An Acad Bras Cienc (2023) 95(Suppl. 3): e20210622 DOI 10.1590/0001-3765202320210622
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ECOSYSTEMS

Glacier retreat effects on the distribution of benthic assemblages in Martel Inlet (Admiralty Bay, Antarctica)

MONICA A.V. PETTI, PAULA F. GHELLER, SANDRA BROMBERG, PAULO C. PAIVA, MICHEL M. MAHIQUES & THAIS N. CORBISIER

Abstract: The Antarctic environment has special characteristics that influence the local marine life. The benthic organisms, adapted to these extreme conditions of life, are subject nowadays to effects of climate change. Recently, the consequences of glacier retreat on these assemblages have been observed in many West Antarctic Peninsula (WAP) regions, including King George Island (KGI). This study described the spatial variation of the benthic macrofauna in different areas of the Martel Inlet (Admiralty Bay - KGI), at depths around 25-30 m. Sampling was done in January 2001 at ten stations classified in localities according to their proximity to ice-margin/coastline in marine-terminating glacier (MTG), terrestrial-terminating glacier (TTG) and ice-free area (IFA). The total density and the abundance of annelids, nematodes, peracarid crustaceans and bivalves were higher at IFA stations. The locality discrimination by taxa and species was independent of available environmental/sedimentary conditions or was the result of unmeasured variables or species life history processes not assessed herein. Considering that our findings were obtained 21 years ago, they will be especially useful for comparing future studies of benthic assemblage responses to the influence of climate change and continuous glacier retreats in the WAP region.

Key words: Benthic ecology, Climate change, Glacier influence, King George Island.

INTRODUCTION

The Antarctic environment has unique characteristics that influence the local marine life. Among these are low and stable water temperatures, small fluctuations in salinity and other drivers, such as the great seasonality of light and food resources, disturbances caused by ice and variations in circulation patterns (Arntz 1994, Gutt et al. 1996). The benthic organisms, adapted to these extreme conditions of life, are increasingly subject nowadays to effects of climate change. The West Antarctic Peninsula (WAP) is considered the most rapidly warming region from the International Geophysical Year 1958 to the late 20th century (Sato et al. 2021), a hotspot of climate-driven environmental change (Robinson et al. 2021). This warming is also manifesting in changes to benthic coastal communities as a result of ice shelf disintegration and glacial retreat (Rogers 2020), which can result in variations of seawater temperature and salinity, turbidity and ice-scouring with significant influence on the biodiversity of these areas (Valdivia et al. 2020).

More recently, the consequences of glacier retreat on the benthic environment have been observed in many regions of the WAP, including some bays and coves of King George Island (KGI), such as Potter Cove (Quartino et al. 2013, Pasotti et al. 2015, Sahade et al. 2015, Lagger et al. 2017, Hoffmann et al. 2018, Braeckman et al. 2019, 2021, Torre et al. 2021), Marian Cove (Park et al. 2020, Bae et al. 2021, Kim et al. 2021) and Fildes/Maxwell Bay (Ko et al. 2020, Valdivia et al. 2020). These studies used different approaches to assess the role of glacier retreat on benthic communities' structuration, but only a few were dedicated to the effects of this retreat on the distribution of soft-bottom macrofauna assemblages (Pasotti et al. 2015, Hoffmann et al. 2018, Braeckman et al. 2021).

Despite the intensifying glacial retreat process over the last two decades (Oliveira et al. 2019, Pasik et al. 2021) in Admiralty Bay (KGI), and the considerable knowledge concerning benthic communities acquired since the 1980s (Sicinski et al. 2011), observations regarding the influence of this process on benthic communities were made only in Ezcurra, one of its three inlets (Sicinski et al. 1996, Pabis et al. 2011, Pabis & Sobczyk 2015, Potocka et al. 2019).

A glacial retreat mapping in Martel Inlet (Admiralty Bay), between 1979 and 2011, showed 13.21% loss of area, mostly between 1979 and 2000 (Rosa et al. 2014). Considering these rapid glacier shifts, this study described the spatial variation of the benthic macrofauna in different areas of Martel Inlet (Admiralty Bay - KGI), according to the proximity of ice-margin/ice-free areas, at depths of around 25-30 m. Allowing to assess their influence on macrobenthic communities, these findings were obtained 21 years ago (2001), and thus will be especially useful for monitoring glacier retreat impact on future surveys of benthic assemblages in this area.

STUDY AREA

King George Island (KGI), the largest island of the South Shetlands Archipelago, is in the West Antarctic Peninsula (WAP) region (Figure 1a-b). Admiralty Bay, its largest embayment, is a fjord-like bay, presenting a central basin and three inlets: Ezcurra, Mackellar, and Martel (Figure 1b-c).

Admiralty Bay is approximately 120 km^2 and has a maximum depth of 600 meters (Jazdzewski et al. 1986). Its connection with the Bransfield Strait is given through an entrance facing the south. The water circulation between the bay and the strait is essential to maintain the chemical and hydrographic conditions, directly affecting the living organisms (Rakusa-Suszczewski 1995). Tides are semidiurnal and the main factors responsible for the water mixing between the bay and the strait and inside the bay (Pruszak 1980). Water salinity and temperature in the austral summer (2009-2012) showed values between 33.9 and 34.4 and -0.4^{o}C and 1.8^{o}C on the surface and at 30 m depth (Cascaes et al. 2012). This stability does not affect the water circulation in the bay (Jazdzewski et al. 1986). The movement of icebergs indicates a permanent surface current flowing towards NE and ENE in the Bransfield Strait, and ice blocks are frequently seen, entering or leaving Admiralty Bay (Madejski & Rakusa-Suszczewski 1990).

