island ($S' = 32$) was still lower than that reported for the whole cove using the same methodology and at similar depths (Sahade et al. 2008), but much higher, especially for megafaunal groups, than that reported by successional studies, using panels or following natural disturbances caused by icebergs, carried out in Antarctic or Arctic systems (Dayton 1989, Pearse and Pearse 1991, Rauschert 1991, Stanwell-Smith and Barnes 1997, Barnes and Kuklinski 2005, Bowden 2005, Bowden et al. 2006, Konar 2007, Beuchel and Gulliksen 2008, Gerdes et al. 2008). Successional panels have also shown high coverage after some years but were dominated by encrusting taxa such as bryozoans or polychaetes, with assemblages exhibiting an almost two-dimensional structure (Bowden et al. 2006, Stark 2008). The high colonisation observed in two 20 x 20 cm tiles recovered after three years in Maxwell Bay could throw light on what was observed on the new island. These tiles showed dense colonisation and large sizes of ascidians, especially the species *M. pedunculata*, but unfortunately such results were never registered again (Rauschert 1991). However, the island showed not only high coverage but also high complexity, with a well-developed three-dimensional structure and epibiotic relationships (Supplementary material Appendix 4, Video S4).

Despite the fact that dominant faunal groups (especially ascidians and sponges) were common in both the cove and the island, there were marked differences among taxa in abundance distribution and in assemblage structure (Sahade et al. 2015). The island showed a higher dominance profile than the cove: on the island, ascidians were dominant across all depths surveyed, except for the non-analysed video-transect at 5 m depth, where visual inspection showed higher macroalgae abundance. The other taxa present showed much lower coverage values, reaching all together almost 15% at 10 m depth, with ascidians exceeding 45%. A major aspect of the island assemblages was the consistently high abundance of few taxa, with dense ascidian aggregations and some sponges composing the main bulk density and coverage of fauna. Indeed, the density registered for ascidians is, to our knowledge, among the highest reported so far in polar benthic ecosystems. A mean of ~310 ascidians (individuals per square metre) was registered, while *C. verrucosa* showed 126 individuals/m² followed by *M. pedunculata*, the species considered pioneer, with 92 individuals/m². These values are more than an order of magnitude higher than the total megafaunal abundances recorded in Larsen ice-shelves after collapse or those registered after iceberg disturbances (Teixidó et al. 2007, Gutt et al. 2011). Moreover, in Larsen A South, *M. pedunculata* had a median abundance of 9 individuals/m², while the median abundance of *C. eumyota* was 1.2 individuals/m², 12 years after the disintegration of the Larsen A ice-shelf (Fillinger 2013). Although areas opened by ice-shelf collapses and by glacier retreat are both different systems, in terms of distance to source populations, depths and oceanographic conditions, the similarity in shared and dominant species (mainly ascidians) provides a basis for interesting comparisons. In this sense, Larsen could be considered favoured, with a higher local primary production than Potter Cove (Gutt et al. 2011, Schloss et al. 2012), and the process observed there may be considered as a secondary succession, in

contrast to Potter Cove, which would be a primary succession. While Potter Cove *a priori* would be favoured by the smaller scale and shorter distance to source populations, however the local populations at Potter Cove suffered a marked shift related to increased sedimentation rates due to glacier retreat that especially affected ascidians (Sahade et al. 2015) and thus potential source populations. In fact, the most affected ascidians in areas with higher sediment influence of Potter Cove were *M. pedunculata* and *C. verrucosa*, two of the most abundant species in the island. This again indicates that the assemblages observed in Potter Cove were at least surprising.

Only six ascidian species were recorded on the island, of a total of 17 species reported for Potter Cove (Tatián et al. 1998). Thus ascidians exhibited high abundance in terms of coverage and density, but only a few species compared to the rest of the cove. It is important to note that the majority of ascidian species reported for Potter Cove can colonise from soft to hard substrate types. The species *C. verrucosa*, *M. pedunculata*, *C. antarctica*, *A. challengerii* and *S. gaimardi* were also reported on soft substrates at Potter Cove (Sahade et al. 1998), and *P. bouvetensis* was found exclusively on moraine deposits at 30 m depth (Tatián et al. 1998). Interestingly, only one colonial species, *S. gaimardi*, was recorded on the island out of seven colonial species present in the cove, including species such as *Synoicum adareanum* that shows a strong affinity to hard bottoms and is well-represented in the cove. This difference between colonial and solitary forms could be an interesting indicator of recent colonisation, since colonial and solitary ascidians present different reproductive strategies. Ascidians are hermaphrodites and have lecithotrophic larvae, but solitary species are, in general, broadcast spawners with external fertilisation while colonial forms are brooders with internal fertilisation. This favours a longer pelagic larval duration of solitary forms, allowing increased dispersal potential compared to colonial species (Svane and Young

