Pita, M., Indacochea, A. G., & Moreno, B. (2025). Emergent sampling of Bryozoa in Mackellar glaciomarine fjord, 62°S maritime Antarctic. *Ukrainian Antarctic Journal*, *23*(1), 32–50.
https://doi.org/10.33275/1727-7485.1.2025.742

Emergent sampling of Bryozoa in Mackellar glaciomarine fjord, 62°S maritime Antarctic

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Abstract. Bryozoans are sessile suspension feeding metazoans which represent an important component of Antarctic macrozoobenthic communities. These ectotherm modular organisms are present in a wide variety of habitats subjected to strong gradients, such as those found in polar glaciomarine fjords. This study focused on the diversity of bryozoans opportunistically collected via van Veen grab deployments during four summer campaigns (2017–2019 and 2023) in Mackellar Inlet (62°S, King George Island) by Peruvian ANTAR expeditions. The cumulative taxa richness and diversity patterns were evaluated, revealing an overall number of 36 taxa, representing 84% of the estimated richness (Chao2 = 43). From the six recognised growth forms, the membraniporiforms (calcified encrusting unilaminar) dominated the bryozoan assemblage, followed by cheilostomes with flustriform growth habit. The highest diversity, cumulative taxonomic richness (26 taxa), and all growth forms herein recorded (6) were found in the outer section of the fjord. The erect flexible basibiont *Nematoflustra flagellata* (Waters, 1904) was the most abundant flustriform and hosted the highest abundance of epizoozoans, which preferred the rear surface of their host fronds for settlement. Unconsolidated deposits such as gravels and coarse sand grains were essential substrates for bryozoan assemblages; however, habitat-facilitating growth forms increased the overall values of abundance and taxonomic and functional richness at a local scale. This work, which is opportunistic in nature, represents a baseline for future studies aiming to create an annotated checklist of bryozoans in the area that would require diverse sampling methodologies focused specifically on bryozoans and their substrates (e.g., scuba diving, rock dredges). Although we aimed to cover a basic functional analysis based on growth forms, a deeper understanding of the ecology of bryozoans in Mackellar Inlet is needed, considering different ecological implications and life strategy adaptations to environmental gradients.

Keywords: cheilostome, colonial, epizoozoan, secondary substrate, zoobenthos

1 Introduction

Antarctic macrobenthos can be broadly classified into two core communities: one dominated by sessile and sedentary suspension feeders and the other dominated by infauna and motile epifauna (Gutt, 2007). However, environmental gradients across spatial scales, such as depth, substrate type, food availability, temperature, and sea ice cover, give rise to a broad range of mixed assemblages, conditioning faunistic gradients (Gutt et al., 2019). Fjords are estuarine basins with an intertwined mixture of environmental conditions and processes. Subpolar Antarctic fjords, such as those found along the West Antarctic Peninsula (WAP), are relatively young ecosystems that are still being colonised (Sahade et al., 2015; Barnes et al., 2020) and are considered hotspots of benthic biodiversity due to their comparatively lower sedimentation disturbance (Grange & Smith, 2013). However, at least 90% of WAP fjords are undergoing a process of warming, and therefore their neighbouring glaciers are retreating (Cook et al., 2016). Due to the proximity to glacial influence, the seabed of glaciomarine fjords receives the haphazard delivery of drop-stones and lithoclasts of different dimensions, creating small islands surrounded by unconsolidated soft bottoms (Ziegler et al., 2017). Sessile suspension-feeding benthic assemblages are important for carbon cycling since they enable the pelago-benthic coupling by capturing and ingesting their planktic prey from the water column (Gili & Coma, 1998). This, and their sessile nature, also make suspension feeders bioindicators of spatial variability in food sources in fjords (Alurralde et al., 2020), especially since this functional group is abundant and, thus, a substantial contributor to zoobenthic carbon storage in ecosystems such as WAP fjords where dropstones host higher morphotaxa richness (Frinault & Barnes, 2024).

Among the Antarctic sessile suspension feeders, the phylum Bryozoa is one of the most important representatives (Bader & Schäfer, 2005). The number of species of bryozoans south of the polar front is currently greater than 400 (Barnes & Downey, 2014). However, it is estimated to be higher considering more recent descriptions and unexplored areas/depths (De Broyer et al., 2011). Antarctic cheilostomes (order Cheilostomatida) are primarily represented on the shelf (Barnes et al., 2009), reaching a high degree of species endemism (57%) (Barnes & Griffiths, 2008). Depending on their taxonomic affiliations and life strategy (e.g., ontogeny, capacity for spatial interference competition), bryozoans can either be found as pioneers of early colonisation during primary succession (Barnes & Downey, 2014) or dominate spatial competition battles (overgrowing neighbouring colonies) in mature assemblages during more advanced phases of ecological succession (Barnes & Kuklinski, 2005; Gutt, 2007).

Another ecologically important aspect exhibited by some bryozoans is their bioconstructional capacity (Lombardi et al., 2020), which promotes habitat complexity and can, therefore, behave as secondary substrate and offer shelter for many other marine invertebrates in timescales that may cover years to decades (Stebbing, 1971; Barnes, 1994; Hayward, 1995). Such is the case of the erect flexible cheilostome *Nematoflustra flagellata* (Waters, 1904) in the Southern Ocean. These colonies are adapted to environmental conditions such as higher turbulence, either in shallow or deep waters, allowing the zoarium to bend and agitate following the flow and direction of currents of the surrounding environment (Moyano, 1986). The growth form and foliose geometry of *N. flagellata* facilitate the settlement of the so-called *epizoozoans* (i.e., animals using other animals as substrate, *sensu* Taylor & Wilson, 2002). This secondary assemblage includes other sessile suspension feeders that inhabit the fronds of the basibiont zoaria (Barnes, 1994), potentially increasing the levels of local diversity.

For the last decades, the Antarctic Peninsula has been going through a phase of rapid regional warming because of the effects of climate change on the ecosystem (Clarke et al., 2007), including an increase in atmospheric temperature, collapse of ice shelves, and particularly, the retreat of marine-terminating glaciers (Stammerjohn et al., 2008). In Admiralty Bay (62°S, maritime Antarctic), there have been shown strong spatial gradients due to the influence of freshwater inflow from glacial retreat, which can further affect density stratification (temperature and salinity) and increase sedimentation, which, in turn, influence benthic assemblages that inhabit glacial bays (Krzeminska & Kuklinski, 2018). Such is the case of bryozoans, which make up one of the most abundant groups of sessile fauna and participate, like ascidians, in the benthic colonisation of newly ice-free areas available due to glacial retreat (Lagger et al., 2017). The high richness and abundance of encrusting bryozoans have been reported in upper sublittoral areas, while in areas of greater depth, bryozoans with erect-flexible/foliose colonies tend to predominate (Krzeminska et al., 2018).