The morphology of Admiralty Bay is complex, both in its coastline and seafloor topography. The heterogeneity of the seafloor in Admiralty Bay largely determines the local hydrodynamics, in conjunction with the circulation in the Bransfield Strait (Szafranski & Lipski 1982). The presence of calving glacier fronts, along with the frequent generation of icebergs and ice growlers, is one of the leading causes of the significant seafloor heterogeneity that provides a wide variety of habitats for benthic communities (Sicinski et al. 2011). Glaciers and icefalls correspond to approximately 40 km of the bay's shoreline and have been retreating in recent decades (Rosa et al. 2020).

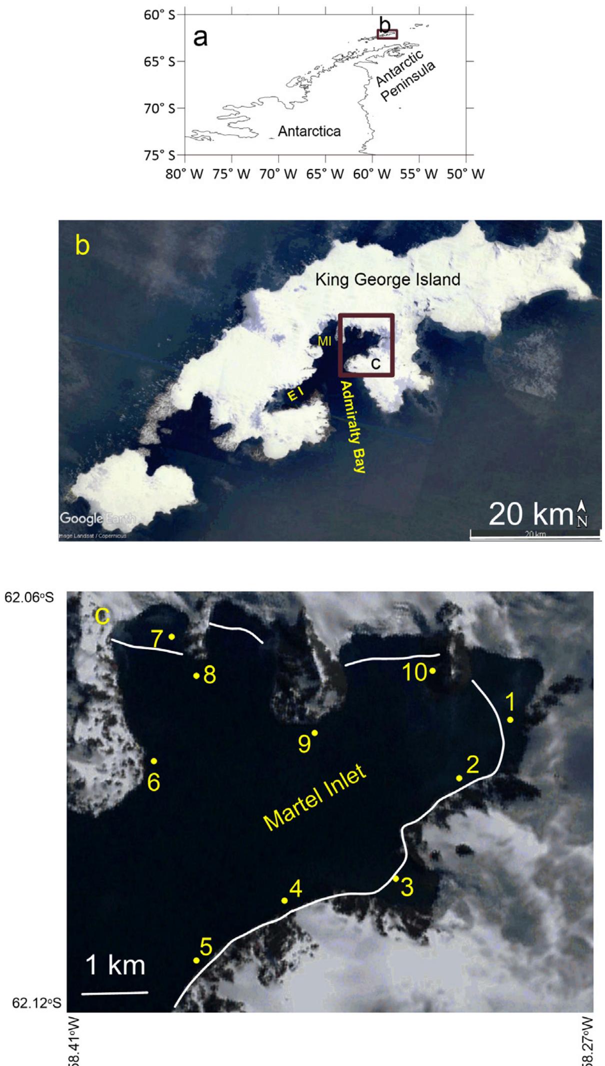

Figure 1 - Location of King George Island in the context of the Antarctic Peninsula (a). Location of the study area in the context of King George Island and Admiralty Bay (b). Location of the sampling stations inside the Martel Inlet (c) with the location of glaciers in 1979 (white line) based on Rosa et al. (2014) who provide further details. Abbreviations: MI: Mackellar Inlet; EI: Ezcurra Inlet. Satellite image source: Google Earth December 2000. Coastline source: http://ngdc.noaa.gov (last accessed March 31st, 2021).

Martel Inlet, located in the northern sector of Admiralty Bay, has an area of around 18 km^2 (Figure 1c) and a variety of geomorphologic features characterized by sharp differences at a small spatial scale and an extremely irregular seafloor affected by local geology and tectonics as well as by glacial erosive processes. The bottom is mainly composed of pebbles and gravels, changing to sandy mud or mud towards the deeper areas (Nonato et al. 2000).

Most of Martel Inlet is surrounded by dynamic tidewater glaciers with intense crevassing and steep slopes characterized by rapid ice flow. These glaciers are marine-terminating, such as Stenhouse, Goetel, Dobrowolski, and Krak Glacier (Perondi et al. 2020). Others are land-terminating, such as Wanda, Dragon, and Professor Glacier (Rosa et al. 2013). This classification was used to identify the stations according to the area of influence of glaciers: marine-terminating glacier (MTG), terrestrial-terminating glacier (TTG) and ice-free area (IFA). The historical analysis of the location of glacier termini allowed for developing a glacial retreat map, with evidence of a total retreat of 13.21% between 1979 and 2011, with the interval between 1979 and 2000 being the most intense in terms of ice retreat (Rosa et al. 2014, Oliveira et al. 2019).

MATERIAL AND METHODS

Sampling and laboratory analysis

Sediment samples were collected with a Van Veen grab (0.03m^2), sampling volume of 3L, at ten stations in Martel Inlet (Figure 1c). At each station, three samples were taken for macrofauna and one for sediment analysis. We only considered successful samples those with more than 2.5 liters of sediment with no indications of improper closing. All samplings were conducted during a single day (January 5th) of the austral summer of 2001. The stations were determined at different areas of Martel Inlet, according to the proximity of ice-margin/ice-free areas, at depths of around 25-30 m. They were numbered and classified as marine-terminating glacier (MTG): Dobrowolski (1), Krak

(3), Stenhouse (7) and Goetel (10); terrestrial-terminating glacier (TTG): Professor (2), Wanda (4) and Dragon (5); and ice-free area (IFA): in front of the Brazilian Station Comandante Ferraz (6), O´Connor Rock (8) and Punta Ullman (9) (Figure 1c). The distance from the station to the closest ice-margin or shoreline was calculated directly in a Google Earth image, dated December 2000 (Table I).