1989, Ayre et al. 1997, Lambert 2005). In the polar Arctic and Antarctic species that have been studied, solitary ascidians showed a lower genetic structure than colonial or brooding species (Demarchi et al. 2008, Demarchi et al. 2010).

Although sessile and mobile groups presented a similar number of species, sessile fauna were much more abundant in terms of coverage and densities, contrasting with the very low densities of mobile species, with the exceptions of the limpet *N. conncina*, the seastar *O. validus* and the snail *Neobuccinum eatoni*. This pattern of high dominance by few species is expected in initial colonisation and succession stages (Barnes and Conlan 2007, Teixidó et al. 2007, Gutt et al. 2011), but one would also expect major representation of mobile fauna compared with sessile species. Although benthic faunal assemblages on the island appear to be representative of fauna of the cove, some common species were not recorded on the island. As expected, two of the most abundant cove species, the sea pen *Malacobelemnion daytoni* and the bivalve *Laternula elliptica*, were absent due to their preference for soft substrates. However, other groups able to colonise hard substrates, such as crinoids, some sponges and colonial ascidians, were also not present in the island. Moreover, the ubiquitous sea urchin *Sterechinus neumayeri* was not found on the island, although it is a mobile and common species in the cove.

Numerous studies about Antarctica have suggested that benthic community structures in shallow subtidal zones (0–50 m depth) are arranged in discrete zones and change along a bathymetric gradient (see Smale 2008 for review). This typical discrete pattern was not observed in the island but a zonation in benthic assemblages was still observed. A sharper division was evident at shallower areas, where a transition between macroalgae to faunal dominance was registered at around 8 to 10 m depth. At greater depths, the zonation was not as sharp and marked as that described in Antarctic coastal

benthos (Gambi et al. 1994, Sahade et al. 1998, Nonato et al. 2000, Barnes and Brockington 2003, Smale 2008, Sahade et al. 2015). Species richness, diversity and evenness showed slight differences with depth, but differed from the pattern exhibited by these factors in the cove and in the majority of Antarctic coastal areas, where a marked trend of increased diversity with increasing depth was reported (Dayton et al. 1969, Sahade et al. 1998, Nonato et al. 2000, Barnes and Brockington 2003, Smale 2008). Multivariate analysis showed that assemblage structure varied with depth but along a continuum pattern. Cluster and MDS analysis indicated high similarities between samples belonging to the same depth and also between contiguous depths. This was confirmed by ANOSIM and SIMPER analyses, which showed high similarities with slight differences as indicated by R values, but significant differences especially between interspersed depths (e.g. between 15 and 30 m or 10 and 25 m). Macroalgae and ascidians were the taxa responsible for these differences between 10 m and the deeper areas, while ascidians and sponges were the main taxa causing differences among the other depths sampled as indicated by SIMPER analysis.

These results suggest a gradual, continuously shifting pattern in structure and diversity that differs from the typical discrete zonation characteristics of many Antarctic shallow benthic communities including those at Potter Cove, albeit similar to that described in Adelaide Island (Sahade et al. 1998, Barnes and Brockington 2003, Smale 2008). This pattern could be related to the steep slope of the island wall, which includes overhangs and crevices, and drops to 30 m depth where it encounters the horizontal soft bottom. This inclination could have an important buffer effect on two of the main disturbance factors for shallow Antarctic benthos. Usually depth attenuates ice disturbance, which is the main factor in driving the zonation pattern (Dayton et al. 1970, Sahade et al. 1998, Barnes 1999, Gutt 2001, Gutt and Piepenburg 2003, Smale et al.

