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Growth form classification for sessile suspension feeders and their distribution in Antarctic fjord, King George Island

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Abstract: Sessile suspension feeders depend primarily on availability of a space to settle and access to the water column. Their sessile nature incapacitates displacement during disturbances thus they rely on their morphology to overcome selective processes. We classified the assemblage of SSF from Mackellar Inlet (King George Island, Antarctica) according to their growth forms (GF) and epibiotic association type, the latter based on direct observation of the epibiotic behaviour of every individual. Organisms that did not comply with any previously established GF were grouped into 'other GF'. Sampling stations were distributed across the fjord following a gradient based primarily on the distance to Domeyko Glacier (inner, middle, outer sections). Seven GF were recognised in the glaciomarine fjord: tree, bush, stalk, mound, flat, runner, and sheet. Four types of epibiotic associations were identified: basibiont, both facultative epibiont and basibiont, facultative epibiont (non-basibiont), and epibiont. Our results showed that the tree GF were found in the inner and middle sections, mound in middle and outer, and flat across all fjord sections. These GF enhanced GF-diversity since they constituted additional substrate for most of the 'other GF' which had primarily an epibiotic strategy. Contrastingly, bush, runner and stalk GF were only found in the outer section of the fjord, thus the most distanced from periglacial disturbances. The GF distribution was consistent with distance to glacier, both in number and strategies. These results highlight the potentialities of the morpho-functional classification applied to Antarctic sessile suspension feeders to help understand their distribution based on adaptive capabilities.

Keywords: Antarctica, macrozoobenthos, functional morphology, life strategies, soft bottom.

Introduction

Antarctic sessile suspension feeders (SSF) are characterised by high species richness, diversity, and biomass (Brey and Gerdes 1997; Gutt 2007; Clarke 2008; Pabis *et al.* 2011). Bryozoans, cnidarians, ascidians, and sponges contribute considerably to the benthic structure in the Southern Ocean, and are key components of energy transfer *i.e.,* pelagic-benthic coupling (Brey and Gerdes 1997; Gutt and Starmans 1998; Gili *et al*. 2001; Tatián *et al*. 2008a; Alurralde *et al.* 2019). The functioning of taxa feeding actively or passively on organic particles and small living organisms in the water column transported by sea currents depends on the influx of particulate material (organic and inorganic) and physical disturbances (Gutt 2007; Pabis *et al*. 2011). The increase of ocean temperature in recent decades caused by climate change enhances sedimentation and ice scouring, have a direct impact on SSF assemblages (Meredith and King 2005; Barnes and Souster 2011; Rückamp *et al.* 2011; Barnes 2017).

Understanding the mechanisms that regulate species adaptive capacities is essential for predicting which populations are likely to be affected, benefited, or remain neutral to changing environmental conditions (Morley *et al.* 2019). For SSF, the morphology is a valuable functional trait through which they cope with environmental pressures (Momo *et al.* 2008; Tatián *et al.* 2008b; Torre *et al.* 2014). Basic patterns are repeated between phylogenetically distant taxa that may represent convergent adaptations to cope with similar environmental conditions (Jackson 1979; Kott 1989). Jackson (1979) proposed a classification of growth forms (GF) that divides colonial organisms into six groups based on space occupancy: tree, plate, mound, vine, runner, and sheet. This model was based on geometric parameters (size and shape) that enabled the interpretation of their adaptive significance and specific potential for survival. Some growth forms had increased commitment with survival (trees ≥ plates > mounds > sheets) while the other GF, such as runners and vines, were considered as 'fugitives' by exhibiting a refuge-seeking strategy (Jackson 1979).

In an environment with high sediment discharge, such as inner parts of fjords, diversity of functional traits is lower and increases with distance from disturbance, as reflected in peak biological parameter values (Pęcherzewski 1980; Włodarska-Kowalczuk *et al.* 2005). The GF approach has been used before in polar latitudes for the assessment of distributions and adaptive strategies of benthos in disturbed environments (Teixidó *et al*. 2004; Momo *et al.* 2008; Pabis *et al.* 2014; Torre *et al*. 2014; Krzemińska and Kukliński 2018). Teixidó *et al.* (2004) examined macrobenthic recovery patterns after ice disturbance in the Weddell Sea and concluded that GF cover patterns changed along successional stages.

GF classification has the potential to summarize and characterize local-to-regional distributions along environmental gradients (Stach 1936; Schopf 1969; Ryland and Warner 1986; Nelson *et al.* 1988) as well as to increase the understanding of the environmental pressures and opportunities faced by organisms (Chapin *et al*. 2000; de Bello *et al*. 2010; Díaz *et al.* 2013; Pérez-Harguindeguy *et al.* 2013). This knowledge is also essential for understanding the changes that can occur in an ecosystem caused by changing environmental conditions (Smith 1995; Amini *et al.* 2004). In this study, we aimed to classify the SSF assemblage of Mackellar Inlet into a GF classification and evaluate their spatial distribution. We hypothesize that the distance to the glacier influences the distribution of GF in Mackellar Inlet.

Study area

Mackellar Inlet is a glaciomarine fjord of approximately 16 km^2 surface area found within Admiralty Bay, the largest bay of King George Island (KGI) (Fig 1). KGI is situated on the border of Antarctic and Subantarctic climatic zones. Westerly winds predominate in Admiralty Bay, with west-southwest reaching high velocities and generating strong downfall winds (Kowalski 1985; Zwolska and Janecki 1999). These winds induce an outflow of surface waters into the Bransfield Strait and inflow of deep waters that prevents the formation of any distinct parameters (Pruszak 1980; Lipski 1987; Lipski and Rakusa-Suszczewski

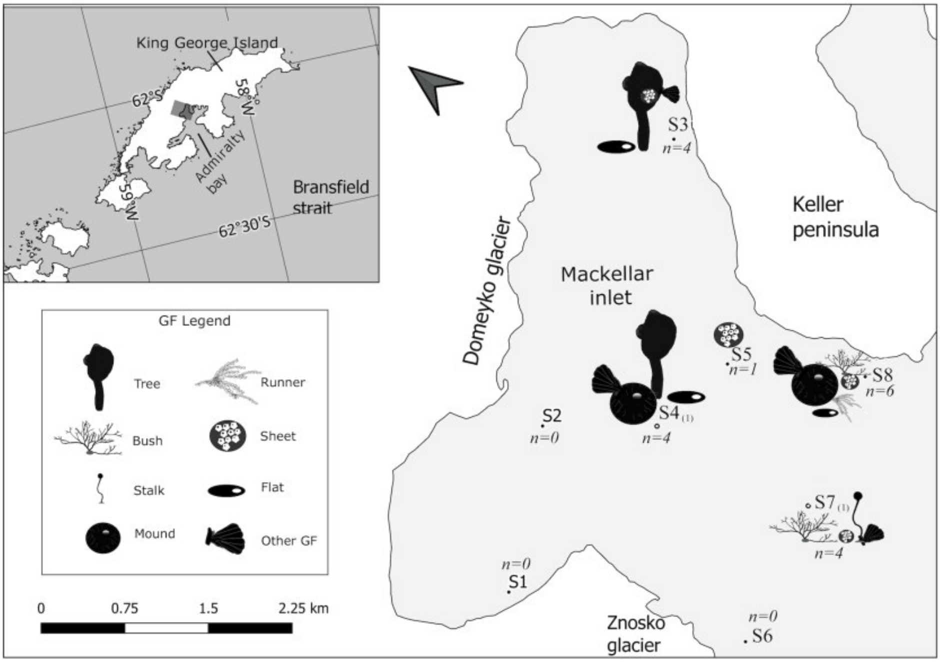

Fig. 1. Growth forms (GF) distribution and composition across Mackellar Inlet in King George Island during austral summer 2017 (n = number of GFs). Subscripts in S4 and S7 indicate single samples with no replicates.

1990; Robakiewicz and Rakusa-Suszczewski 1999). Currents in the center of the bay are more intense than within inlets which are low-energy due to tides (Campos *et al.* 2012).