Macrofauna samples were washed through a 0.5-mm mesh; the material retained was fixed in 10% borax-buffered formalin and preserved in 70% ethanol. Samples were examined at the Antarctic Benthic Laboratory of the Oceanographic Institute of the University of São Paulo (IOUSP). Macrofauna was counted and identified at the higher taxonomic level, with polychaetes and bivalves identified at the species level. Although nematodes are typical of the meiofauna community, they were considered in our analysis because meio- vs. macrobenthic nematodes represent different communities (Sharma et al. 2011). The biomass (wet weight) of each taxonomical group from each replicate was weighed after blotting on filter paper for 2 min with a 1-mg precision scale. We used two measurements of biomass for analyses: total and partial, the latter excludes large-size taxonomic groups and those with hard shells (sea urchins, ophiuroids, bivalves, gastropods, and ascidians). The macrofauna was deposited in the Biological Collection "Professor Edmundo F. Nonato" (ColBIO-IOUSP).

Grain size analysis of sediment was done by the sieving and pipetting techniques described in Suguio (1973), using the Folk & Ward (1957) classification. Carbonate percentage was calculated by weight difference in sediment before and after HCl dissolution (Gross 1971). Organic matter percentage was calculated from the weight difference in sediment before and after oxidation using H_2O_2 (30%).

Data Analysis

Owing to the high collinearity among sedimentary variables, they were submitted to a Principal Component Analysis (PCA) in R (R Core Team 2021) to reduce them from 12 to only four more orthogonal related: mud, pebbles, sorting and $CaCO_3$. Mud is a proxy of organic matter and lower coarse sand content, while $CaCO_3$ is a proxy of mean/fine sand. These four sedimentary variables plus depth, distance from the closest ice-margin/coastline and locality were used for further analysis. Dependence among community measurements (density, biomass and abundance of taxonomic groups) and selected environmental variables were assessed through Generalized Linear Models (GLM, Burnham & Anderson 2002) with log-link function (Poisson family) for count data, and identity link (Gaussian) for the log of biomass. The best models were selected through the criteria of delta AICc < 2 (Burnham & Anderson 2002), and the average of the best models was provided. Both analyses were performed in the R environment 4.03 (R Core Team 2021) with model selection performed through the 'MuMIn' package (Bartón 2020). Multivariate analyses were also performed to compare stations and localities for three sets of data: environment, taxonomic groups, and dominant polychaete/bivalve species. Nonmetric multidimensional scaling (MDS) was performed separately for each set, using Bray-Curtis similarity matrix on log-transformed biotic data. Euclidean distance was used to calculate the matrix on normalized/standardized variables of environmental data. Results were compared through the Procrustes test (PROTEST) when the mean-square of rotated configurations were tested against null-models through permutation (Peres-Neto & Jackson 2001). Comparison among areas were assessed by means of PERMANOVA with 999 permutations. Three comparisons were

Table I. **Characteristics of each station: distance from to the closest ice-margin/coastline, depth, sediment characteristics, total density, total and partial biomass, and density of each taxonomic groups. Ice-free area (IFA): in front of the Brazilian Station "Comandante Ferraz" (6), O´Connor Rock (8) and Punta Ullman (9); terrestrial terminating glacier (TTG): Professor (2), Wanda (4) and Dragon (5); and marine terminating glacier (MTG): Dobrowolski (1), Krak (3), Stenhouse (7) and Goetel (10).**

CLASSIFICATION	IFA stations			TTG stations			MTG stations			
STATIONS	**6**	**8**	**9**	**2**	**4**	**5**	**1**	**3**	**7**	**10**
Distance (m)	144	337	195	330	286	178	398	712	338	784
Depth (m)	23.4	25.0	25.7	20.3	31.4	21.9	23.4	25.5	21.7	27.7
SEDIMENT										
Pebbles (%)	0.0	12.3	34.4	17.0	8.2	11.6	1.6	0.6	41.4	18.0
Granules (%)	2.5	8.8	2.6	8.0	5.3	6.8	3.5	2.1	7.4	4.2
Very Coarse Sand (%)	2.5	2.5	1.4	3.9	3.5	2.2	1.7	1.2	3.5	3.1
Coarse Sand (%)	2.5	2.4	1.7	4.6	5.6	2.6	2.5	1.2	4.0	2.7
Medium Sand (%)	2.5	1.6	1.4	3.5	11.9	7.5	2.5	1.2	2.4	3.3
Fine Sand (%)	2.5	1.8	1.8	4.6	21.1	20.8	2.5	1.2	2.3	5.7
Very Fine Sand (%)	2.5	3.2	3.1	5.0	13.0	16.9	2.5	1.2	3.2	11.1
Mud (%)	85.1	67.4	53.5	53.5	31.4	31.7	83.4	91.5	35.8	51.9
Organic Matter (%)	10.5	9.1	9.8	8.8	8.0	4.3	7.1	8.0	6.7	7.7
$CaCO_3$ (%)	12.3	11.8	12.0	13.6	23.3	12.0	8.4	8.8	10.9	12.4
Mean Diameter (ϕ)	6.7	5.4	5.8	4.5	3.8	4.2	6.3	6.9	4.4	5.1
Sorting (ϕ)	2.5	3.5	3.2	3.6	3.1	3.2	2.5	2.2	3.8	3.2
DENSITY/BIOMASS (ind.0.09 m^{-2}/g.0.09 m^{-2})										
Density	1069	1033	654	54	959	357	82	349	62	867
Total Biomass	102.9	17.4	18.8	37.2	166.9	12.7	18.7	18.7	0.2	7.7
Partial Biomass	3.0	7.4	3.1	5.9	2.1	12.2	18.7	3.5	0.2	5.1
TAXONOMIC GROUPS (ind.0.09 m^{-2})										
Nematodes	584	468	162	1	370	17	2	181	2	20
Polychaetes	114	249	138	10	104	86	13	29	4	772
Oligochaetes	211	135	215	5	81	7	0	0	0	0
Bivalves	22	142	42	22	40	14	3	38	2	16
Amphipods	33	3	17	2	49	151	2	7	49	19
Cumaceans	31	3	33	6	53	26	49	61	0	3
Tanaids	3	0	0	3	164	15	11	25	0	1
Priapulids	20	28	6	0	6	3	1	1	1	13
Gastropods	0	0	3	0	36	12	0	1	4	0
Ophiuroids	49	2	3	0	1	0	0	0	0	0
Ascidians	0	0	29	0	19	1	0	3	0	0
Isopods	1	0	3	3	21	19	0	3	0	0
Nemerteans	0	0	0	0	1	2	0	0	0	22
Ostracods	0	0	3	0	8	1	0	0	0	0
Copepods	0	0	0	0	4	3	1	0	0	1
Others	1	3	0	2	2	0	0	0	0	0