2007a, 2007b, Teixidó et al. 2007, Torre et al. 2017). In this case, the slope of the wall would reduce the probability of ice impact, allowing the development of high megapibenthic abundance at shallow depths. A second important factor is sediment run-off, especially in areas located close to the glacial termini (Siciński et al. 2012, Torre et al. 2012, Sahade et al. 2015). This would probably impose a shallow distribution limit on macroalgae, due to light penetration (Clark et al. 2013, Quartino et al. 2013, Deregibus et al. 2015). The slope itself could also reduce sedimentation effects on the macrofauna, since lower amounts of inorganic matter per square metre would reach the bottom compared with horizontal substrates. This effect, though, would not be as important in reducing the organic matter supply, as this is lighter than inorganic material and can remain suspended for longer periods (Schloss et al. 1999). Taking into account that the benthic ecosystem at Potter Cove is probably fuelled by allochthonous organic matter of detrital origin (Tatián et al. 2004, Quartino and Boraso de Zaixso 2008), it is also possible that the island, as a complex structure, influences the hydrographical conditions, retarding currents and increasing the water column residence time over it. This phenomenon could thus increase the organic matter supply for these assemblages, which showed a much higher secondary production than those in the cove. Increasing residence time of water column over the island could also favour a higher larvae settlement and further recruitment.

Despite the above-mentioned differences, the island assemblages were more similar to those found in the inner cove, characterised by soft and moraine deposit bottoms, than those in the rocky outer cove. It should be noted that the higher similarity with the cove assemblages was established through observations in the early 90s at 30 m depth, before a marked shift related to increased sedimentation seriously diminished ascidian populations (Sahade et al. 2015). It was also suggested that the assemblages observed

could cope with high sediment loads, until a threshold limit pushed the system to another stage not dominated by ascidians (Sahade et al. 2015). Whether the island assemblages suffer a similar shift, with local ascidian extinction processes, or if they can cope with current sedimentation rates, is an interesting topic to be addressed in the next few years.

The Antarctic benthos are often considered stable due to the apparent persistence of assemblages structural patterns over multiple years in the presence of a relatively constant oceanographic regime. At the same time, biological processes in Antarctica are considered to be slow at different organisational levels, from molecules to communities (Barnes and Conlan 2007, Clarke et al. 2007, Pörtner et al. 2007). Colonisation and succession are no exception, and previous reports either based on artificial substrates or following areas devastated by iceberg impacts are in line with this image (Gutt et al. 1996, Stanwell-Smith and Barnes 1997, Gutt and Starman 2001, Brown et al. 2004, Teixidó et al. 2007). Also benthic assemblages with much longer recovery times as those affected by volcanic activity at Deception Island did not reach richness and abundances of close areas after more than 30 years or the newly opened Larsen areas that after 12 years still shows low diversity and abundances patterns (Cranmer et al. 2003, Lovell and Trego 2003, Gutt et al. 2011). However, fast growth rates, population bursts, rapid colonisation and shifts in benthic structure have also been reported in a few species (Dayton 1989, Rauschert 1991, Gutt et al. 2011, Barnes 2013, Dayton et al. 2013, Dayton et al. 2016). Fillinger et al. (2013) reported a rapid glass sponge expansion in a pre-existing community in a time lapse of four years; this increase was from 0.79 to 1.31 individuals/m² in glass sponge densities, and Dayton et al. (2016) also reported massive recruitment and high growth in glass sponges. In Potter Cove, we registered sponges of up to 0.02 m³ that, if we estimate they have developed in 6 years,

present a growth faster than previously reported (Fillinger et al. 2013, Dayton et al. 2016).

There are many indications that the assemblages found in the new island may have developed in these few years. The dominating species have been indicated as pioneers in several works (Gutt et al. 1996, Teixidó et al. 2004, Gutt et al. 2011, Moon et al. 2015). There is an almost complete absence of colonial ascidian species, and it is possible that such assemblages may have developed due to the absence or scarcity of predators. The latter has been indicated as a potential factor allowing fast growth (Rauschert 1991, Dayton et al. 2016) and, although potential predators, sea stars and sea slugs, were detected in our sampling, it is possible that they arrived after the assemblages were well developed. However, other indicators suggest an assemblage could have developed under the glacier, in ice-free refuges favoured by the island structure. These include the high species richness, coverage and densities recorded, and the large size of some sponges, i.e. big sponges more than 50 cm in height (which with some exceptions are expected to exhibit slow growth rates).