From the monitoring efforts undertaken by the Universidad Científica del Sur and the Peruvian Antarctic Program, the first reports of Bryozoa in the Mackellar glaciomarine fjord started with Moreno (2015) and later with Thorne et al. (2022). The former reported the Bryozoa only to the phylum level since the authors' focus was soft-bottom macrobenthos. Given this gap in taxonomical knowledge, Thorne et al. (2022) increased the taxonomic resolution and identified bryozoans to the species level whenever possible. Additionally, they studied different ecological aspects focusing on the spatial distribution of sessile suspension feeders from a morpho-functional point of view. Therefore, the aim of the present study was to adopt recent functional approaches to describe the diversity of bryozoan assemblages along the axis of Mackellar fjord (inner, middle, outer sections) by expanding the temporal coverage of samples collected from van Veen grabs between 2017–2019 and 2023. We refer to this effort as emergent (opportunistic) sampling (Palinkas et al., 2015) since the deployments were not originally planned for studying bryozoans. However, the cumulative occurrence of lithoclasts in the samples has enabled further ecological investigation on this assemblage.

2 Materials and methods

2.1 Study area

The formation of Mackellar Inlet arose from postglacial hanging valleys (Rakusa-Suszczewski, 1995). It is one of the three tributary fjords of Admiralty Bay in King George Island (KGI) (South Shetland Islands, maritime Antarctic). It is the closest fjord to the Peruvian Antarctic research station, Machu Picchu (ECAMP) (Fig. 1). Nine sampling sites were distributed along the fjord. Here, we used the same nomenclature (S1–S8) as Thorne et al. (2022) but included the analysis of one additional site (SMP) located near the ECAMP. Following a gradient based on the linear distance to Domeyko Glacier (Thorne et al., 2022) and a supporting cluster classification (Moreno, 2015), sampling sites were categorised according to the section of the fjord: inner, middle, and outer (Appendix Table).

2.2 Biological sampling

The samples used for this study were obtained during the Peruvian Antarctic expeditions ANTAR XXIV, XXV, XXVI, and XXIX in 2017, 2018, 2019, and 2023, respectively. Samples were collected using a van Veen grab (0.05 m^2) at nine sites, three replicates each, distributed in the inner (S1, S2, S3), middle (S4, SMP, S5), and outer (S6, S7, S8) sections of the Mackellar Inlet. The macrobenthic fraction was sorted and separated using a 500 µm sieve, and the biological material was fixed in 10% formalin for taxonomic identification. Data on environmental variables were also obtained using a Niskin bottle at each sampling site, including physicochemical parameters such as temperature, pH, turbidity, and dissolved oxygen.

2.3 Taxonomic and morphological identification

Bryozoans were identified to the lowest possible taxonomic level based on closely examining of the external morphological characters using a ZEISS Stemi 305 stereomicroscope and specialised literature (Hayward, 1995; Cecchetto et al., 2019). The taxonomic nomenclature was verified using WoRMS (World Register of Marine Species). When identification to the species level was impossible, organism identity was limited to a higher operational taxonomic unit. Bryozoan zoaria were also counted and photographed using an AmScope ME1400 camera. For the morphological description and morphospecies grouping, we adopted the

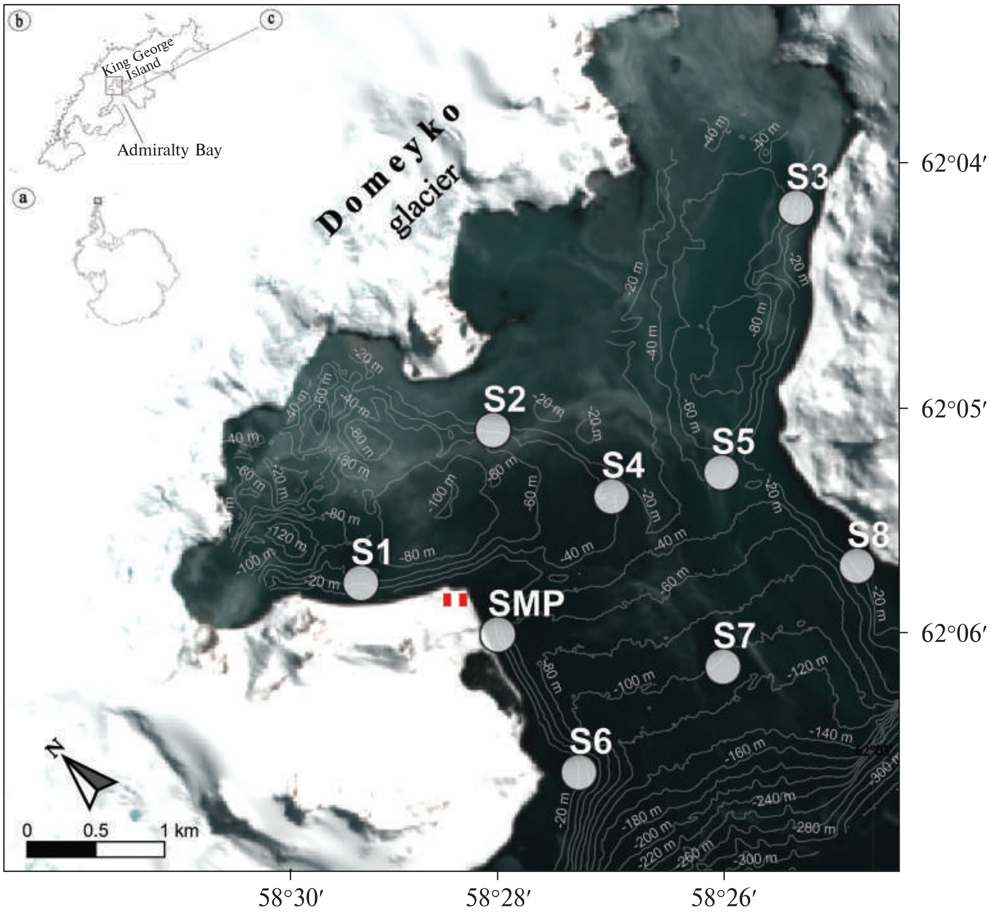

Figure 1. Sampling sites in the Mackellar glaciomarine fjord showing 20-m isobaths; the red/white flag indicates the Peruvian Antarctic research station Machu Picchu (ECAMP) in Crépin Point. Inset maps: a) Antarctica, b) King George Island (KGI), c) Mackellar Inlet (Admiralty Bay). The main map was generated using a Landsat 9 satellite image natural colour composite from 2021-01-12 (downloaded from https://glovis.usgs.gov/app). Maps were made in Quantarctica v. 3.2 (Matsuoka et al., 2021)

morpho-functional approach used by Thorne et al. (2022), which includes the classification of the functional traits of bryozoans based on Stach (1936) and Hageman et al. (1998).