performed: for taxonomic groups, species composition and environmental variables. For taxonomic groups and species composition a Bray-Curtis similarity matrix on log-transformed biotic data were used. While for environmental variables, analysis was performed on a matrix of Euclidean distances applied to standardized (x-mean/standard deviation) data (Anderson 2001). All multivariate analyses were performed using the package 'vegan' (Oksanen et al. 2020).

RESULTS

Environment

The relative position of stations to the ice-margin and ice-free areas is likely to be realistic since Figure 1c was taken from Google Earth in December 2000, one month before our sampling survey. Station 7 (MTG) is the only station covered by a glacier (Stenhouse) before 1995. Stations 1, 3 and 10 (MTG) are close to places previously occupied by glaciers in 1979: Dobrowolski, Krak and Goetel, respectively (see Figure 4, Rosa et al. 2014). (Table I, Figure 2).

Most sediment samples were classified as mud (7 of 10 stations); the other three were classified as sand (stations 4 and 5) or pebbles with sand (station 7). The percentage of pebbles varied from 0 to 41.4%, indicating a high variability of this fraction. The mean grain size (Folk & Ward 1957) of the sand-mud fraction can be classified as coarse to medium silts, while the sorting coefficient indicates poorly to extremely poorly sorted sediments (Table I).

The calcium carbonate content varied from approximately 8% to 23%, indicating a lithogenic character to the samples. The organic matter content varied from 4% to more than 10.5%, with the lowest value measured at the outermost station (5) and the highest located in front of the "Comandante Ferraz" station (6) (Table I).

Considering localities, TTG was rather different from IFA and MTG stations owing to its higher sand and calcium carbonate content, resulting in more heterogeneous sediment. IFA and MTG differ only by organic matter content, which was much higher in IFA (Table I, Figure 2).

Benthic macrofauna

A total of 5,486 individuals were found from nine phyla. Annelids were the most abundant (39.6%, of which 27.7% were polychaetes and 11.9% oligochaetes), followed by nematodes (32.9%), crustaceans (16.2%, of which 6.1% were amphipods, 4.8% cumaceans, and 4.0% tanaids) and mollusks (7.2%, of which 6.2% were bivalves and 1.0% gastropods).

The density and biomass values were quite different among sampling stations and even in stations within localities (Table I, Figure 3). Considering the division in localities, the macrofauna density (mean±sd) was higher in the IFA stations (306.2±137.5 inds/0.03m^2) than the TTG (152.2±150.7 inds/0.03m^2) and MTG (113.3±233.4 inds/0.03m^2) stations (Table II, Supplementary Material - Table SI). Regarding the total and partial biomass, the differences among localities were not significant (Table II, Table SI). The highest mean value of total biomass in TTG stations (24.1±32.7 g/0.03m^2) was due to the presence of several bivalves and ascidians in a single replicate, differing from IFA (15.5±19.8 g/0.03m^2) and MTG (3.8±7.0 g/0.03m^2). Regarding the partial biomass, the mean values were more similar among localities: IFA (1.5±1.0 g/0.03 m^2), TTG (2.2±2.7 g/0.03 m^2) and MTG (2.3±5.2 g/0.03 m^2). However, the MTG stations showed a high variability due to the occurrence of large polychaetes (*Amphitrite kerguelensis* and *Aglaophamus trissophyllus*) in one unique replicate of station 1 (Figure 3).