The experimental work with artificial and natural cleaned substrates on the island, as a control for the natural experiment represented by the new island, after six years showed no indication of recruitment and fast development of megafaunal species, but rather some encrusting taxa, such as bryozoans and spirorbid polychaetes, with a pattern more similar to those described by other colonisation studies than to those found on the island. The experimental set-up offered no conclusive answer to whether the assemblages observed were pre-existing or the result of new colonisation and succession, since the patterns observed were not even close to those observed on the island and episodic recruitment processes cannot be discarded. Panels are still in place at Potter Cove and are currently being sampled to help addressing this question.

It is thus still not clear if the assemblages observed are the result of extraordinary and unexpected fast colonisation, or if they were just uncovered and exposed to open-sea conditions. The first scenario of a rapid response would be important for enabling the conservation and survival of these threatened coastal benthic ecosystems along the Antarctic Peninsula, especially inside fjords that are also important biodiversity hotspots (Grange and Smith 2013). In contrast, the second case would be the exposure of these previously protected assemblages to new unfavourable conditions.

The current warming process of the Antarctic Peninsula, causing the retreat of the vast majority of glaciers and ice-shelf collapses, presents coastal ecosystems with environmental changes that are unprecedented in recent millennia, and in the last years, long-term observations in Arctic and Antarctica have revealed profound changes in benthic communities structure associated with climate-driven regime shifts (Kortsch et al. 2012, Sahade et al. 2015, Dayton et al. 2016). Therefore a better knowledge of possible responses is crucial to improving our current understanding and ability to predict outcomes.

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Table Legend

Table 1. Taxonomic list of taxa present on the new island at Potter Cove.

Phylum	Class	Species	Depth (m)				
			10	15	20	25	30
Porifera	Demospongiae	<i>Mycale (Oxymycale) acerata</i>	•	••	•	•	•
		<i>Haliclona</i> sp.1			•	•	•
		<i>Haliclona</i> sp.2	••	••	•	••	•
		<i>Haliclona</i> sp.3	•	•	••	•	•
Cnidaria	Anthozoa	<i>Artemidactis victrix</i>	•				
		<i>Hormosoma scotti</i>	•		•		
		Indet. anthozoa				•	
Nemertea	Anopla	<i>Parborlasia corrugatus</i>	•	•			
Mollusca	Gastropoda	<i>Doris kerguelensis</i>			•		
		<i>Nacella concinna</i>	•	•	•	•	
		<i>Neobuccinum eatoni</i>	•	•	•		•
		<i>Marseniopsis mollis</i>					•
Ctenophora	Tentaculata	<i>Lyrocteis flavopallidus</i>				•	•
Bryozoa	Gymnolaemata	Indet. bryozoa 1	•	•	•	•	••
		Indet. bryozoa 2	•	•	•	•	•
Echinodermata	Asteroidea	<i>Odontaster validus</i>	•	•	•	•	•
		<i>Odontaster meridionalis</i>	•	•	•		
		<i>Perknaster aurorae</i>		•			•
		<i>Perknaster fuscus</i>	•		•	•	•
		Indet. asteroidea 1	•				
		Indet. asteroidea 2			•		
Chordata	Ascidiacea	<i>Sycozoa gaimardi</i>					•
		<i>Ascidia challengerii</i>	••	••	••	••	••
		<i>Corella antarctica</i>	••	••	••	•••	••
		<i>Cnemidocarpa verrucosa</i>	•••••	•••••	•••••	•••••	•••••
		<i>Molgula pedunculata</i>	•••	•••	•••••	•••••	••
		<i>Pyura bouvetensis</i>			•	•	
Rhodophyta	Florideophyceae	<i>Plocamium cartilagineum</i>	•••	•	•		•
		<i>Palmaria decipiens</i>	•		•		
Ochrophyta	Phaeophyceae	<i>Desmarestia</i> sp.	•	•	•	•	
		<i>Himantothallus grandifolius</i>	•				
Chlorophyta	Ulvophyceae	<i>Monostroma hariotii</i>			•	•	

The percentage cover classes at each depth are represented by: • ≤1%; •• 1.01–5%; ••• 5.01–10%; •••• 10.01–15%; ••••• 15.01–20%; •••••• ≥ 20.01%.