2.4 Secondary substrate and epizoozoans

We evaluated the zoaria of the erect flexible (Smith & Key, 2019) *N. flagellata* that behaves as basibiont (i.e., organism whose surface is colonised by other organisms; Barnes, 1994). The taxa richness of epizoozoans (i.e., animals using other animals as substrate) was determined and differentiated according to the surface to which they were found attached (front or rear).

2.5 Data analysis

Abundance values were determined by the colony (zoaria) count of each bryozoan taxa. The taxonomic richness (S) was determined by sampling site, and alpha diversity was obtained using the Shannon diversity index ($H' - \log_e$) and Simpson's dominance (D). The Chao2 index was calculated to estimate the expected number of species in the study area. The data was fourth-root-trans-

Table 1. Taxonomic list of recorded bryozoan taxa, sampling sites, and settlement substrate. Growth form/zoarial type/growth habit classification according to Stach (1936) and Hageman et al. (1998): adeoniform – erect bilaminar branches; buguliform – flexible lightly-calcified bushy tufts; flustriform – erect foliaceous inherently flexible zoaria; fungiform – zooids concentrated at typically flaring ends; membraniporiform – encrusting unilaminar morphotype with entire basal lamina attached by cementation; vinculariform – erect, rigid, subcylindrical branches. Sections of the fjord: inner: S1–S3; middle: SMP, S4, S5; and outer: S6–S8

Taxonomy				Growth form	Sampling sites where occurring	Substrate				
Class	Order	Family	Taxa			Gravels (2–64 mm fraction)	Coarse sands (0.5–2 mm)	*Nematoflustra flagellata* (Waters, 1904)	*Himantozoum* (*Himantozoum*) *antarcticum* (Calvet, 1909)	Ascidian
1	2	3	4	5	6	7	8	9	10	11
Gymnolaemata	Cheilostomatida	Beaniidae	*Beania erecta* Waters, 1904	Membraniporiform	S8			×		
		Buffonellidae	*Aimulosia* sp.1	Membraniporiform	S2, S3, S8	×				
			Aimulosia sp.2	Membraniporiform	S2	×				
			Hippadenella inerma (Calvet, 1909)	Membraniporiform	S2, S3, S8	×				
		Bugulidae	*Himantozoum (Himantozoum) antarcticum* (Calvet, 1909)	Buguliform	S4, S5, S8	×				
			Himantozoum sp.	Buguliform	S1, S8	×				
			Camptoplites sp.	Buguliform	SMP, S7, S8		×			
		Calloporidae	*Amphiblestrum familiaris* Hayward & Thorpe, 1989	Membraniporiform	S2	×				
		Chaperiidae	*Chaperiopsis* sp.	Membraniporiform	S2, S4	×				
		Cribrilinidae	*Filaguria spatulata* (Calvet, 1909)	Membraniporiform	S2, S6			×		
			Filaguria sp.	Membraniporiform	S6			×		
		Electridae	*Harpecia spinosissima* (Calvet, 1904)	Membraniporiform	S1, S8				×	
		Ellisinidae	*Ellisina antarctica* Hastings, 1945	Membraniporiform	S2, S3	×				
		Exochellidae	*Escharoides tridens* (Calvet, 1909)	Membraniporiform	S2	×				
		Fenestrulinidae	*Fenestrulina proxima* (Waters, 1904)	Membraniporiform	S5, S6	×				×
			Fenestrulina rugula Hayward & Ryland, 1990	Membraniporiform	S2, S3, S8	×				

1	2	3	4	5	6	7	8	9	10	11
		Flustridae	*Nematoflustra flagellata* (Waters, 1904)	Flustriform	S2, SMP, S4, S5, S6, S8	×				
			Isosecuriflustra tenuis (Kluge, 1914)	Flustriform	S6	×				
			Klugeflustra antarctica (Hastings, 1943)	Flustriform	S6, S7	×				
			Isosecuriflustra sp.	Flustriform	S2	×				
		Hippothoidae	*Antarctothoa* sp.	Membraniporiform	S3, S5, S7, S8			×		
		Inversiulidae	*Inversiula nutrix* Jullien, 1888	Membraniporiform	S2, SMP, S5, S6, S8	×				
		Lacernidae	*Lacerna eatoni* (Busk, 1876)	Membraniporiform	S6, S8			×		
		Microporidae	*Micropora brevissima* Waters, 1904	Membraniporiform	S2, S5, S8	×				
			Micropora notialis Hayward & Ryland, 1993	Membraniporiform	S2	×				
		Sclerodomidae	*Cellarinella* sp.1	Adeoniform	S7		×			
			Cellarinella sp.2	Adeoniform	S7		×			
		Smittinidae	*Smittina* sp.1	Adeoniform	S2, SMP, S5	×				
			Smittina sp.2	Adeoniform	S2, S6, S8	×				
			Smittina sp.3	Adeoniform	S2, S4	×				
Stenolaemata	Cyclostomatida	Cytididae	*Supercytis tubigera* Busk, 1886	Vinculariform	S8			×		
		Lichenoporidae	*Disporella canaliculata* (Busk, 1876)	Fungiform	S2, S8			×		
		Tubuliporidae	*Idmidronea antarctica* Borg, 1944	Vinculariform	S7, S8			×		
			Idmidronea sp.	Vinculariform	S3				×	×
			Tubulipora organisans d'Orbigny, 1842	Fungiform	S8			×		
			Tubulipora sp.	Fungiform	S8			×		

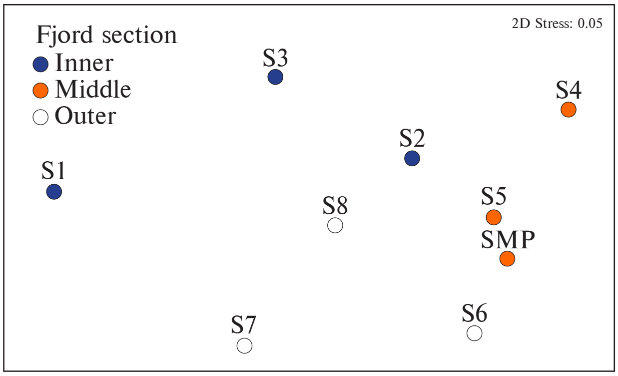

Figure 2. Non-parametric multidimensional scaling of bryozoan composition from nine sampling sites differentiated by sections of the Mackellar fjord. The stress value (0.05) indicates a very good and reliable representation of the bryozoan assemblage structure