Main taxonomic groups showed great variation in density within each station and

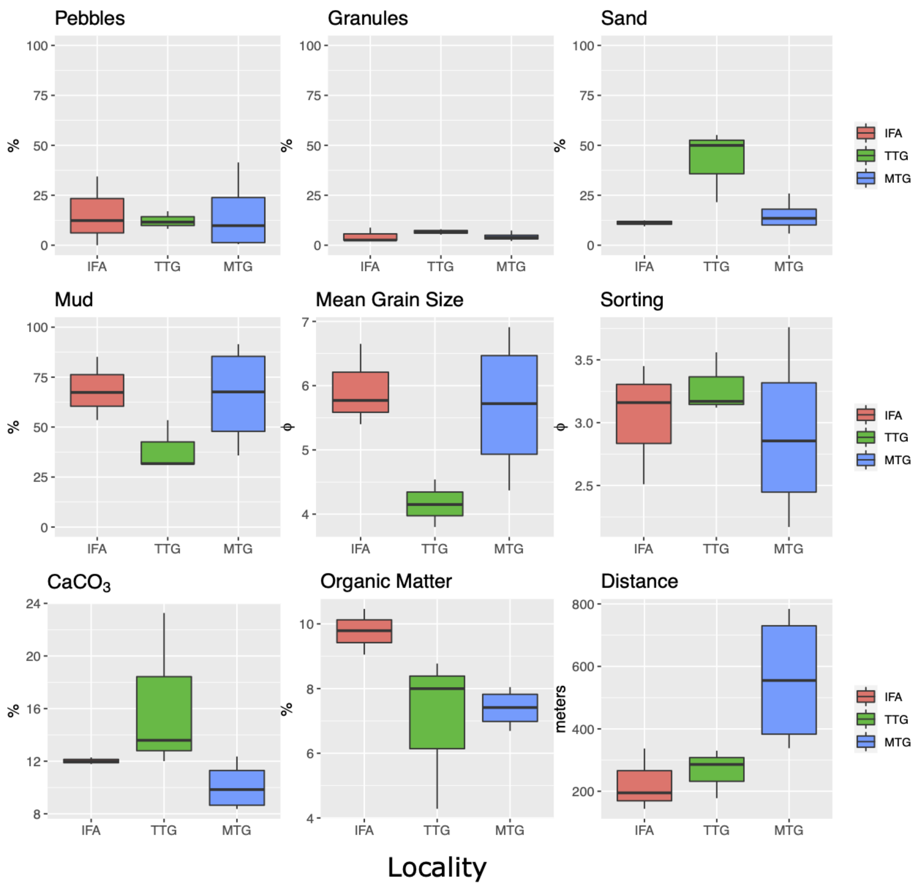

Figure 2 - Boxplot of sediment characteristics and distance from the coast. The stations were grouped into localities: IFA, TTG and MTG.

localities (Figure 4). Nematodes, oligochaetes, and polychaetes were dominant in IFA and TTG stations, representing 82.6% and 58.8% of the total macrofauna, respectively. Peracarid crustaceans (37.4%) were also important in TTG stations. The polychaetes were dominant in the MTG stations (60.1%), mainly due to station 10, followed by the peracarid crustaceans (16.9%) and nematodes (15.1%). The absence of oligochaetes and ophiuroids in the MTG stations was noticeable (Table I).

Within the polychaetes, at least 24 different morphotypes, being eleven identified at species level, were recorded, and within the bivalves, four species (Table SII). Younger individuals of these groups could not be identified. Some patches of surface deposit-feeder polychaete species were found at MTG station 10 (*Aphelochaeta* spp. and *Apistobranchus glacierae*) and IFA station 8 (*Levinsenia gracilis*).

Environmental drivers of biotic variability

The effect of environmental variables, locality and distance from glaciers on assemblage descriptors (biomass and total density) and density of the main taxonomic groups were noticeable. But there were differences in intensity (coefficients) and relation (positive or negative) among groups (Table II, Table SI). The sedimentary variables sorting and mud (a proxy of grain-size range) were selected for almost all groups, total density, and biomass (total and partial). While total density and most taxa density were associated with more homogeneous sediments with higher sand content (i.e., negatively related to sorting and mud), biomass

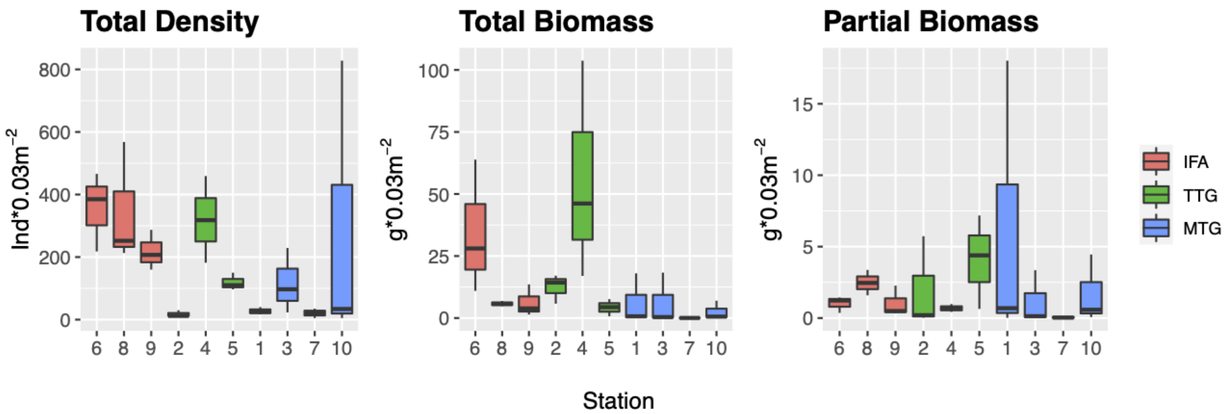

Figure 3 - Boxplot of total density and biomass, and partial biomass by stations. Colors represent the classification of stations in localities (IFA, TTG and MTG).

Table II. Coefficients of average models for community variables (for average model calculation, only those models with Δ AICc < 2 were included). Ice-free area (IFA); terrestrial terminating glacier (TTG); and marine terminating glacier (MTG).

Variable	Intercept	Locality	Distance	Depth	Mud	Pebbles	Sorting	$CaCO_3$
Total biomass	-12.95	IFA = TTG = MTG	-0.002	0.609	0.029	-0.061	2.219	-0.657
Partial biomass	-4.881	IFA = TTG = MTG	-0.001	0.231	0.055	-0.007	-0.476	0.031
Total density	17.53	IFA > TTG = MTG	0.004		-0.085	-0.069	-1.557	
Polychaetes	19.77	IFA > MTG > TTG	0.006		-0.142	-0.100	-1.558	
Amphipods	21.79	IFA > MTG > TTG		-0.148	-0.097		-2.971	
Bivalves	2.98	IFA > MTG > TTG	0.008				-0.673	
Gastropods	5.375	IFA = TTG = MTG	-0.004	0.131	-0.09		-1.989	0.099
Nematodes	-6.65	IFA > MTG > TTG	0.014	0.216			-3.621	
Cumaceans	14.25	TTG > IFA = MTG	-0.001		-0.035		-3.131	
Tanaids	-3.13	IFA = TTG = MTG		0.177		0.221		
Priapulids	15.62	IFA > MTG > TTG			-0.148	-0.177		

presented a different pattern, being related with mixed and finer sediments, dominated by larger animals. Pebble content seems to inhibit fauna, except for tanaids, while $CaCO_3$ was only selected positively for gastropods and partial biomass and negatively for total biomass. Effect of distance from glaciers/coastline and depth, despite its restricted range, were variable and complex, but the main pattern suggests more abundance and less biomass furthest from the ice-margin/coastline. Both biomass (total and partial) and gastropod and tanaid abundances did not differ among groups of stations (IFL=TTG=MTG).