Subglacial streams bring melted waters into the fjord that contain large amounts of suspended mineral matter (Pęcherzewski 1980). The total amount of inorganic suspended matter in Admiralty Bay over a year varies from 32 264 to 171 000 tons (Rakusa-Suszczewski 1995), and due to climate-induced phenomena a tendency to of increased sedimentation has been reported (Gilbert *et al.* 2002; Sanders *et al.* 2010; Cook *et al.* 2016). The belt of hard-bottom is narrow in Mackellar Inlet, and it quickly changes to soft-bottom dominated by silt and mud (Zielinski 1990). Calving of glaciers also delivers dropstones to nearby areas, enhancing heterogeneity and influencing on benthic biodiversity (Gutt 2001; Ziegler *et al.* 2016). Some oceanographic phenomena typical for coastal waters are recognized, such as the circulation generated by tides and the nearshore upwelling (Pruszak 1980; Lipski 1987).

Material and methods

Sampling design. — The fjord was intentionally divided into three sections in a distance gradient to Domeyko Glacier, and eight sampling stations across sections were surveyed (Table 1, Fig. 1). In each station four replicates of soft-bottom macrozoobenthos were collected from an inflatable boat by manually deploying a 0.05 m² Van Veen grab sampler, except in stations S4 and S7 where

Table 1

Sampling stations from Mackellar Inlet, King George Island (WGS84 geographic system) and environmental data measurements. Subscripts in S4 and S7 indicate single samples, no replicates.

Sampling stations	Latitude (°W)	Longitude (°S)	Distance from Domeyko Glacier front (m)	Fjord section	Depth (m)	Folk classification
S1	62.0906	58.4839	1000	inner	~41	gravelly mud
S2	62.0808	58.4650	900	inner	~34	gravelly mud
S3	62.0667	58.4221	1300	inner	~34	gravelly mud
$S4_{(1)}$	62.0853	58.4487	2000	middle	~41	silt
S5	62.0839	58.4333	2400	middle	~47	gravelly mud
S6	62.1033	58.4541	400*	outer	~20	gravelly mud
$S7_{(1)}$	62.0966	58.4337	3600	outer	~106	sandy silt
S8	62.0902	58.4147	3500	outer	~16	muddy gravel
* Distance to Znosko Glacier						

only one sample in each was collected ($S4_{(1)}$ and $S7_{(1)}$). Sessile suspension feeding organisms were retrieved and fixed with 4% formalin, and few grab samples were preserved in 70% ethanol for genetic research.

Three parameters relevant to the distribution of the GF are presented in Table 1. Approximate linear distances of each station to the front of the Domeyko Glacier (Znosko Glacier end for S6) were measured in ArcMap 10.7 using a WorldView-2 satellite image from March 2012 (see acknowledgments). Depth corresponds to the first grab deployed at each station and samples for grain-size analysis were collected by the INGEMMET during the ANTAR XXV Expedition in 2018. Folk (1954) grain-size classification and nomenclature were used (Table 1). For other single measurements of environmental parameters taken at the moment or same week of sampling (Appendix 1).

Growth form classification. — Specimens classified as SSF following classification by Barnes and Sands (2017) were taxonomically identified following Monniot and Monniot (1983), Primo and Vázquez (2007) and Monniot *et al.* (2011) and for ascidians (Appendix 2) and Hayward (1995) and the Atlas of Antarctic Bryozoa (http://www.iopan.gda.pl/ekologia/Antarctica/index.php?go=Taxa) for bryozoans (Appendix 3). Additionally, some identities were confirmed by specialists (see acknowledgments). Samples are stored in the scientific collection of the Universidad Científica del Sur (Peru) (Appendix 4).

We adapted the GF classification by Jackson (1979) distinguishing tree, plate, vine, mound, runner and sheet forms to suit better the shallow Antarctic assemblages with morpho-functional descriptions of other authors (*i.e,* bush, stalk and flat) (Connell and Keough 1985; Hageman *et al*. 1998; Torre *et al.* 2014) (Table 2). Eleven taxa have not been previously described morphofunctionally, therefore they were classified as 'other GF'. The attributes of each GF are focused on the disposition of the colony or body in relation to the water column and substrate, thus in how they occupy space (Connell and Keough 1985). Additionally, we report the type of epibiotic association (*i.e.,* organism-substrate relationship) found for each taxa, which included: 1) basibiont [b]; 2) both facultative epibiont and basibiont [fe–b]; 3) facultative epibiont (non-basibiont) [fe]; and 4) epibiont [e] (strict epibiont on this study) (Wahl and Mark 1999).

Data analysis. — Each station was described by GF number (n), GF relative abundance, and number of taxa (S') per GF. The proportion of GF (%) was calculated for each station. GF number and number of taxa per GF in each station were discussed in relation to distance to the glacier as glacier disturbance is one the most important structural forces for zoobenthic assemblages in Admiralty Bay (Siciński *et al.* 2011). For distribution analysis, GF abundance data was transformed into presence/absence to produce a two-way cluster analysis (Q-mode for stations, and R-mode for GF) using Sørensen (dis)similarity matrix. Routines were performed in PRIMER 6 (Clarke and Gorley 2006).

Table 2.

Descriptions and ecological implications of the growth forms found in a shallow soft-bottom Antarctic fjord. Classification based on Jackson (1979) but adapted to suit the Antarctic assembly: tree, plate, vine, mound, runner, and sheet proposed by Jackson (1979), bush by Connell and Keough (1985), stalk by Hageman *et al*. (1998) and flat Momo *et al*. (2008).

Growth Form (GF)		Description	Ecological implications
Tree		Large and erect solitary or colonial organisms with a limited area of adhesion to the substrate by a main trunk (Jackson, 1979). In colonial organisms highly calcified skeleton are recognised and can have zooecial apertures from the tip of the base (Hageman et al., 1998).	Exploits different ranges of flow in the water column (Ryland & Warner, 1986; Abelson et al., 1991), escape from burial by high sedimentation or resuspension and evade competitors. High-risk growth form because of its dependence on a small attachment area (Jackson, 1979).
Plates		Flattened, foliose more or less parallel to the substratum colonial organisms and projecting into the water column from a limited zone of basal attachment (Jackson, 1979).	With high degree of isolation of surface tissues from substratum, but with high commmitment to attachment and area of settelement. Flattened surfaces may be effective in obtaining resuspended resources, but vulnerable to strong water (Jackson, 1979).
Vine		Linear or irregulary branched, erect, semierect, or colonial climbing forms, with one or more restricted zones of attachment to the substratum (Jackson, 1979).	Their low commitment to their point of settlement and elevated disposition, helps in the avoiding potential disadvantages of substratum, and accesibility to fine particles in the water column (Jackson, 1979; Abelson et al., 1991).
Bush		Erect and flexible colonial organisms that can branch from the base but with a main point of adhesion to the substrate (Connell & Keough, 1985).	Exploits the environmental energy through the withstand of multidirectional or turbulent waters by its high flexibility (Jackson, 1979; Ryland & Warner, 1986). Not very competitive for space (Connell & Keough, 1985) but can have epibiont habit (Rubin, 1987).
Stalk		Solitary and colonial organisms with a peduncle much longer and thinner than their body. In colonial organisms they do not have zooids on the peduncle (Hageman et al., 1998).	This growth form enambles the exploitation of particles of the water column and the escape from burial.
Mound		Solitary or colonial organisms that occupy an important part of the bottom relative to their surface tissue, with vertical and horizontal growth (Jackson, 1979).	Can occupy an important area of attachment. Good competitors for space. Dominance of this GF is expected in late stages of colonisation (Teixidó, 2004).
Flat		Solitary organisms with a depressed morphological appearance. They may have siphons, or other respiratory apparatus that protrude the body.	Some species do not need adherence to a hard substrate, this facilitates recruitment were substrate is a limited resource. Instead they contribute as one.
Runner		Linear or branched colonial organisms that grow along the substrate. They can be fully, or only attached at some points (Jackso, 1979).	Its directional growth allows for rapid growth rates and shelter search strategies, which in turn helps avoide competitors and environmental disturbances (Buss, 1979; Jackson, 1979; Rubin, 1987).
Sheet		Colonial organisms fully adhered to the substrate with unlimited or limited horizontal growth (Jackson, 1979).	This form prevents mechanical or predatory damage (Berril, 1955). Can occupy cryptic habitats and colonize quickly (Goodbody, 1963; Jackson, 1977).
Other GFs		Organisms that present morphological features that have not been previously described as traits influencing over their fitness.	