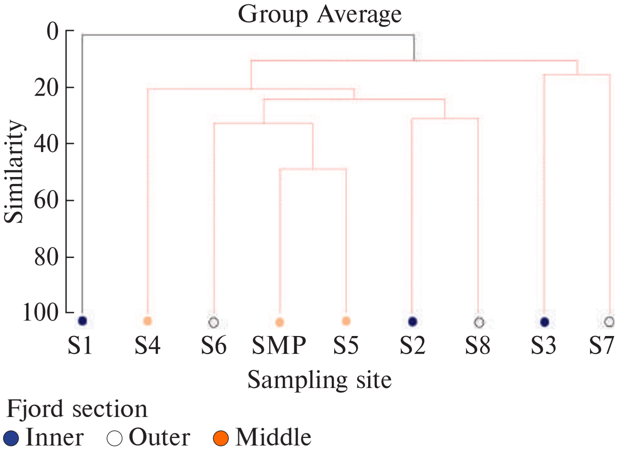

Figure 3. Hierarchical cluster analysis (Bray-Curtis, group-averaged) of the composition of the bryozoan assemblages. Red clusters indicate arrangement according to similarity between sampling sites, identified by the SIMPROF test

formed, and an analysis of similarity (ANOSIM) was performed to test the significance of the assemblage composition according to the factor fjord section (inner, middle, and outer). For the multivariate data analysis, a similarity matrix was constructed from abundance data using the Bray-Curtis distance to produce similarity dendrograms between sampling sites, including the bootstrap procedure to obtain the probability values of the dendrogram clusters. A similarity profile test (SIMPROF) was also applied to identify significant differences between the clusters. To analyse the relationship between the bryozoan samples collected from different sites, a non-metric multidimensional scaling (nMDS) based on the Bray-Curtis distance was performed to generate an ordination plot that would represent the similarity of the assemblages between sites on a simplified two-dimensional plane. To evaluate which species were mainly responsible for the differentiation between assemblages from different sampling sites, we used the similarity percentage test (SIMPER) based on abundance data (Clarke et al., 2014). All routines were performed in PRIMER v.6.0 (Clarke & Gorley, 2006).

3 Results

3.1 Taxonomic species richness

Overall, the taxonomic richness of bryozoans in Mackellar fjord yielded 36 taxa. The richest order was Cheilostomatida, with 30 species distributed in 17 families, followed by Cyclostomatida, with 6 taxa distributed in 3 families (Table 1). Representatives of the order Ctenostomatida were not observed in our samples. The richest families were Flustridae and Tubuliporidae, with 4 species each, followed by Buffonellidae, Bugulidae, and Smittinidae, with 3 species each. The highest species richness value was recorded at S8 (20 species), followed by S2 (18 taxa) and S6 (9 taxa). The highest diversity (H') was also recorded in S8, with a value of 2.78, followed by S2 (2.57) and S6 (2.20), while the lowest diversity was recorded in S1 (0.69) (Table 2). The outer section sites (S6, S7, and S8) had the highest cumulative taxonomic richness (26 taxa), followed by the inner (22) and, lastly, the middle section (10). Additionally, the calculated Chao2 index was 43, indicating that the observed represented 84% of the estimated richness.

3.2 Bryozoan assemblage composition

The results of the ANOSIM showed a significant difference in species composition according to the fjord section but not for the depth ranges (Table 3).

This is visually represented in the nMDS, with only a slight difference in the groupings according to the fjord sections (Fig. 2). The most similar sites (50% between SMP and S5) belonged to the middle section of the fjord (Fig. 2); however, there was no other marked grouping with high similarity between sites from same fjord section. The site with the lowest diversity and richness recorded (S1) was found to be an outgroup from the rest of the sites evaluated (Fig. 3).

The SIMPER analysis showed that the middle section sites were more similar in composition, with an average similarity of 34.81% (Table 4). These results also showed species from each section that contributed to the most similarity across the sites, indicating a more important predominance of bryozoans with a membraniporiform growth form for the inner section. In contrast, in the other two sections, the growth forms contributing more to inter-site similarity were flustriform and adeoniform growth forms, as well as the membraniporiform.

On the other hand, according to the dissimilarity analysis, the main difference was observed when comparing the middle and inner sections (90.92%). The species that contributed the most to this differentiation were the cheilostomes *I. nutrix* (Appendix Fig. 2b)*, N. flagellata, Smittina* sp.1, and *Himantozoum (Himantozoum) antarcticum* (Appendix Fig. 2f) (Table 5). Another bryozoan that contributes to the differentiation between the outer and inner and the outer and middle sections (dissimilarity = 88.1 and 80.4, respectively) was the cyclostome *I. antarctica*, which was only recorded in the outer section of the fjord (S7 and S8) and absent in the other sections (Table 5).

3.3 Growth forms

Six growth forms in bryozoans were recognised: membraniporiform, buguliform, flustriform, adeoniform, vinculariform, and fungiform. The predominant growth form was membraniporiform, which included calcified encrusting species, followed by the flustriform growth with erect flexible zoaria, of which *N. flagellata* was the most important representative in terms of abundance. Additionally, it was observed that S8 (outer section) contained the highest number of growth forms when compared with the rest of the sampling sites, especially those of the inner section (S1 and S3) where only two growth forms were registered (Fig. 4). In S2, the section with the second highest richness (18), the number of growth forms was lower than in other sites, resulting in lower morpho-functional diversity.

Table 2. Bryozoan diversity indices and abundance in the sampling sites

Sampling site	S	N	d	J’	H’($\log_e$)	D
S1	2	2	1.44	1	0.69	0.50
S2	18	48	4.39	0.89	2.57	0.11
S3	6	6	2.79	1	1.79	0.17
SMP	4	4	2.16	1	1.39	0.25
S4	4	5	1.86	0.96	1.33	0.28
S5	7	11	2.50	0.86	1.67	0.26
S6	9	9	3.64	1	2.20	0.11
S7	6	8	2.40	0.93	1.67	0.22
S8	20	39	5.19	0.93	2.78	0.08

Note: S — taxonomic richness, N — abundance, d — Margalef index, J’ — Pielou’s evenness, H’ — Shannon diversity index, D — Simpson’s dominance

3.4 Secondary substrate

Two types of substrata were found colonised by bryozoans. Abiotic, composed by coarse sands (0.5–2 mm) and gravels (2–64 mm); and natural secondary substrate (i.e., basibionts) *Nematoflustra flagellata, Himantozoum (Himantozoum) antarcticum*, *Camptoplites* sp., and ascidians. The highest number of epizoozoic taxa was hosted by the flustriform *N. flagellata* and mostly included other cheilostomes and cyclostomes. However, foraminiferans, solitary ascidians, calcareous tubeworms, entoprocts, and cnidarians were also found to a lesser extent. Epizoozoans were registered exclusively on the rear side surface of *N. flagellata* fronds (Appendix Fig. 1). The buguliform bryozoan *H. antarcticum* was also colonised by only two taxa of bryozoans (a membraniporiform electrid and a vinculariform tubuliporid) (Appendix Fig. 2a and 1e, respectively) and a foraminiferan. The smaller bush-like *Camptoplites* sp. registered only one foraminifera taxon (Table 1).