Nevertheless, the abundance of all other groups and total density was higher in IFA and the lowest densities, depending on taxa, were found in TTG or MTG. It is noteworthy that this pattern was related only to locality differences since we controlled for environmental variables. This means that such observed differences are likely related to other variables not included in the model.

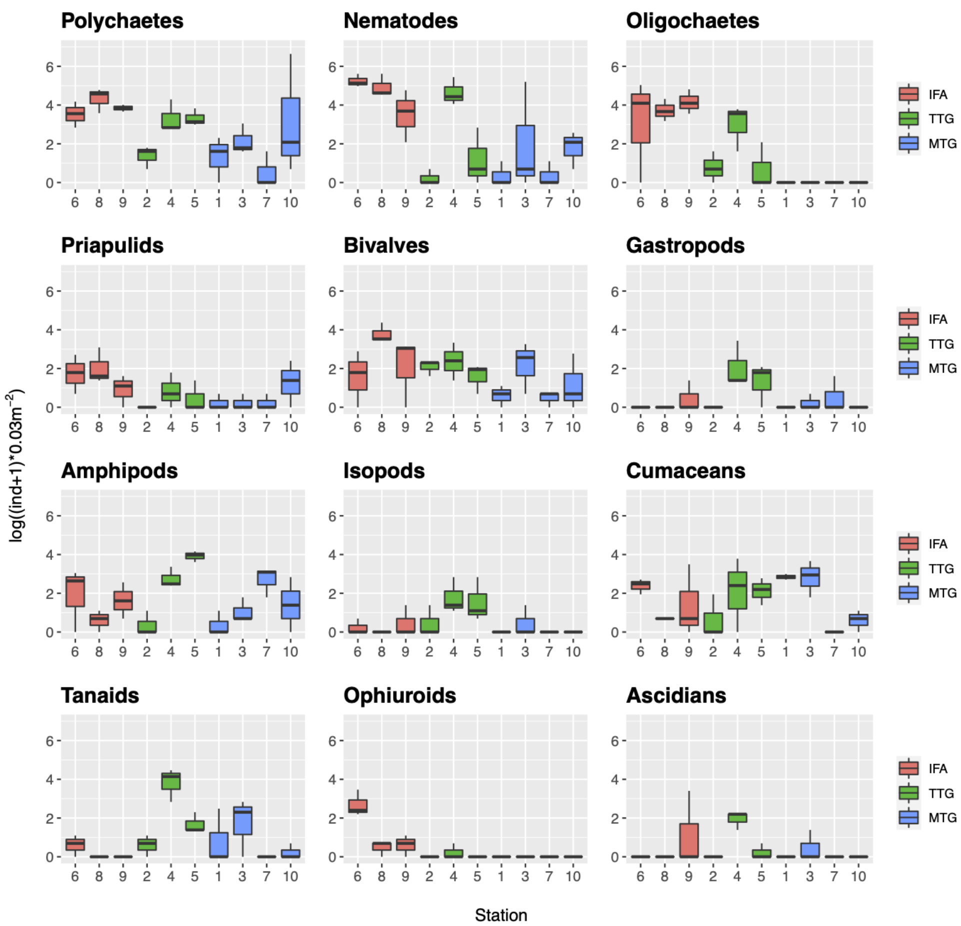

Figure 4 - Boxplot of the main taxonomic groups by the stations. Colors represent the classification of stations in localities (IFA, TTG and MTG).

Assemblage patterns

The pattern of environmental similarity among localities was rather different from those observed for taxonomic groups or species (Figure 5). The locality groups were not recovered by environmental characterization (Table III), especially due to the higher $CaCO_3$ and medium/fine sand contents in station 4 for TTG and more heterogeneous sediments (>pebbles and sorting) in station 7 from MTG. IFA stations were rather different from other localities, being homogeneous both environmentally (Figure 5a) and regarding community composition (Figure 5b-c). This result corroborated the univariate modeling analysis above, which indicated that it is still possible to distinguish localities regarding total faunistic density and several taxonomic groups after factoring out environmental variables.

Taxonomic patterns showed that MTG station 3 was more related to the TTG group (Figure 5b), characterized by the dominance of peracarids (isopods, tanaids and cumaceans), while in other MTG stations, polychaetes and amphipods were more common. IFA stations were more cohesive regarding community composition and were more diverse regarding the number of taxonomic groups.

Community patterns at higher taxonomic groups showed a lower correlation with environment than those based on species level (polychaetes and bivalves) (Table IV, Figure 5b-c). IFA was still more cohesive, and within similarities between TTG stations were higher than for groups. Nevertheless, we can still