Results

Of the total number of individuals and colonies collected (390), 87% were ascidians and 13% bryozoans within 18 and 13 taxa, respectively. Seven GF were identified for Mackellar Inlet: tree, bush, stalked, mound, flat, runner and sheet; and an additional group was considered ('other GF') (Table 3). The latter was the most speciose with eleven taxa, represented mostly by epibiotic colonial ascidians with small rounded or elongated forms, and only one bryozoan taxon was placed in this group as Tubuliporidae (Johnston, 1837). Seven taxa had sheet GF, three taxa had mound and bush GF, and two had tree and flat GF. Each stalk and runner GF were represented by one taxon (Table 3). With the exception of 'other GF', all growth forms were composed either by ascidians or bryozoans.

All taxa from the same GF shared an epibiotic association type, except for mound which had both solitary *Pyura setosa* (Sluiter, 1905) and colonial *Aplidium* spp. representatives, classified as basibiont and without epibiotic association type (non-epibiont non-basibiont), respectively. Additionally, some GF shared their epibiotic association type: tree, flat and the solitary mound were basibionts; bush and runner were facultative epibionts and basibiont; stalk and sheet were facultative epibionts and the majority of 'other GF' were epibionts (Table 3).

No sessile suspension feeders were found in stations S1, S2, and S6. Station S8 had the highest GF number followed by S7, both in the outer section of the fjord. Only one GF was found in S5, located in the middle section of the fjord. Sheet GF had the widest distribution, found at five stations (absent only in $S4_{(1)}$) (Figs. 1 and 2). Sheet and flat were found in all three sections of the fjord, while bush ($S7_{(1)}$ and S8), runner (S8) and stalk ($S7_{(1)}$) were only found in the outer stations of the fjord.

The most abundant station was $S4_{(1)}$ with 307 organisms of which > 97% were epibiotic living over an aggregation of basibionts (Fig. 2). In S3 the abundance was low (11), but tree and flat GF allowed for the presence of some epibiotic forms. In S5 sheet was the only GF, with 15 colonies. Stations $S7_{(1)}$ and S8 had 19 and 13 taxa, respectively. Of the total abundance across stations (390 individuals and colonies) 84% were classified as 'other GF' (329), and the majority of which (234) were *Tylobranchion* sp.1 zooids were found individually embedded in their own tunic and were thus counted as such.

The number of GF and taxa changed in relation to the distance from the glacier (Fig. 3). GF number was the highest in station S8, the most distant to Domeyko Glacier, while the inner S1, S2 did not present any SSF. No GF were found in S6 located in the outer section of the fjord but the closest to Znosko Glacier. On the other hand, S3, $S4_{(1)}$ and $S7_{(1)}$ stations from the inner, middle, and outer sections presented the same number of GF (Fig. 3). The number of taxa constantly increased with the distance from the glacier, except for S5 (see Appendix 5).

Table 3

Classification of ascidians and bryozoans found in Mackellar Inlet (King George Island) during the austral summer 2017 (ANTAR XXIV) based on growth forms; and their corresponding epibiotic association type: basibiont (b), facultative epibiont and basibiont (fe–b), facultative epibiont only (fe) (non-basibiont), epibiont (e). A – Ascidiacea, B – Bryozoa.

Growth Forms (GF)	taxa	taxonomic group		epibiotic association type			
		A	B	b	fe-b	fe	e
Tree	*Molgula pedunculata* (Herdman, 1881)			x			
	Cnemidocarpa verrucosa (Lesson, 1830)			x			
Bush	*Nematoflustra flagellata* (Waters, 1904)				x		
	Himantozoum sp. 1 (Harmer, 1923)				x		
	Camptoplites sp. (Harmer, 1923)				x		
Stalk	*Sycozoa gaimardi* (Herdman, 1886)					x	
Mound	*Pyura setosa* (Sluiter, 1905)			x			
	Aplidium sp. 2 (Savigny, 1816)						
	Aplidium sp. 3 (Savigny, 1816)						
Flat	*Ascidia challengeri* (Herdman, 1882)			x			
	Corella eumyota (Traustedt, 1882)			x			
Runner	*Himantozoum* sp. 2 (Harmer, 1923)				x		
Sheet	*Fenestrulina* sp. 1 (Jullien, 1888)					x	
	Fenestrulina sp. 2 (Jullien, 1888)					x	
	Micropora sp. (Gray, 1848)					x	
	Inversiula nutrix (Jullien, 1888)					x	
	Antarctothoa sp. (Moyano, 1987)					x	
	Patinella sp. (Dall, 1871)					x	
	Bryozoa sp. 1					x	
	Bryozoa sp. 2					x	
Other GF	*Tylobranchion speciosum* (Herdman, 1886)						x
	Tylobranchion sp. (Herdman, 1886)						x
	Aplousobranchia sp. 1						x
	Aplousobranchia sp. 2						x
	Aplousobranchia sp. 3						x
	Cnemidocarpa sp. (Huntsman, 1913)				x		
	Styelidae (Herdman, 1881)						x
	Polyclinidae sp. 1 (Milne Edwards, 1841)						x
	Aplidium sp. 1 (Savigny, 1816)						x
	Molgula enodis (Sluiter, 1912)						x
	Tubuliporidae (Johnston, 1837)						x

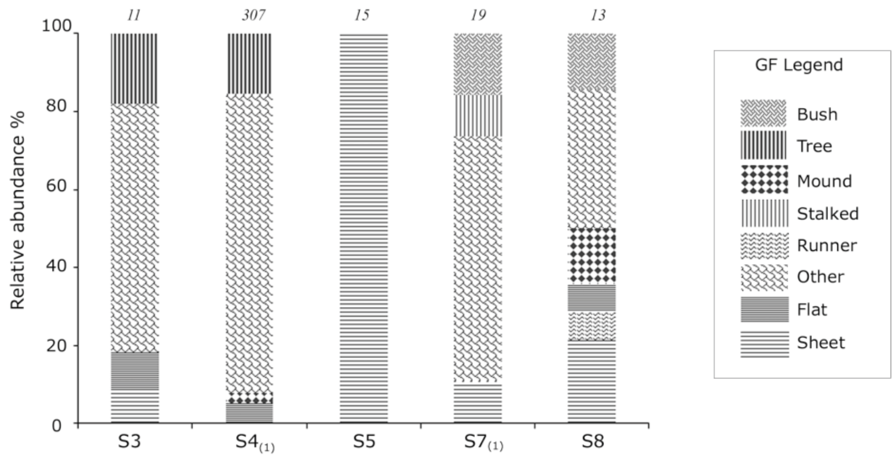

Fig. 2. Relative (%) and total abundance (number on top of the bar) of growth forms (GF) in each sampling stations across Mackellar Inlet in King George Island during austral summer 2017. Subscripts in S4 and S7 indicate single samples (no replicates).

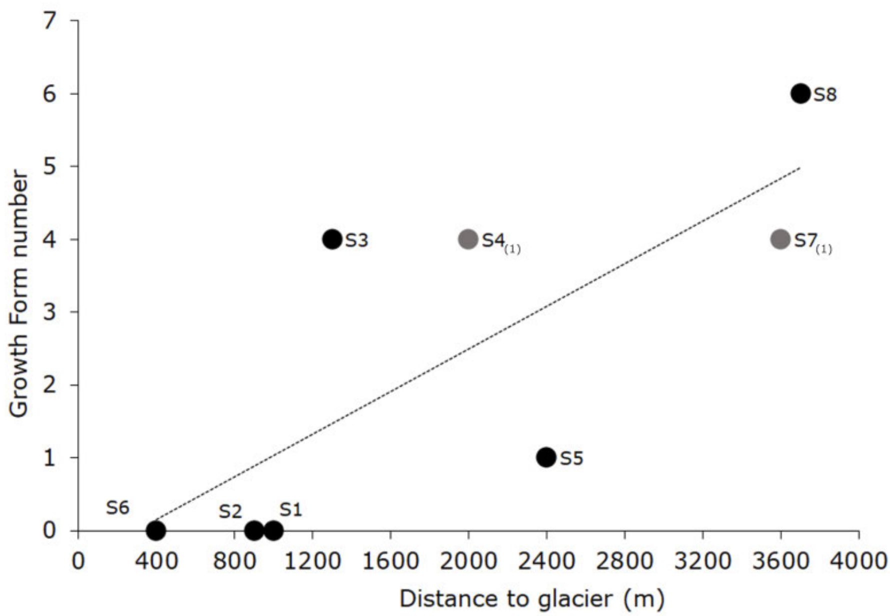

Fig. 3. Number of growth forms (GF) in each sampling stations in relation to distance to the glaciers. Light-grey dots and subscripts in S4 and S7 indicate single samples (no replicates).