Table 3. Results of the ANOSIM test of the bryozoan assemblages. Sampling sites were grouped according to fjord sections and depth range

Factor	Significance level	p-value	R
Fjord section (inner, middle, and outer)	3.9%	0.03	0.292
Depth range, m (<30, >30 and >100)	52%	0.52	−0.05

4 Discussion

4.1 Bryozoan assemblage composition

Substrate availability and its characteristics are important factors for the settlement of lithophilic assemblages (Kuklinski et al., 2006; Krzeminska &

Table 4. Similarity percentage (SIMPER) test results (SD: standard deviation)

Taxa	Average abundance	Average similarity	Similarity/SD	Contribution percentage	Cumulative percentage
Inner section					
Fenestrulina rugula	0.80	2.01	0.58	25	25
Ellisina antarctica	0.91	2.01	0.58	25	50
Aimulosia sp. 1	1.00	2.01	0.58	25	75
Hippadenella inerma	0.67	2.01	0.58	25	100
Middle section					
Nematoflustra flagellata	1.14	18.64	4.19	53.55	53.55
Inversiula nutrix	1.08	5.45	0.58	15.65	69.21
Smittina sp. 1	0.67	5.45	0.58	15.65	84.86
Himantozoum (*Himantozoum*) *antarcticum*	0.67	5.27	0.58	15.14	100
Outer section					
Klugeflustra antarctica	0.67	4.24	0.58	20.7	20.7
Idmidronea antarctica	1.05	2.84	0.58	13.85	34.56
Antarctothoa sp.	0.91	2.01	0.58	9.80	44.35
Camptoplites sp.	0.67	2.01	0.58	9.80	54.15
Nematoflustra flagellata	1.22	1.88	0.58	9.17	63.32
Inversiula nutrix	0.67	1.88	0.58	9.17	72.49

Kuklinski, 2018). Many opportunistic species can colonise medium size lithoclasts since they are readily available in gravelly sediments of fjords. The most diverse site in Mackellar Inlet (S8) was also the shallowest (<30 m) and was composed mainly by gravelly bottoms, differing from most of the other sites, which were composed mostly by unconsolidated sediments (Moreno & Herrera, 2025). Gravels characterised by gravelly-mud substrate were also present around S2 (Moreno & Herrera, 2025), offering potential settlement surfaces for a wider variety of epilithozoans and other organisms, such as large brown macroalgae (Moreno & Szeligowska, 2023). In our study, these two sites (S8 and S2) harboured the highest taxa richness and diversity, confirming that local differences in substrate heterogeneity influence the shaping of bryozoan assemblages (Kuklinski et al., 2017). The flustriform *N. flagellata* was the most abundant in S8, which could be explained by the shallow depth, the availability of hard substrata for settlement, and the distance from Domeyko Glacier as important factors contributing to the

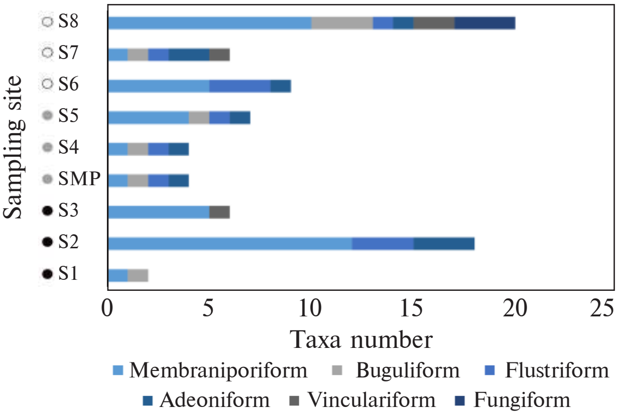

Figure 4. Number of taxa according to growth form classification by sampling site

Table 5. Dissimilarity results of the SIMPER test according to the fjord section (inner and middle, inner and outer, middle and outer). SD = Standard deviation

Taxa	Average abundance	Average abundance	Average dissimilarity	Dissimilarity SD	Contribution percentage	Cumulative percentage
Inner and middle (dis = 90.9)	Inner	Middle				
Inversiula nutrix	1.15	1.08	9.61	1.26	10.57	10.57
Nematoflustra flagellata	0.33	1.14	8.93	1.16	9.83	20.40
Smittina sp. 1	0.47	0.67	5.60	0.98	6.16	26.56
Himantozoum (*Himantozoum*) *antarcticum*	0.00	0.67	5.33	0.97	5.86	32.42
Aimulosia sp. 1	1.00	0.00	5.00	1.24	5.50	37.92
Inner and outer (dis = 88.1)	Inner	Outer				
Idmidronea antarctica	0.00	1.05	5.61	0.82	6.37	6.37
Inversiula nutrix	1.15	0.67	4.88	1.34	5.54	11.92
Klugeflustra antarctica	0.00	0.67	4.53	1.04	5.15	17.06
Nematoflustra flagellata	0.33	1.22	4.35	1.09	4.95	22.01
Middle and outer (dis = 80.4)	Middle	Outer				
Idmidronea antarctica	0.00	1.05	6.28	0.96	7.81	7.81
Klugeflustra antarctica	0.00	0.67	5.10	1.29	6.35	14.16
Nematoflustra flagellata	1.14	1.22	5.10	1.24	6.34	20.50
Inversiula nutrix	1.08	0.67	5.07	0.99	6.31	26.82
Antarctothoa sp.	0.33	0.91	4.16	1.11	5.18	32.00

availability of suitable conditions and provision of optimal habitat for erect flexible bryozoans. On the other hand, in the inner section of the fjord, which is more susceptible to disturbances due to its proximity to the Domeyko Glacier, encrusting membraniporiform bryozoans were the most common and abundant. Even though some sampling sites, such as S2, registered high species richness, the functional diversity was not necessarily correlated to this descriptor.

One of the most frequent encrusting taxa was *Inversiula nutrix*; an early coloniser and fast-growing species in the early stages of ecological succession (Moyano, 1972; Barnes, 1995). Moreover, *I. nutrix* has been found to grow well on horizontal surfaces, exhibiting a tolerance to sedimentation, which is less usual among other bryozoans (Clark et al., 2017). Another frequent taxon was the encrusting cheilostome *Fenestrulina* sp., common in several sampling sites in the study area. These early-colonising and opportunist species are commonly found in habitats with a higher disturbance frequency, as opposed to less disturbed areas where slow-growing but more competitive bryozoans are observed, resulting in an assemblage composition more towards equilibrium (Barnes & Clarke, 1998).