Figure Legends

Figure 1. Location of the area of investigation. a) Map of the location of South Shetland Island on the Antarctic Peninsula (black square). b) Location of Potter Cove in 25 de Mayo/King George Island and c) satellite image of Potter Cove (Google Earth, 2011). The dotted line marks the position of the Fourcade Glacier in 2003: the new island is framed in red.

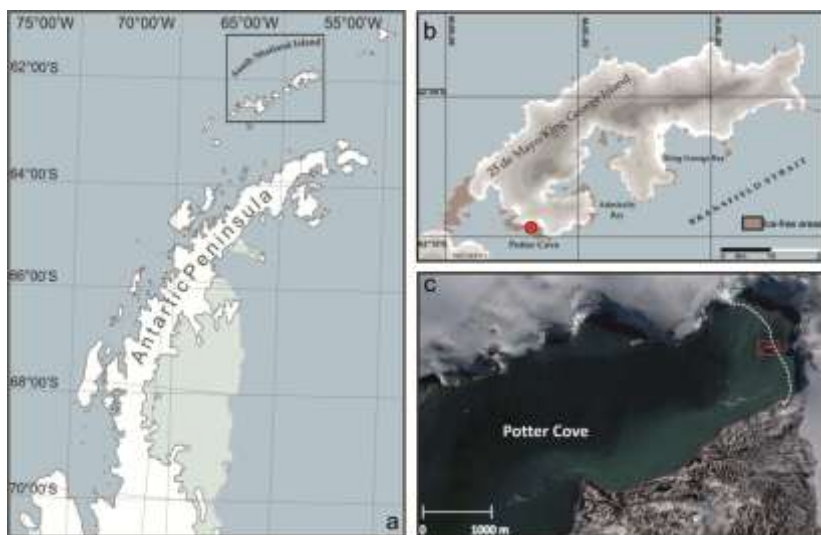


Figure 2a) Faunal and macroalgae abundance (percent cover) at the depths sampled (metres) at Potter Cove. Bars represent \pm SE. **b)** Sessile and mobile faunal group abundance (percent cover) at the depths sampled (metres) at Potter Cove. Bars represent \pm SE.