The Q-mode (stations) cluster analysis performed on Sørensen dissimilarity matrix shows that S3 and $S4_{(1)}$ were the most similar stations (75% similarity), followed by $S7_{(1)}$ and S8 (60%). These subgroups shared 49% of similarity, and 27% with the outgroup S5 (Fig. 4A). On the other hand, the R-mode (GF) cluster analysis showed two groups: tree, mound, flat and 'other GF' at 65% similarity,

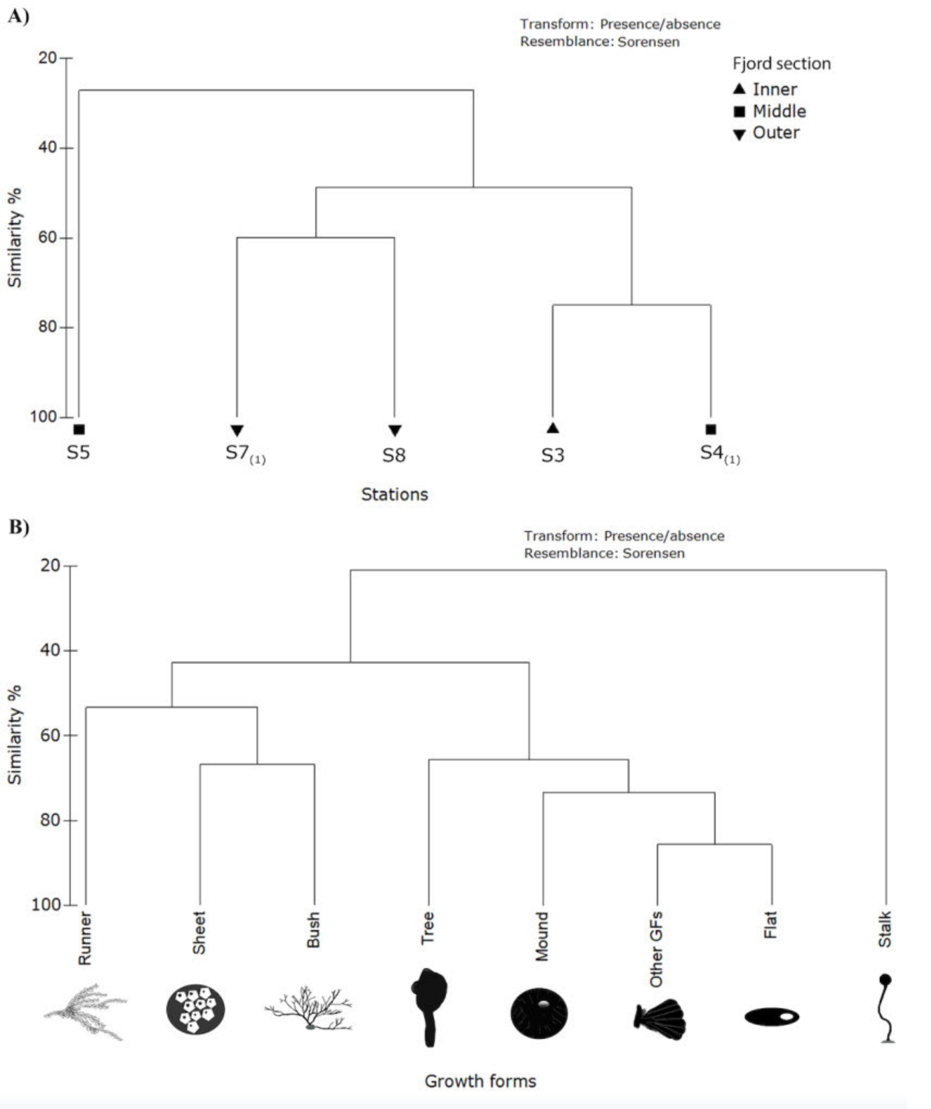

Fig. 4. Two-way cluster analysis using Sorensen similarity and group-average linking for presence/absence data. A. Grouping based on sampling stations (Q-mode) categorized by fjord section. Subscript in S4 and S7 indicates only one sample collected on those stations. B. Grouping based on growth forms (R-mode).

and, runner, bush, and sheet at 53% similarity (Fig. 4B). Stalk GF was an outgroup of the previous sharing 20% similarity. The first group is composed by GF found along the fjord while the second group is composed by GF found in the outer section plus the sheet GF with a more opportunistic strategy.

Discussion

Glacier disturbance in the Southern Ocean has been reported as one of the most important factors structuring macro and megazoobenthic assemblages in shallow areas (Echeverría *et al.* 2005; Echeverría and Paiva 2006; Smale *et al.* 2008; Siciński *et al.* 2011; Pabis *et al*. 2014). Glacier disturbance in fjords can reduce biomass and the local diversity of benthic communities by means of mechanical impact (ice scour), and by the lithogenic input of large amounts of inorganic particles (Pęcherzewski 1980; Barnes and Souster 2011). Encrusting species were reported to dominate inner and shallow sections of fjords, while branched and tuft-like were better represented in deeper and less disturbed areas (Barnes 1995; Pabis *et al*. 2014). Therefore, spatial distribution of GF could serve as an indicator of the level of disturbance. Glacier disturbances in Mackellar Inlet also seemed to have an influence for diversity and distribution of GF confirmed by positive relationship between the number of GF, and the distance to the glaciers. This result is consistent with other studies that report higher, taxonomic and functional diversity that increase with depth and distancing from source of disturbance (Barnes 1995; Gutt and Starmans 1998; Gutt 2001; Włodarska-Kowalczuk *et al.* 2005; Krzemińska *et al.* 2018).

In the present study, the tree-like *Molgula pedunculata* (Herdman, 1881) and flat *Ascidia challengeri* (Herdman, 1881) were found in the inner section of the fjord. Tree GF allow their siphons to escape from sediment resuspension, heavy sedimentation and other deleterious processes as these structures usually hover between 10–30 cm above the bottom (Jackson 1979; Tatián *et al.* 2008b; Torre *et al*. 2012; Torre *et al.* 2014), while flat GF were found to cope with high concentration of inorganic particles (200 mgL^{-1}) (Tatián *et al.* 2008b; Torre *et al.* 2014). Although through different mechanisms both GF seem to resist high sedimentations, but within some limits. A population decrease of *Cnemidocarpa verrucosa* (Lesson, 1830) and *M. pedunculata* and the flat ascidians *Corella eumyota* (Traustedt, 1882) and *A. challengeri* were reported from 1994–2010 in Potter Cove as a result of increased sedimentation (Sahade *et al.* 2015).

A more abundant assemblage was found in the middle section of the fjord in station $S4_{(1)}$ with various tree individuals (*C. verrucosa*), two flats (*A. challengeri*) and a solitary mound (*P. setosa*). Mound GF were found to be dominant in undisturbed areas, while tree GF were usually observed in areas with varying disturbance intensity (Teixidó *et al*. 2004). Dominance of a GF in a determined environment undoubtedly reflects its success but parameters which control presence/absence also have ecological significance (Hageman *et al.* 1997). Conditions in this station allowed for the presence of three types of habitats forming GF: tree, flat and mound. These diversified the inner and middle section of the fjord by acting as basibionts for other organisms, especially for the ‘other GF’. Most of these organisms were ascidians with diverse morphologies, from small globulars, as *Molgula enodis*, to irregular forms, as

Tylobrachion speciosum or *Aplidium* spp. Previous studies have proved that growth morphologies can influence community development (Nelson 2009). It is assumed that elevated positions are advantageous to feeding on drifting particles due to current increase and in an environment with substratum scarcity epibiosis is essential (Gutt and Schickan 1998).