4.2 Growth forms

Encrusting membraniporiform (50% of total taxa found) followed by adeoniform colonies (erect and rigid branching) were among the most frequent growth forms of bryozoans in Mackellar Inlet. The latter was represented by 5 taxa, such as *Cellarinella* sp.1 and *Cellarinella* sp.2, both with erect delicate zoaria. These were only recorded at S7, the site with the maximum recorded depth, 113 m, which indicate lower levels of mechanical disturbance in deeper waters. Some environmental conditions, such as the physical action from waves, currents, and iceberg scouring, could explain why these erect and rigid bryozoans with more fragile and delicate colonies are absent in the shallower areas (Kuklinski et al., 2005; Liuzzi et al., 2018). Meanwhile, erect, flexible, and branching bryozoans (e.g., flustriforms) can live in moderate to high energy waters (Stach, 1936). These findings coincide with the growth form patterns found in Ezcurra Inlet, where the number of encrusting species was very high in the inner area of the fjord, while in other areas, growth-form diversity was much higher (Pabis et al., 2014). However, as mentioned before, many factors are involved during the colonisation history of bryozoans, including substrate stability, which is dependent on the frequency of disturbance forcings (Kuklinski et al., 2006), nearby larval supply sources, and epizoozoan loading (Barnes, 1999).

4.3 Secondary substrate

In this study, the most important settlement substrates were gravels and basibiont bryozoans (Table 1). *Nematoflustra flagellata* was the basibiont with the highest abundance of epizoozoans, including other cheilostome and cyclostome bryozoans (5 taxa each). This erect flexible species, therefore, represents a habitat facilitator, serving as an important substrate for other sessile suspension feeders (Thorne et al., 2022). Our observations demonstrated that most epizoozoans preferred the rear surface of *N. flagellata* rather than the frontal surface (Appendix Fig. 2). This can be explained by the presence of frontal setiform avicularia – autozooids with defence and cleaning functions to avoid the accumulation of sediment or detritus. These results agree with Moyano and Cancino (2002), and Barnes (1995).

Additionally, although cyclostomes are typically found settled on unconsolidated sediments in Antarctic fjords (Pabis et al., 2014; Krzeminska et al., 2018; Krzeminska & Kuklinski, 2018), the cyclostomes we report (6 taxa) were found settled as only epizoozoans (i.e., none was found on gravels, nor coarse sands). Therefore, the presence of secondary substrate in fjordic basins where soft bottoms predominate represents an important service in providing an elevated three-dimensional layered refuge for taxa that are less adapted to sediment burial, as well as providing a higher perch and better access to food items for suspension feeders (Winston, 2009). In the South Orkney Islands (60.7°S), seven species of epizoozoic cheilostomes have been reported fouling Antarctic pycnogonids — zooid-level predators of bryozoans (Mckinney et al., 2003). However, no cyclostome representatives were found fouling the motile basibionts (Key et al., 2013). The reason for our finding epizoozoic cyclostomes could be the higher complexity and surface characteristic of the lightly calcified bushy-forming basibionts reported here (*N. flagellata* and *H. antarcticum*, flustriform and buguliform growth forms, respectively). It must be noted, however, that the strength of longer but thinner colonies may be considerably reduced when high epizoozoan loading weighs the basibiont down (Barnes, 1999), thus also having possible implications in the strategies and overall structure of the bryozoan assemblage from a functional perspective.

4.4 Carbonate production

Beyond the factors discussed, the remains of epizoozoic bryozoans are also important as potential contributors to carbonate sediment production in cold-water environments (Rejimen, 2021), mainly due to the calcitic nature of their skeletal mineralogy. In polar ecosystems, the storage and burial of carbonates produced by zoobenthos are closely linked to the surrounding environmental and oceanographic conditions, reflecting an interplay between biogenic activity and the prevailing physical setting (Frank et al., 2014). In addition, for lightly calcified articulated bryozoans, skeletons commonly break apart after death (Lombardi et al., 2020), while the long-lasting carbonate structures produced by epizoozoic bryozoans from ephemeral substrates are preserved as dispersed fragments in sediments (Hageman et al., 2000). This is of particular importance in the context of blue carbon gains from emerging young glaciomarine fjords, where not only storage-to-sequestration efficiencies are relatively high but where zoobenthic carbon is also expected to increase with fjord age (Barnes et al., 2020; 2021; Sands et al., 2023).

5 Conclusions

This study presents an analysis of bryozoan assemblages derived from emergent sampling efforts in Mackellar Inlet, Antarctica. The sites in the glaciomarine fjord's outer section had higher accumulated taxa richness, diversity, and number of growth forms. The membraniporiform growth form was the most abundant across all fjord sections. Cheilostomes showed higher taxonomic richness (30), while cyclostomes (6) were only found as epizoozoans. The basibiont *N. flagellata* hosted, by far, the highest abundance and diversity of epizoozoans, confirming its key role as bioconstructor and habitat facilitator. Our results can be used as the baseline for future studies that include methodologies specifically focused on sampling lithophilic assemblages, such as scuba diving and rock dredges, to investigate further the importance of substrate composition on the structure of antarctic bryozoans, and sessile suspension feeding assemblages in general.

Ethical aspects. The study meets the legal requirements of the Antarctic Treaty. Samples were collected under official permits issued and granted by the Dirección de Asuntos Antárticos—Ministerio de Asuntos Exteriores (MRE) of Peru.

Data availability. Datasets generated for the current study are available from the corresponding authors upon reasonable request.

Author contributions. M. P.: sample collection and curation, conceptualisation, analysis, wrote original draft; A. G. I.: sample collection, funding acquisition, project administration; B. M.: sample collection, conceptualisation, analysis, wrote original draft. All authors reviewed and edited content prior to manuscript submission.

Acknowledgements. This work is part of the MP undergraduate thesis project registered as "Diversidad de briozoos del fiordo glaciomarino Mackellar, Isla Rey Jorge, Antártida" (N°009-2022-PRE5), Universidad Científica del Sur (CIENTIFICA). We thank Dr. Pepe Espinoza, Dr. Báslavi Cóndor-Luján, and MSc. Raul Olaechea for reviewing the thesis work. Thanks are due to the military and scientific staff who helped in the sampling activities during ANTAR XXIV, XXV, XXVI, and XXIX (austral summers of 2017, 2018, 2019, and 2023, respectively), especially boatmen T1 EP Albino Milla and T2 EP Joel García, technical staff of the Compañía de Operaciones Antárticas (COA). We thank the logistical support offered by crew members of the Peruvian Navy Research Vessel B.A.P. "Carrasco" (https://www.dhn.mil.pe/carrasco/en/) during the ANTAR expeditions. We thank José Manuel Herrera for providing the processed isobaths and dr inż. Marlena Szeligowska for creating the satellite composite (2021-01-12) for Fig. 1. We acknowledge Donna Pringle (Dirección General de Investigación, Desarrollo e Innovación, DGIDI, CIENTIFICA) for proofreading the English version of the manuscript.