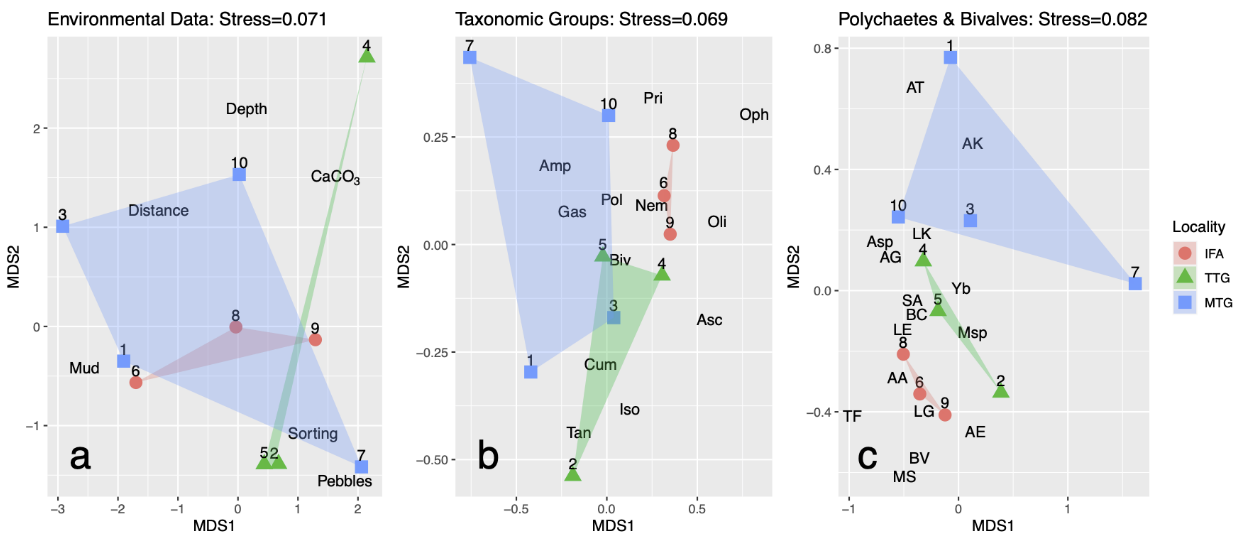

Figure 5 - Nonmetric multidimensional scaling (nMDS) plots for environmental data (a), taxonomic groups (b), and species of polychaetes and bivalves (c). Numbers represent the sampling stations. Abbreviations Figure 5b: Amp = amphipods; Asc = ascidians; Biv = bivalves; Cum = cumaceans; Gas = gastropods; Iso = isopods; Nem = nematodes; Oli = oligochaetes; Oph = ophiuroids; Pol = polychaetes; Pri = priapulids; Tan = tanaids. Figure 5c: Polychaetes: AA = *Asychis amphiglyptus*; AK = *Amphitrite kerguelensis*; AG = *Apistobranchus glacierae*; Asp = *Aphelochaeta* spp.; AT = *Aglaophamus trissophyllus*; BC = *Barrukia cristata*; BV = *Bradabyssa villosa*; LK = *Leitoscoloplos kerguelensis*; LG = *Levinsenia gracilis*; MS = *Maldane sarsi antarctica*; SA = *Sphaerodoropsis arctowskyensis*. Bivalves: AE = *Aequiyoldia eightsi*; LE = *Laternula elliptica*; Msp = *Mysella* spp.; Yb = Young bivalves.

observe heterogeneous composition among MTG stations, especially due to the lower density and small number of taxonomic groups of station 7, located within an area occupied by a glacier until 1995 (Fig. 4 in Rosa et al. 2014). Comparison among areas when compared to permuted data (PERMANOVA) indicates that it was possible to distinguish between all three localities for taxonomic groups but not for species (Table III).

DISCUSSION

Admiralty Bay has one of the most comprehensive data series of Antarctic benthic communities and its past data has been reviewed and synthesized in Sicinski et al. (2011). Around 1,300 benthic species were recorded, representing a great diversity of organisms for a single bay. Based on samples collected in 1993, Sicinski et al. (1996) addressed glacier influence as the main factor for explaining difference among the zoobenthos assemblages of shallow sublittoral waters of Herve Cove (Ezcurra Inlet) and open waters in Admiralty Bay. Further analysis, done in 2008 in the same area, indicated that bottom communities of Herve Cove (Ezcurra Inlet) are progressing towards diversity typical for open waters of Admiralty Bay (Potocka et al. 2019).

Analysis of glacier retreat studies of Martel Inlet (Rosa et al. 2014, Oliveira et al. 2019) and our results from the 2001 survey provide a good opportunity to follow up on the consequence of such shrinkages on benthic communities of Martel Inlet. The wide range of density and biomass, as well as the composition of the taxonomic groups and species, among localities (IFA, TTG and MTG) in the shallow zone of Martel Inlet show a great spatial variation in the structure of communities that can be linked to

Table III. Results of the Permutational Analysis of Variance (PERMANOVA) for taxonomic groups, species, and environmental variables comparing localities.

	Factor	df	Sum of Squares	Pseudo-*F*	R^2	P(perm)
Environment	Locality	2	0.329	1.542	0.306	0.207
	Residuals	7	0.746		0.694	
	Total	9	1.075		1.000	
Taxonomic Groups	Locality	2	0.349	2.024	0.366	**0.044**
	Residuals	7	0.603		0.633	
	Total	9	0.952		1.000	
Species	Locality	2	0.373	1.245	0.262	0.212
	Residuals	7	1.051		0.737	
	Total	9	1.424		1.000	

their position relative to the different types of ice-margins/coastlines.

Comparing our data with previous ones is a difficult task since different sampling gear and approaches were used. Furthermore, the seasonal and interannual changes in the shallow benthic communities in Admiralty Bay (Sicinski et al. 2011) must be evaluated. It is important to emphasize that our survey was done in a single day, which allows us to eliminate possible changes due to storms and other short-term temporal variability that could influence the results. Despite all the difficulties in comparing data, our density and biomass results (extrapolated to m^2) are in the range of previous surveys done at similar depths in Admiralty Bay (Jazdzewski et al. 1986, Bromberg et al. 2000, Sicinski et al. 2011). Most abundant macrofauna organisms (polychaetes, oligochaetes, nematodes, bivalves and amphipods) were the same as these previous surveys, although variation in dominant groups was observed. All polychaete and bivalve species here identified are very common and abundant in Admiralty Bay (Sicinski et al. 2011). Differences in benthic distribution are due to specific environmental characteristics (depth, type of sediment) and disturbances of each sampling site (ice impact, proximity to sewage outfall), as we have seen in Martel Inlet (Nonato et al. 2000, Skowronski & Corbisier 2002, Echeverria et al. 2005, Petti et al. 2006, Corbisier et al. 2014, Gheller & Corbisier 2022). The highest values of organic matter observed in IFA stations were also recorded by Skowronski et al. (2009) and was attributed to the sheltered condition of such environment while the stations closer to the influence of glaciers had lower values.