In the eastern part of the middle section (S5), the low number of GF may be reflecting some degree of physical disturbance. Only small bryozoans with sheet GF were found colonising small rocks (primary substratum) where the cheilostome *Inversiula nutrix* Jullien, 1888 was dominant with ten colonies. Due to its low two-dimensional profile this species was recorded successfully inhabiting impacted sites (Clark *et al.* 2017; Krzemińska *et al*. 2018). Sheet GF are dominant during the first stages of colonisation and are favoured by availability of free surface (Boyer *et al.* 1990) and diverse substrata (Barnes *et al.* 1995; Amini *et al.* 2004; Pabis *et al.* 2014). In addition, sheet GF was found in all stations except for $S4_{(1)}$, the most abundant one due to a high aggregation of *Tylobranchion* sp., indicating a low competitive capacity for space, as suggested by Teixidó *et al*. (2004). Competition for space have been reported to be less relevant for structuring communities in shallow subtidal (0–15 m) and intermediate circalittoral zones (15–30 m) because of the predominance of much more recurrent glacier-related disturbance factors (Dayton *et al.* 1974), although competition do occur and might have more significant role in these assemblages.

Some GF, such as bush of *Nematoflustra flagellata* (Waters, 1904), *Himantozoum* sp. 1 and *Camptoplites* sp., stalk of *Sycozoa gaimardi* (Herdman, 1886), and runner GF as *Himantozoum* sp. 2, were found only in the outer section of the fjord and were considered as less competitive (Connell and Keough 1985; Jackson 1979; Teixido *et al.* 2004). The outer part of the fjord located further from glacier disturbances is exposed to faster bottom currents of central basin having has potential greater larval flux and higher concentrations of chlorophyll-*a* essential for sessile suspension feeders (Siciński *et al.* 2011; Campos *et al.* 2012; Jansen *et al.* 2018; Krzemińska and Kukliński 2018; Baylón *et al.* 2019). The morphological flexibility of bush, stalk and runner GF makes them capable for surviving in moderate to high energy waters (Wildish and Kristmanson 1997; Kuklinski 2009). In addition, the presence of gravel in S8 may reduce of impacts by granting protected areas (Krzemińska *et al*. 2018). Contrastingly, the absence of GF in the western outer section of the fjord (S6) could be explained by vicinity of Znosko Glacier (400 m) as important factor providing high amounts of lithogenic material, hindering settlement.

Jackson (1979) interpreted two main strategies in GF, *e.g.*, committed with survival and the fugitives. GF with strong attachment resources and higher tolerance to disturbances present the first strategy (tree>plate>mound>sheet), while GF with a refuge-seeking behaviour present the latter (runner and vines). In Mackellar Inlet, two groups of GF were formed based on distribution similarities.

The first corresponded to those GF that tolerate the harsh processes of the inner and middle section of the fjord: tree, flat, and mound (all defined as basibionts, except for the colonial mounds) and those that benefit from the additional substrata, or epibionts. Antarctic species are known to form as biogenic substrata (basibionts) structuring benthic communities in disturbed areas (Dayton *et al.* 1994). Furthermore, colonial invertebrates are much less fouled and appear to be more affected by high sedimentation than solitary organisms (Jackson 1977). This implies fundamental differences that must be considered for future research for assessing distribution of growth forms. The second group corresponds to GF previously found behaving as facultative epibionts which can also be considered a fugitive strategy: bush, runner, and sheet. The first two were only found in the outer section of the fjord while sheet was found across the fjord and has been defined as having an opportunistic behaviour (Pabis *et al.* 2014).

Conclusions

The composition of GF was different along the fjord: bush, runner and stalk were only found in the outer sections, while tree, flat, sheet and the 'other GF' were found in the inner section. Mound GF was found in the middle and outer sections. Sheet GF was distributed along the fjord, attributable to its tolerance to physical processes, but showed reduced competitive capacities compared to the 'other GF' with epibiotic strategy. These findings support previous interpretations of GF attributes such as 'resistant' and fugitives. The structure of the benthic communities in shallow Antarctic fjords can be influenced by the epibiotic associations of the GF. The presented GF classification may provide relevant insights to deal with uncertainties when projecting responses of Antarctic sessile suspension feeders to future ecological changes and disturbances. However, future research should also be focused on larger spatiotemporal scales and higher resolution to achieve a better understanding of the biological response to environmental processes in Antarctic fjords.

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Appendix

Appendix 1.

Single measurements of four environmental parameters taken from the bottom of the water column of sampling stations the day or week of sampling in Mackellar Inlet, King George Island. Current speed and direction, salinity and temperature obtained with an Aanderaa SEAGUARD RCM CTD. Dissolved oxygen (mg. L-1) measured with a multiparameter HANNA HI 9828 in water samples collected with a 5L Niskin bottle approximately at the depth of grab samples.

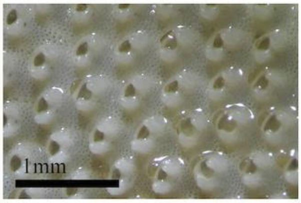
Sampling stations	Latitude (W)	Longitude (S)	Current speed (cm/s)	Current direction (degrees)	O2 Bottom (mg. L1)	Salinity (‰)	Temp (°C)
S1	62.0906	58.4839	2.81	185.7	9.12	34.2	0.67
S2	62.0808	58.4650	2.59	121.6	9.22	34.1	0.92
S3	62.0667	58.4221	4.47	284.6	9.36	34.2	1.02
$S4_{(1)}$	62.0853	58.4487	1.08	295.5	9.64	34.2	0.93
S5	62.0839	58.4333	3.38	142.6	9.08	34.2	0.87
S6	62.1033	58.4541	10.36	58.1	9.5	34.1	1.42
$S7_{(1)}$	62.0966	58.4337	5.86	75.1	9.43	34.3	0.78
S8	62.0902	58.4147	1.66	86.8	7.05	34.1	1.3

Appendix 2.

Ascidians (Chordata: Ascidiacea) found during the austral summer 2017 in Mackellar Inlet, King George Island, indicating their growth form and their epibiotic association type. **b**: basibiont; **fe–b**: both facultative epibiont and basibiont; **fe**: facultative epibiont; and e: epibiont.

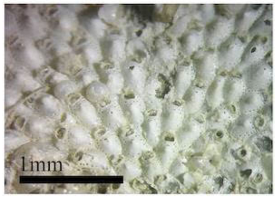
Appendix 3.

Bryozoans (Bryozoa) found during the austral summer 2017 in Mackellar Inlet, King George Island, indicating their growth form and their epibiotic association type. **b**: basibiont; **fe–b**: both facultative epibiont and basibiont; **fe**: facultative epibiont, and e: epibiont.

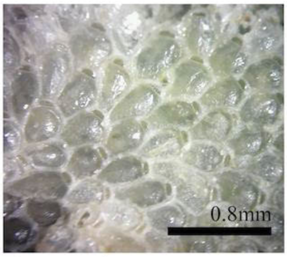


Inversiula nutrix
Sheet, [fe]

Antarctothoa sp.
Sheet, [fe]



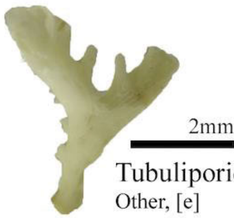
Micropora sp.
Sheet, [fe]



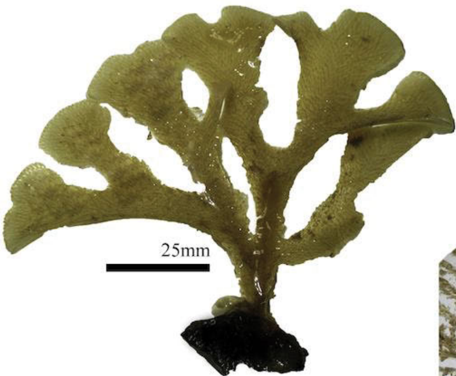
Fenestrulina sp.
Sheet, [fe]

Patinella sp.
Sheet, [fe]

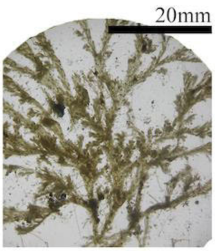
Himantozoum sp.2
Runner, [fe-b]



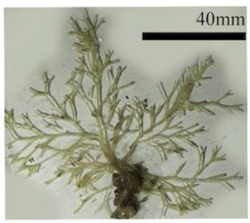
Tubuliporidae
Other, [e]



Nematoflustra flagellata
Bush, [fe-b]



Camptoplites sp.
Bush, [fe-b]



Himantozoum sp.1
Bush, [fe-b]

Appendix 4. Collection information of samples at the Universidad Cientifica del Sur.