Funding. Samples for this study were collected under the research projects executed by Universidad Científica del Sur (CIENTIFICA), funded by the Dirección de Asuntos Antárticos–Ministerio de Relaciones Exteriores (MRE, Peru): "Environmental factors governing the distribution of macrobenthos in Mackellar Inlet, King George Island, Antarctica" and "Polychaeta as biological indicators on the trophic interactions of macrobenthos in Mackellar Inlet, King George Island–Antarctica".

Conflict of Interest. The authors declare no conflict of interest.

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Received: 25 January 2025
Accepted: 12 May 2025

Поступ дослідження фауни Bryozoa у післяльодовиковому фйорді бухти Макеллара, 62°S

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Реферат. Моховатки – багатоклітинні тварини, що ведуть прикріплений спосіб життя та харчуються суспендованими у воді частинками органіки. Це важливий компонент антарктичних макрозообентосних угруповань. Ці холоднокровні модульні організми присутні в широкому спектрі середовищ існування, для яких характерні великі градієнти умов (наприклад, у полярних фйордах льодовикового походження). Ця робота присвячена різноманіттю моховаток, виявлених у зразках, принагідно відібраних за допомогою ковша ван Вина в бухті Макеллара (62°S, острів Кінг-Джордж) протягом чотирьох сезонів (2017–2019 та 2023) Перувійськими експедиціями ANTAR. Оцінка кумулятивного таксономічного багатства та патернів різноманіття виявила 36 таксонів, що представляють 84% оціненої різноманітності (Chao2 = 43). З шести визначених життєвих форм домінували мембраніпориформні (колоніальні, що утворюють сланкі обростання) (кальцифіковані кіркоподібні однопластинчасті), на другому місці були хейлостомні з флустриформною будовою (колоніальні з гнучкими злегка кальцифікованими гілками). Найбільша різноманітність, кумулятивне багатство (26 таксонів) та всі наразі відмічені життєві форми (6) знайдено в зовнішній частині фйорду. Прямостоячий гнучкий базибіонт *Nematoflustra flagellata* (Waters, 1904) був найпоширенішим серед моховаток флустриформної будови. Різноманіття тварин, які обростали представників цього виду, також було найбільшим; вони переважно заселяли зворотню сторону віяла. Незакріплені гравій чи крупнозернистий пісок були необхідним субстратом для наростання моховаток, проте присутність середовищеадаптивних життєвих форм збільшувала загальні показники чисельності та таксономічного і функціонального багатства в локальному масштабі. На основі цього по суті опортуністичного дослідження (збір зразків не був основною метою експедиційних виїздів) можливі подальші роботи з укладення анотованого переліку місцевих моховаток. Такі дослідження вимагають різноманітних методів відбору проб, адаптованих для моховаток та їхніх субстратів (наприклад, дайвінг чи драгування скель). Автори ставили за мету фундаментальний функціональний аналіз на основі життєвих форм, проте необхідно глибше зрозуміти екологію моховаток в бухті Макеллара, зважаючи на нюанси екологічного значення знахідок та адаптацій життєвих форм до градієнтів довкілля.

Ключові слова: вторинний субстрат, зообентос, колонія, обростання інших моховаток, хейлостоми

APPENDIX

Table. Details of the sampling sites, eight as found in Thorne et al. (2022) and adding the *SMP site. In brackets, coded E01—11 is the station nomenclature used by the Peruvian project

Sampling site	Latitude	Longitude	Fjord section	Distance to Domeyko, m	Depth range, m	Depth from bathymetry data, m
S1 (E-01)	-62.0906	-58.4839	Inner	970	>30	40
S2 (E-02)	-62.0808	-58.4650	Inner	400	>30	42
S3 (E-04)	-61.0667	-58.4221	Inner	800	10—30	30
*SMP (E-05)	-62.0942	-58.4697	Middle	2200	10—30	45
S4 (E-06)	-62.0853	-58.4887	Middle	1500	>30	40
S5 (E-07)	-62.0839	-58.4333	Middle	1700	>30	50
S6 (E-09)	-62.1033	-58.4541	Outer	3500	>30	17.9
S7 (E-10)	-62.0966	-58.4337	Outer	2900	>30	113
S8 (E-11)	62.0902	-58.4147	Outer	3000	<10	16