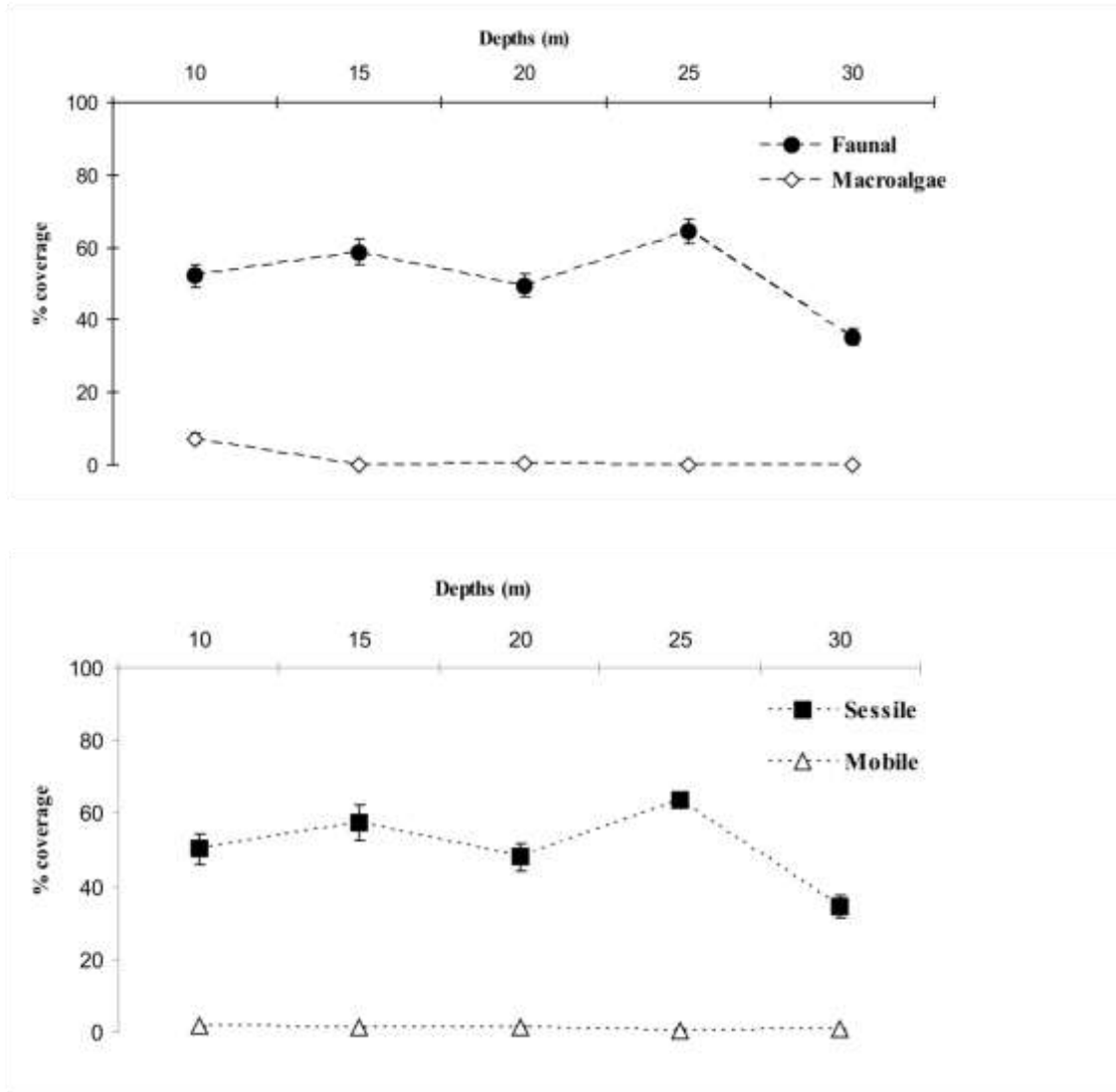


Figure 3. Density (individuals m^2) of the most abundant solitary ascidian species on the new island at Potter Cove. Bars represent \pm SE.

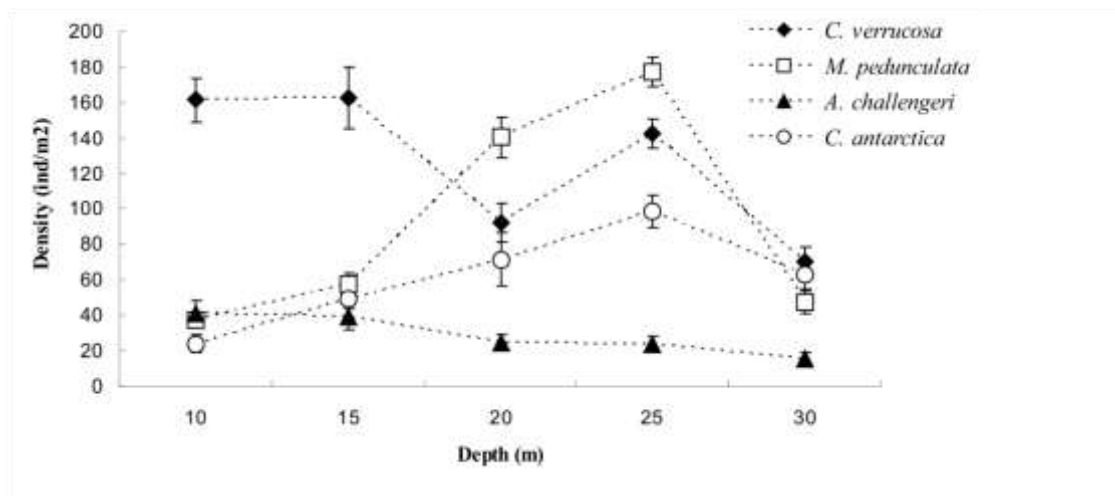


Figure 4. Percentage of coverage of major taxa present on the new island by depth (m) at Potter Cove.