Colection code	Project	Year	Date	Station	Taxon	Growth form	Abun-dance
UCSUR 09 000001	Antar XXIV	2017	8.02.2017	S3	*Tylobranchion speciosum*	Other	2
UCSUR 09 000002	Antar XXIV	2017	8.02.2017	S3	*Styelidae* sp.1	Other	2
UCSUR 09 000003	Antar XXIV	2017	8.02.2017	S3	*Molgula pedunculata*	Tree	3
UCSUR 09 000004	Antar XXIV	2017	8.02.2017	S3	*Tylobranchion* sp.	Other	14
UCSUR 09 000005	Antar XXIV	2017	8.02.2017	S3	*Ascidia challengueri* cf.	Flat	1
UCSUR 09 000006	Antar XXIV	2017	15.02.2017	S4(1)	*Aplousobranchia* sp. 1	Other	1
UCSUR 09 000007	Antar XXIV	2017	15.02.2017	S4(1)	*Tylobranchion* sp.	Other	223
UCSUR 09 000008	Antar XXIV	2017	15.02.2017	S4(1)	*Tylobranchion speciosum*	Other	56
UCSUR 09 000009	Antar XXIV	2017	15.02.2017	S4(1)	*Cnemidocarpa verrucosa*	Tree	4
UCSUR 09 000010	Antar XXIV	2017	15.02.2017	S4(1)	*Molgula pedunculata*	Tree	2
UCSUR 09 000011	Antar XXIV	2017	15.02.2017	S4(1)	*Molgula enodis*	Other	16
UCSUR 09 000012	Antar XXIV	2017	15.02.2017	S4(1)	*Pyura setosa*	Mound	1
UCSUR 09 000013	Antar XXIV	2017	15.02.2017	S4(1)	*Ascidia challengeri*	Flat	2
UCSUR 09 000014	Antar XXIV	2017	15.02.2017	S4(1)	*Aplousobranchia* sp.2	Other	1
UCSUR 09 000015	Antar XXIV	2017	15.02.2017	S7(1)	*Sycozoa gaimardi*	Stalk	2
UCSUR 09 000016	Antar XXIV	2017	15.02.2017	S7(1)	Polyclinidae	Other	2
UCSUR 09 000017	Antar XXIV	2017	15.02.2017	S7(1)	*Molgula enodis* cf.	Other	1
UCSUR 09 000018	Antar XXIV	2017	15.02.2017	S7(1)	*Tylobranchion sp.*	Other	1
UCSUR 09 000019	Antar XXIV	2017	15.02.2017	S7(1)	Aplousobranchia sp.3	Other	1
UCSUR 09 000020	Antar XXIV	2017	11.02.2017	S8	*Aplidium* sp. 1	Other	2
UCSUR 09 000021	Antar XXIV	2017	11.02.2017	S8	*Aplidium sp.* 2	Mound	1
UCSUR 09 000022	Antar XXIV	2017	11.02.2017	S8	*Aplidium* sp. 3	Mound	1

Colection code	Project	Year	Date	Station	Taxon	Growth form	Abun-dance
UCSUR 09 000023	Antar XXIV	2017	11.02.2017	S8	*Tylobranchion sp.*	Other	1
UCSUR 09 000024	Antar XXIV	2017	11.02.2017	S8	*Molgula enodis*	Other	1
UCSUR 09 000025	Antar XXIV	2017	11.02.2017	S8	*Corella sp.*	Flat	1
UCSUR 10 000001	Antar XXIV	2017	8.02.2017	S3	*Antarctothoa sp.*	Sheet	1
UCSUR 10 000002	Antar XXIV	2017	11.02.2017	S5	*Inversula nutrix*	Sheet	10
UCSUR 10 000003	Antar XXIV	2017	11.02.2017	S5	*Micropora sp.*	Sheet	1
UCSUR 10 000004	Antar XXIV	2017	11.02.2017	S5	*Fenestrulina* sp.	Sheet	1
UCSUR 10 000005	Antar XXIV	2017	11.02.2017	S5	*Antarctothoa sp.*	Sheet	1
UCSUR 10 000006	Antar XXIV	2017	15.02.2017	S7(1)	*Antarcthotoa sp.*	Sheet	1
UCSUR 10 000007	Antar XXIV	2017	15.02.2017	S7(1)	*Patinella sp.*	Sheet	1
UCSUR 10 000008	Antar XXIV	2017	15.02.2017	S7(1)	Tubuliporidae	Other	7
UCSUR 10 000009	Antar XXIV	2017	15.02.2017	S7(1)	*Nematoflustra flagellata*	Bush	1
UCSUR 10 000010	Antar XXIV	2017	15.02.2017	S7(1)	*Camptoplites sp.*	Bush	1
UCSUR 10 000011	Antar XXIV	2017	15.02.2017	S7(1)	*Himantozoum sp. 1*	Bush	1
UCSUR 10 000012	Antar XXIV	2017	11.02.2017	S8	*Himantozoum sp. 2*	Runner	1
UCSUR 10 000013	Antar XXIV	2017	11.02.2017	S8	*Nematoflustra flagellata*	Bush	2
UCSUR 10 000014	Antar XXIV	2017	11.02.2017	S8	*Inversula nutrix*	Sheet	3
UCSUR 10 000015	Antar XXIV	2017	11.02.2017	S8	*Antarctothoa sp,*	Sheet	8
UCSUR 10 000016	Antar XXIV	2017	11.02.2017	S8	*Camptoplites sp.*	Bush	1
UCSUR 10 000017	Antar XXIV	2017	11.02.2017	S8	*Patinella sp.*	Sheet	1
UCSUR 10 000018	Antar XXIV	2017	11.02.2017	S8	*Fenestrulina sp.2*	Sheet	2
UCSUR 10 000019	Antar XXIV	2017	11.02.2017	S8	Briozoa sp. 1	Sheet	1
UCSUR 10 000020	Antar XXIV	2017	11.02.2017	S8	Briozoa sp. 2	Sheet	3

References

Alurralde G., Fuentes V.L., MaggionI T., Movilla J., Olariaga A., Orejas C., Schloss R. and Tatián M. 2019. Role of suspension feeders in Antarctic pelagic-benthic coupling: Trophic ecology and potential carbon sinks under climate change. *Marine Environmental Research* 152: 104790. doi:10.1016/J.MARENVRES.2019.104790

Amini Z.Z., Adabi M.H., Burrett C.F. and Quilty P.G. 2004. Bryozoan distribution and growth form associations as a tool in environmental interpretation, Tasmania, Australia. *Sedimentary Geology* 167: 1–15. doi:10.1016/j.sedgeo.2004.01.010

Barnes D.K.A. 1995. Sublittoral epifaunal communities at Signy Island, Antarctica. II. Below the ice-foot zone. *Marine Biology* 121: 565–572. doi:10.1007/BF00349467

Barnes D.K.A. 2017. Polar zoobenthos blue carbon storage increases with sea ice losses, because across-shelf growth gains from longer algal blooms outweigh ice scour mortality in the shallows. *Global Change Biology* 23: 5083–5091. doi:10.1111/gcb.13772

Barnes D.K.A and Sands C.J. 2017. Functional group diversity is key to Southern Ocean benthic carbon pathways. *PLoS ONE* 12: e0179735. doi:10.1371/journal.pone.0179735

Barnes D.K.A and Souster T. 2011. Reduced survival of Antarctic benthos linked to climate induced iceberg scouring. *Nature Climate Change* 1: 365–368. doi:10.1038/nclimate1232

Baylón M., Hernández-Becerril D.U., Indacochea A. and Purca S. 2019. Variabilidad espacio-temporal del fitoplancton de la ensenada Mackellar, Bahía Almirantazgo, Isla Rey Jorge, Antártida, durante el verano austral 2012/2013. *Revista de Biología Marina y Oceanografía* 54: 151–165. doi: 10.22370/rbmo.2019.54.2.1809 https://doi.org/https://doi.org/10.22370/rbmo.2019.54.2.1809

Boyer M., Matricardi G. and Pisano E. 1990. Zoarial forms in the development of a bryozoan community. *Anales de Biología Murcia* 16: 155–162.