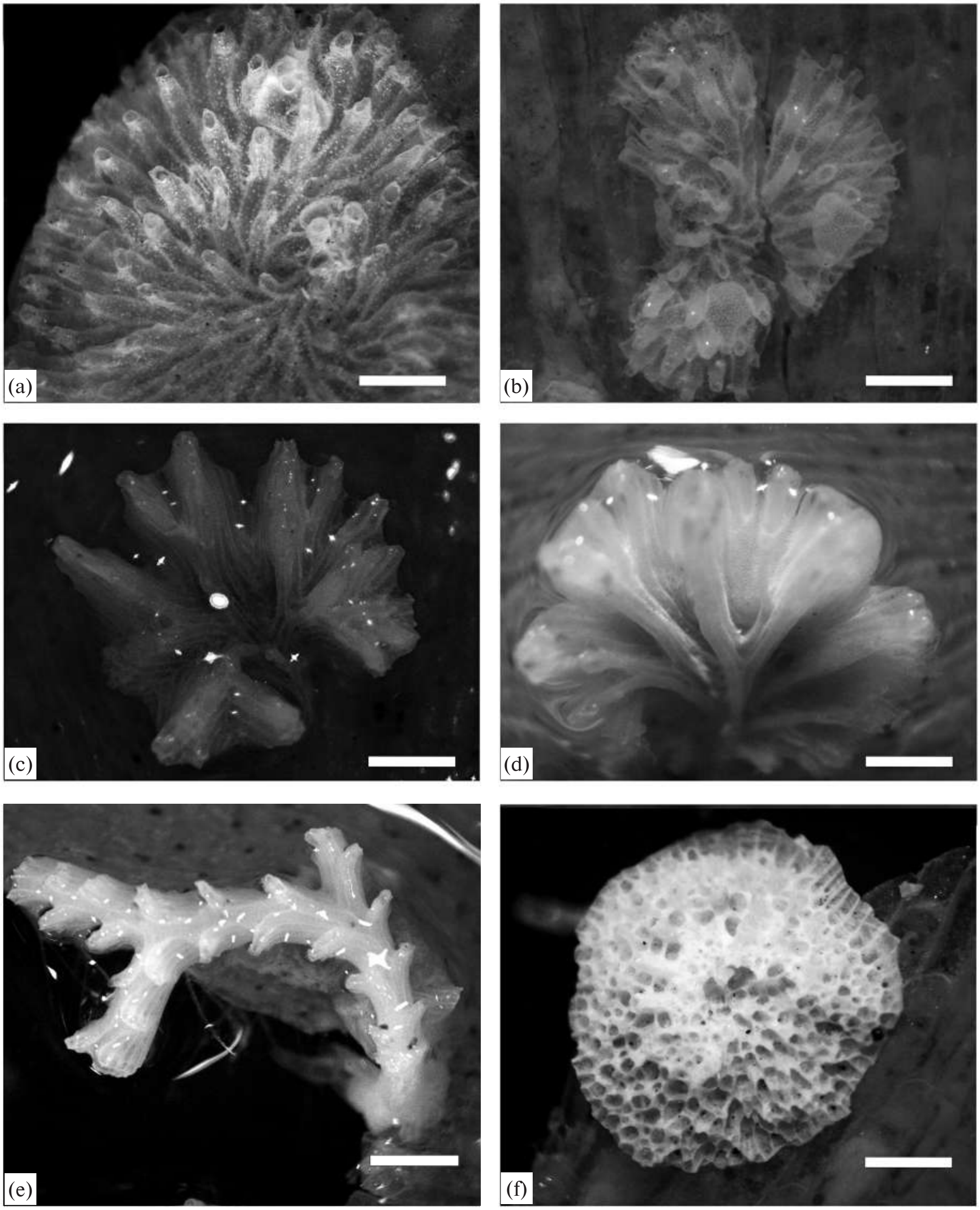

Figure 1. Some cyclostomes (and their growth forms) registered in the study found growing as epizoozoans on the rear surface side of *Nematoflustra flagellata*: (a)–(b) *Tubulipora organisans* (fungiform); (c)–(d) *Supercytis tubigera* (vinculariform); (e) *Idmidronea* sp. (vinculariform); (f) *Disporella canaliculata* (fungiform). Scale bars: 0.5 mm (a)–(c), 1 mm (d)–(f)

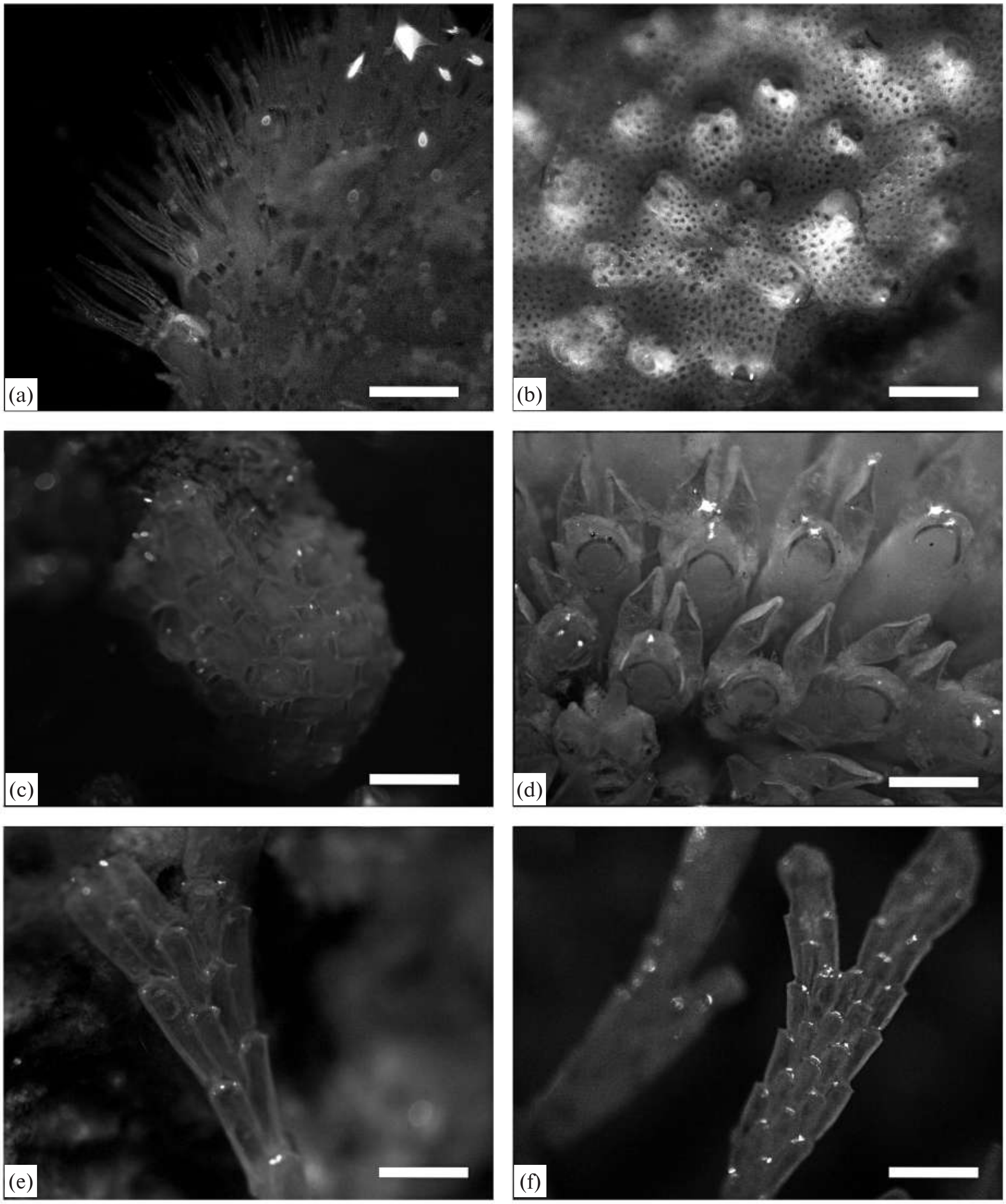

Figure 2. Some cheilostomes (and their growth forms) registered in the study: (a) *Harpecia spinosissima* (membraniporiform) growing on the frond of *Himantozoum* sp., scale bar: 0.6 mm; (b) *Inversiula nutrix* (membraniporiform), scale bar: 0.5 mm; (c) *Micropora brevissima* (membraniporiform), scale bar: 1 mm; (d) *Beania erecta* (membraniporiform), scale bar: 0.5 mm; (e) *Camptoplites* sp. (buguliform), scale bar: 0.8 mm; (f) *Himantozoum* sp. (buguliform), scale bar: 1.6. mm