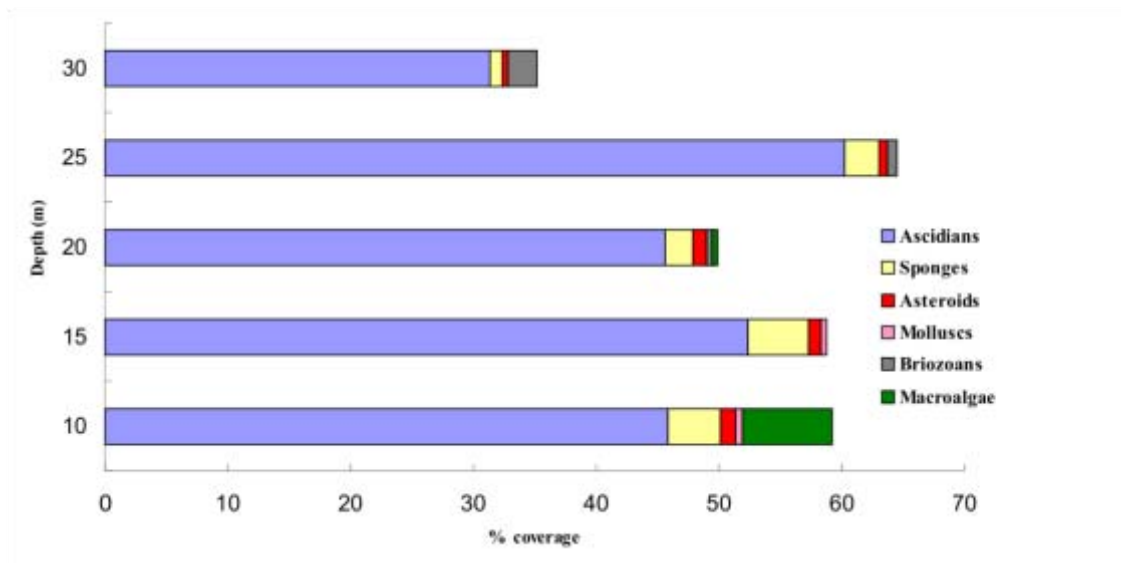


Figure 5. Multivariate assemblage analysis based on Bray–Curtis similarity matrix of square-root transformed abundance data (% cover). The original 50 samples per depth were pooled (10 consecutive images) resulting in 5 replicates to facilitate visualisation of cluster dendrogram (UPGMA).

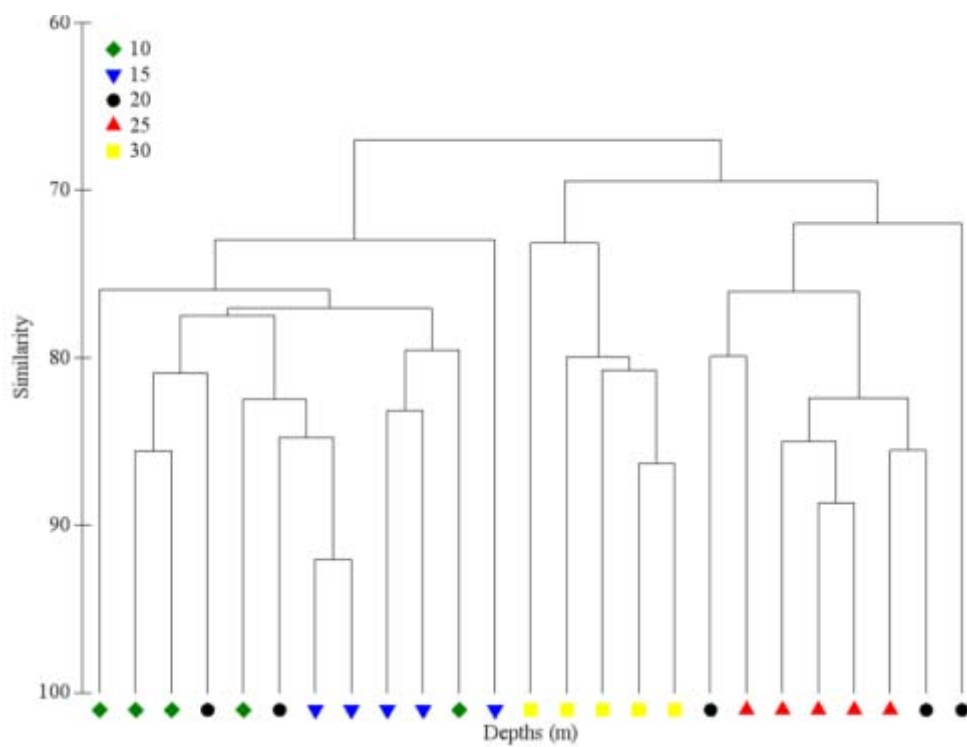


Figure 6. Multivariate assemblage analysis based on Bray–Curtis similarity matrix of square-root transformed abundance data (% cover). The original 50 samples per depth were pooled (10 consecutive images) resulting in 5 replicates to facilitate visualisation of nMDS.