Brey T. and Gerdes D. 1997. Is Antarctic benthic biomass really higher than elsewhere? *Antarctic Science* 9: 266–267. doi:10.1017/s0954102097000357

Campos L.S., Barboza C.A.M., Bassoi M., Bernardes M., Bromberg S., Corbisiert N., Fontes R.F. C., Gheller P.F., Hajdu E., Kawall H.G., Lange P.K., Lanna A.M., Lavrado H.P., Monteiro G. C.S., Montone R.C., Morales T., Moura R.B., Nakayama C.R., Oackes T., Paranhos R., Passos F.D., Petti M.A.V., Pellizariv H., Rezende C.E., Rodrigues M., Henrique Rosa L., Secchi E., Tenenbaum D.R. and Yoneshigue-Valentin Y. 2012. Environmental processes, biodiversity and changes in Admiralty Bay, King George Island, Antarctica. *Adaptation and Evolution in Marine Environments* 2: 127–156. doi:10.1007/978-3-642-27349-0_8

Chapin F.S., Zavaleta E.S., Eviner V.T., Naylor R.L., Vitousek P.M., Reynolds H.L., Hooper D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M.C. and Díaz S. 2000. Consequences of changing biodiversity. *Nature* 405: 234–242. doi:10.1038/35012241

Clarke A. 2008. Antarctic marine benthic diversity: patterns and processes. *Journal of Experimental Marine Biology and Ecology* 366: 48–55. doi:10.1016/j.jembe.2008.07.008

Clarke K.R. and Gorley R.N. 2006. PRIMER v6: User Manual/Tutorial. Plymouth, UK.

Clark G.F., Stark, J.S. and Johnston E.L. 2017. Tolerance rather than competition leads to spatial dominance of an Antarctic bryozoan. *Journal of Experimental Marine Biology and Ecology* 486: 222–229. doi:10.1016/j.jembe.2016.10.008

Connell J. and Keough M. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. *In*: Pickett S.T. and White P. (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press Inc.: 125–151.

Cook A.J., Holland P.R., Meredith M.P., Murray T., Luckman A. and Vaughan D.G. 2016. Ocean forcing of glacier retreat in the western Antarctic Peninsula. *Science* 353: 283–286. doi: 10.1126/science.aae00

De Bello F., Lavorel S., Díaz S., Harrington R., Cornelissen J.H.C., Bardgett R.D., Berg M.P., Cipriotti P., Feld C.K., Hering D., Martins Da Silva P., Potts S., Sandin L., Sousa J.P., Storkey J., Wardle D. and Harrison P.A. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* 19: 2873–2893. doi:10.1007/s10531-010-9850-9

Dayton P.K., Robilliard G.A., Paine R.T. and Dayton L.B. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs* 44: 105–128.

Dayton P K., Mordida B.J. and Bacon F. 1994. Polar marine communities. *American Zoologist* 34: 90–99.

Díaz S., Purvis A., Cornelissen J.H.C., Mace G.M., Donoghue M.J., Ewers R.M., Jordano P. and Pearse W.D. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* 3: 2958–2975. doi:10.1002/ece3.601

Echeverría C.A. and Paiva P.C. 2006. Macrofaunal shallow benthic communities along a discontinuous annual cycle at Admiralty Bay, King George Island, Antarctica. *Polar Biology* 29: 263–269. doi:10.1007/s00300-005-0049-6

Echeverría C.A., Paiva P.C. and Alves V.C. 2005. Composition and biomass of shallow benthic megafauna during an annual cycle in Admiralty Bay, King George Island, Antarctica. *Antarctic Science* 17: 312–318. doi:10.1017/S0954102005002762

Folk R.L. 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. *The Journal of Geology* 62: 344–359.

Gilbert R., Nielsen N., Möller H., Desloges J.R. and Rasch M. 2002. Glacimarine sedimentation in Kangerdluk (Disko Fjord), West Greenland, in response to a surging glacier. *Marine Geology* 191: 1–18. doi:10.1016/S0025-3227(02)00543-1

Gili J.M., Coma R., Orejas C., López-González P.J. and Zabala M. 2001. Are Antarctic suspension-feeding communities different from those elsewhere in the world? *Polar Biology* 24: 473–485. doi:10.1007/s003000100257

Gutt J .2001. On the direct impact of ice on marine benthic communities, a review. *Ecological Studies in the Antarctic Sea Ice Zone*: 157–168. doi:10.1007/s003000100262

Gutt J. 2007. Antarctic macro-zoobenthic communities: a review and an ecological classification. *Antarctic Science* 19: 165. doi:10.1017/S0954102007000247

Gutt J. and Schickan T. 1998. Epibiotic relationships in the Antarctic benthos. *Antarctic Science* 10: 398–405. doi:10.1017/S0954102098000480

Gutt J. and Starmans A. 1998. Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): Ecological role of physical parameters and biological interactions. *Polar Biology* 20: 229–247. doi:10.1007/s003000050300

Hageman S.J., Bone Y., Mcgowran B. and James N.P. 1997. Bryozoan colonial growth-forms as paleoenvironmental indicators: Evaluation of methodology. *Palaios* 12: 405. doi:10.2307/3515380

Hageman S.J., Bock P.E., Bone Y. and Mcgowran B. 1998. Analysis bryozoan growth habits: classification. SEPM *Society for Sedimentary Geology Paleontological Society* 72: 418–436. doi: 10.1017/S0022336000024161

Hayward P.J. 1995. Antarctic cheilostomatous bryozoa. *Oxford University Press*.

Jackson J.B.C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *The American Naturalist* 111: 743–767

Jackson J.B.C. 1979. Morphological strategies of sessile animals. *Biology and Systematic of Colonial Organisms*: 499–555.

Jansen J., Hill N.A., Dunstan P.K., Mckinlay J., Sumner M.D., Post A.L., Eléaume M.P., Armand L. K., Warnock J.P., Galton-Fenzi B.K. and Johnson C.R. 2018. Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. *Nature Ecology & Evolution* 2: 71–80. doi: 10.1038/s41559-017-0392-3

Kott P. 1989. Form and function in the Ascidiacea. *Bulletin of Marine Science* 45: 253–276.

Kukliński P. 2009. Ecology of stone-encrusting organisms in the Greenland Sea—a review. *Polar Research* 28: 222–237. doi:10.3402/polar.v28i2.6114

Kowalski D. 1985. Wind structure at the *Arctowski Station*. *Polish Polar Research* 6: 391–403.

Krzemińska M. and Kukliński P. 2018. Biodiversity patterns of rock encrusting fauna from the shallow sublittoral of the Admiralty Bay. *Marine Environmental Research* 139: 169–181. doi:10.1016/j.marenvres.2018.03.016

Krzemińska M., Siciński J. and Kukliński P. 2018. Biodiversity and biogeographic affiliation of Bryozoa from King George Island (Antarctica). *Systematics and Biodiversity* 16: 576–586. doi:10.1080/14772000.2018.1457099

Lipski M. 1987. Variations of physical conditions, nutrients and chlorophyll *a* content in Admiralty Bay (King George Island, South Shetland islands, 1979). *Polish Polar Research* 8: 307–332.

Lipski I.M. and Rakusa-Suszczewski S. 1990. Early summer pattern of vertical distribution of chlorophyll *a* (Bransfield Strait Antarctica November 1986). *Polskie Archiwum Hydrobiologii* 37: 287–293.

Meredith M.P. and King J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters* 32: 1–5. doi:10.1029/2005GL024042

Momo F., Sahade R. and Tatián M. 2008. Benthic animal communities of Potter Cove (King George Island, Antarctica): Observed patterns and explanatory models. The Antarctic ecosystem of Potter Cove, King-George Island (Isla 25 Mayo). *Reports on Polar and Marine Research:* 1–411. doi:10.2312/BzPM_0571_2008

Monniot C. and Monniot F. 1983. *Ascidies antarctiques et subantarctiques: morphologie et biogeographie.* Muséum national d'Histoire Naturelle, Paris.