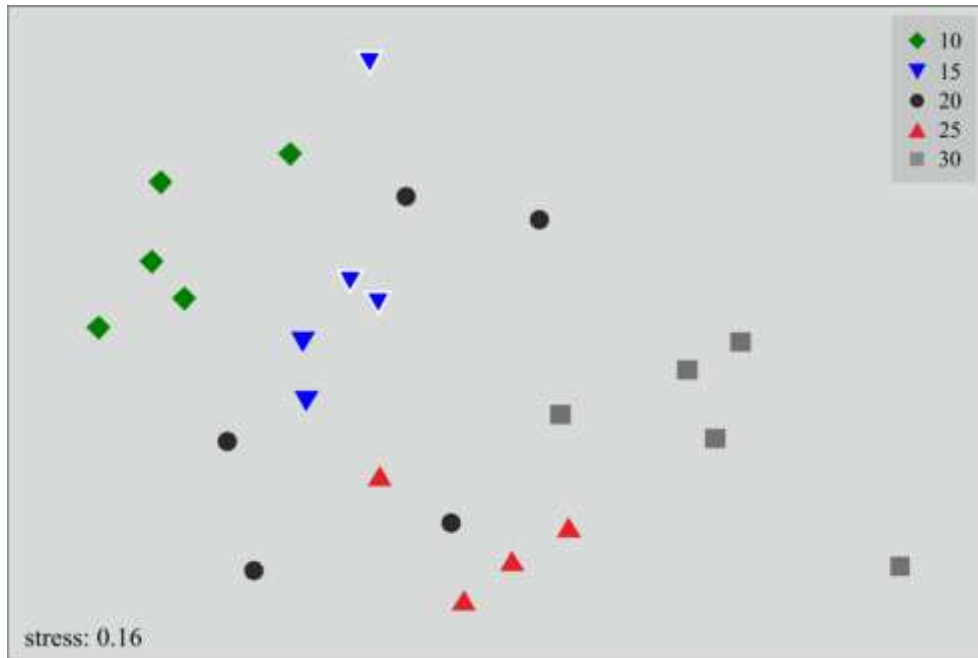


Figure 7. Artificial panels and cleaned natural areas established on the new island of Potter Cove in December 2009. a, b) Two representative examples of panels (33 cm diameter) photographed at 15 m depth after 6 years. c) One of the five natural areas of 40 x 30 cm at 15 m depth after 6 years cleaned.

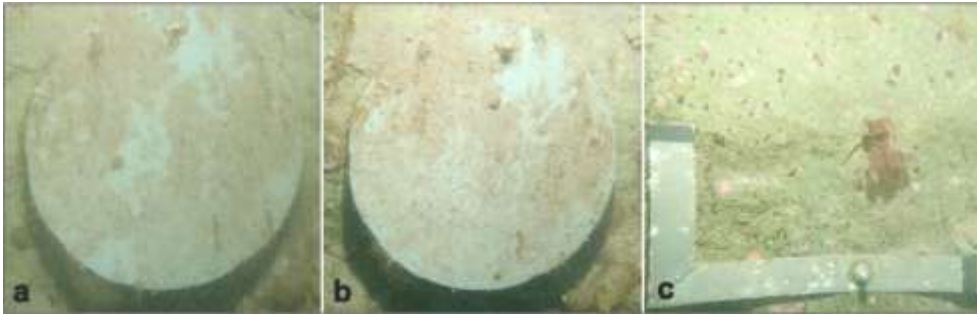


Figure 8. A real picture of the island in front of Fourcade glacier and a schematic drawing of the under-water topography. Pictures of different organisms found on the island are shown in the circles. **a)** Macroalgae and the sea star *O. validus*. **b)** The ascidians *C. verrucosa* and *M. pedunculata*. **c)** *Haliclona* sp.2 and *C. verrucosa*. **d)** *C. verrucosa*. **e)** *M. pedunculata*, sponges and a sea-star.