Monniot F., Dettai A., Eleaume M., Cruaud C. and Ameziane N. 2011. Antarctic Ascidians (Tunicata) of the French-Australian survey CEAMARC in Terre Adélie. *Zootaxa* 54: 1–54. doi:10.11646/zootaxa.2817.1.1

Morley S.A, Barnes D.K.A. and Dunn M.J. 2019. Predicting which species succeed in climate-forced polar seas. *Frontiers in Marine Science* 5: 1–507. doi: 10.3389/fmars.2018.00507

Nelson C.S., Hyden F.M., Keane S.L., Leask S.L. and Gordon D.P. 1988. Application of bryozoan zoarial growth form studies in facies analysis of non-tropical carbonate deposits in New Zealand. *Sedimentary Geology*, 60: 301–322. doi: /10.1016/0037-0738(88)90126-1

Nelson M.L. 2009. Growth morphology and succession in a temperate marine fouling community. Master's thesis, Humboldt State University.

Pabis K., Sicinski J. and Krymarys, M. 2011. Distribution patterns in the biomass of macrozoobenthic communities in Admiralty Bay (King George Island, South Shetlands, Antarctic). *Polar Biology* 34: 489–500. doi:10.1007/s00300-010-0903-z

Pabis K., Hara U., Presler P. and SicinskI J. 2014. Structure of bryozoan communities in an Antarctic glacial fjord (Admiralty Bay, South Shetlands). *Polar Biology* 37: 737–751. doi:10.1007/s00300-014-1474-1

Pęcherzewski K. 1980. Distribution and quantity of suspended matter in Admiralty Bay (King George Island, South Shetland Islands). *Polish Polar Research* 1: 75–82.

Pérez-Harguindeguy N., Díaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P., Bret-Harte M. S., Cornwelf W.K., Craine J.M., Gurvich D.E., Urcelay E.J., Veneklaas E.J., Reich P.B., Poorter L., Wright I.J., Ray P., Enrico L., Pausas J.G., De Vos A.C., Buchmann N., Funes G., Quétier F., Hodgson J.G., Thompson K., Morgan H.D., Ter Steege H., Van Der Heijden A., Sack L., Blonder B., Poschlod P., Vaierentti M.V., Conti G., Staver A.C., Aquino S. and Cornelissen J.H.C. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234. doi:10.1071/BT12225

Primo C. and Vázquez E. 2007. Ascidians collected during the Spanish Antarctic expedition CIEMAR 99/00 in the Bransfield and Gerlache Straits. *Journal of Natural History* 41: 1775–1810. doi:10.1080/00222930701500126

Pruszak Z. 1980. Currents circulation in the waters of Admiralty Bay (region of *Arctowski Station* on King George Island). *Polish Polar Research* 1: 55–74.

Rakusa-Suszczewski S. 1995. Flow of matter in the Admiralty Bay area, King George Island, Maritime Antarctic. *NIPR Symposium on Polar Biology, National Institute of Polar Research, Tokyo* 8: 101–113.

Robakiewicz M. and Rakusa-Suszczweski S.1999. Application of 3D circulation model to Admiralty Bay, King George Island Antarctica. *Polar Research* 20: 43–58

Rückamp M., Braun M., Suckro S. and Blindow N. 2011. Observed glacial changes on the King George Island ice cap, Antarctica, in the last decade. *Global and Planetary Change* 79: 99–109. doi:10.1016/j.gloplacha.2011.06.009

Ryland J.S. and Warner G.F. 1986. Growth and form in modular animals: ideas on the size and arrangement of zooids. *Philosophical Transactions Royal Society of London*, Series B, 313: 53–76. doi:10.1098/rstb.1986.0025

Sahade R., Lagger C., Torre L., Momo F., Monien P., Schloss I., Barnes D.K.A., Servetto N., Tarantelli S., Tatián M., Zamboni N. and Abele, D. 2015. Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. *Science Advances* 1: 1–8. doi:10.1126/sciadv.1500050

Sanders C.J., Santos I.R., Patchineelam S.R., Schaefer C. and Silva-Filho E.V. 2010. Recent 137Cs deposition in sediments of Admiralty Bay, Antarctica. *Journal of Environmental Radioactivity* 101: 421–424. doi:10.1016/j.jenvrad.2010.02.006

Schopf T.J. 1969. Paleoecology of ectoprocts (Bryozoans). *Journal of Paleontology* 43: 234–244.

Siciński J., Jażdżewski K., De Broyer C., Presler P., Ligowski R., Nonato E.F., Corbisier T.N., Petti M.A.V., Brito T.A.S., Lavrado H.P., Błażewicz-Paszkowycz., Pabis K., Jażdżewska A. and Campos L.S. 2011. Admiralty Bay benthos diversity – A census of a complex polar ecosystem. *Deep-Sea Research Part II: Topical Studies in Oceanography* 58: 30–48. doi:10.1016/j.dsr2.2010.09.005

Smale D.A, Brown K.M., Barnes D.K.A., Fraser K.P.P. and Clarke A. 2008. Ice scour disturbance in Antarctic Waters. *Science* 321: 371. doi: 10.1126/science.1158

Smith A.M. 1995. Paleoenvironmental interpretation using bryozoans: a review. *In*: Bosence D. and Allison P. (eds.) *Marine paleoenvironmental analysis from fossils.* Geological Society, Special Publication, London 83: 231–243. doi:10.1144/GSL.SP.1995.083.01.11

Stach L.W. 1936. Correlation of zoarial form with habitat. *The Journal of Geology* 44: 60–65. doi:10.1086/624395

Tatián M., Mercuri G., Fuentes V.L., Antacli J.C., Stellfeldt A. and Sahade R. 2008a. Role of benthic filter feeders in pelagic-benthic coupling: assimilation, biodeposition and particle flux. The Antarctic ecosystem of Potter Cove, King-George Island (Isla 25 Mayo). *Reports on Polar and Marine Research.* Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven: 118–127.

Tatián M., Milozzi A., Sahade R., Mercuri G. and Lagger C. 2008b. Contribution of different seston components to ascidian food in Potter Cove. The Antarctic ecosystem of Potter Cove, King-George Island (Isla 25 Mayo). *Reports on Polar and Marine Research.* Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven: 128–134.

Teixidó N., Garrabou J., Gutt J. and Arntz W.E. 2004. Recovery in Antarctic benthos after iceberg disturbance: Trends in benthic composition, abundance and growth forms. *Marine Ecology Progress Series* 278: 1–16. doi:10.3354/meps278001

Torre L., Servetto N., Eöry M.L., Momo F., Tatián M., Abele D. and Sahade R. 2012. Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. *Polar Biology* 35: 1743–1748. doi:10.1007/s00300-012-1208-1

Torre L., Abele D., Lagger C., Momo F. and Sahade R. 2014. When shape matters: Strategies of different Antarctic ascidians morphotypes to deal with sedimentation. *Marine Environmental Research* 99: 179–187. doi:10.1016/j.marenvres.2014.05.014

Wahl M. and Mark O. 1999. The predominantly facultative nature of epibiosis: experimental and observational evidence. *Marine Ecology Progress Series* 187: 59–66. doi:10.3354/meps187059

Wildish D. and Kristmanson D. 1997. *Benthic suspension feeders and flow*. Cambridge University Press, Cambridge.

Włodarska-Kowalczuk M., Pearson T.H. and Kendall M.A. 2005. Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. *Marine Ecology Progress* Series 303: 31–41. doi: 10.3354/meps303031

Ziegler A.F., Smith C.R., Edwards K.F. and Vernet M. 2017. Glacial dropstones: Islands enhancing seafloor species richness of benthic megafauna in West Antarctic Peninsula fjords. *Marine Ecology Progress Series* 583: 1–14. doi:10.3354/meps12363

Zielinski K. 1990. Bottom macroalgae of the Admiralty Bay (King George Island, South Shetlands, Antarctica). *Polish Polar Research* 11: 95–131.

Zwolska I. and Janecki T. 1999. Weather and hydrological conditions in the region of Admiralty Bay (King George Island, South Shetlands, Antarctica) in 1998. *Polish Polar Studies. XXVI Polar Symposium, June 1999, Lublin*: 329–338.

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