IFA stations, closer to the coastline, differed the most, both in sediment characteristics and macrofauna abundance and composition, when comparing with TTG and MTG stations (Figure 5). The finer sediments and higher percentage of organic matter supported the high densities and dominance of different groups of small worms (nematodes, oligochaetes, polychaetes, priapulids) and bivalves. This difference for small-sized organisms occurred despite the fact that biomass was not significantly different among localities, while density was higher in the IFA. The dominance of surface deposit-feeder polychaetes and bivalves seems to be the result of higher levels of organic content in the sediment (Paiva et al. 2015).

Two of the TTG stations (2 and 5) were remarkably similar in respect to environmental variables but the high amount of $CaCO_3$ in station 4 differed from the others. No environmental difference was noticed in relation to the organisms and species suggesting that other factors are likely to be involved in the benthic community structuration in this area. This group was characterized by sand sediments and presented the highest density of peracarid crustaceans.

The MTG stations showed high differences regarding environmental and biotic variables (Figure 5, Table IV). They likely represent diverse phases of benthic colonization. The innermost station 7 was the poorest in terms of benthic density and biomass. It is the only station that was occupied by glacier in 1979 (Rosa et al. 2014) and can represent the most recent stage of colonization among our samples, as suggested by the dominance of vagile amphipods. The absence of oligochaetes and relatively few nematodes (with exception of station 3), groups without larval stages, also reflects initial stages of colonization in these stations.

Even though environmental characteristics of Potter Cove (KGI) are different from the Martel Inlet, some similarities can be highlighted. The high number of peracarid crustaceans found in some TTG and MTG stations, as well as the presence of the motile carnivores *Aglaophamus trissophyllus* and the scavenger *Barrukia cristata* is consistent with the findings observed in the most recent ice-free area (Pasotti et al. 2015). Furthermore, the abundance of Cirratulidae in the intermediate ice-free area of Potter Cove was also observed at station 10 in the Martel Inlet. In relation to IFA stations, some similarities with the oldest ice-free area in Potter Cove were observed such as the high number of small bivalves (*Mysella* sp, *Aequiyoldia eightsi* and thyasirids), presence of maldanid polychaetes and a lesser contribution of peracarid crustaceans (Pasotti et al. 2015).

Localities were better discriminated by taxa groups than species composition. Thus, a high taxonomic level pattern is likely to be involved on adaptation to the novel environments provided by glacier retreat. Valdivia et al. (2020) when assessing the role of glacier retreat in Potter Cove, King George Island, also noticed a higher taxonomic level pattern, in their case, contrasting the dominance of producers vs. consumers in the colonization of new areas.

The dominance of different groups and the variation in density and biomass values among the localities (IFA, TTG and MTG) reveal the heterogeneity in the distribution of benthic macrofauna in the shallow zone of Martel Inlet, which can be related to the proximity to different types of glaciers and ice-free areas. The presence of glaciers seems to greatly influence the benthic community, which in these MTG areas have lower densities and greater heterogeneity in the distribution on a smaller scale. Differentiation among localities as regards biotic composition (taxa and species) seems to be independent of available environmental/sedimentary conditions, i.e., species and taxa groups do colonize novel areas provided by

Table IV. Procrustes test (PROTEST) for comparison of pairs of configurations. SS = sum of squares of differences, Cor = correlation, p = p-values indicating type-I error of correlation significance based on null models.

Configuration	SS	Cor	p
Environment *vs.* Groups	0.854	0.382	0.508
Environment *vs.* Species	0.777	0.472	0.257
Group *vs.* Species	0.642	0.598	0.078

glacier retreat even when these new areas are not environmentally similar. Successional processes associated with life-history such as reproduction and settlement are likely to be important in the colonization of new retreated areas. But we should consider that other unmeasured variables (e.g., oxygen content, salinity, hydrodynamic conditions, wave impact, ice-scour, suspended particles (Nonato et al 2000, Paiva et al 2015, Valdivia et al 2020) could also be involved in the colonization process.

Baseline knowledge of the bottom fauna associated with sedimentary environments is essential to properly evaluate possible future changes in Admiralty Bay (Sicinski et al 2012). The available climatic scenarios and its continued comprehensive studies suggest that this bay should be an ideal place to recognize further stages of colonization/succession of benthic communities (Potocka et al. 2019). Considering that our findings were obtained 21 years ago, they will be especially useful for comparing future studies of benthic assemblage responses to the influence of climate change and continuous glacier retreats in the WAP region, mainly Martel Inlet, Admiralty Bay.

Acknowledgments

Special thanks to the staff of the Brazilian Antarctic Station “Comandante Ferraz” (OPERANTAR XIX) and the researchers Rodrigo Skowronski and Alessandro Athiê for their help in collecting samples and logistical support. Special thanks goes to Beatriz Grotto for the identification of bivalves. We are also grateful for support of the Secretariat for the Marine Resources Inter-Ministerial Committee (SeCIRM). Financial support for this project was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 680051/00-7). PCP received grants from CNPq (Proc. 304321/2017-6 and 428447/2018-0) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro - FAPERJ - Proc. E-26/202.607/2019 (246952). MM de M acknowledges the CNPq for the Research Grant 300962/2018-5. Jim Hesson copyedited the manuscript (https://academicenglishsolutions.com/editing-service). Finally, we would like to thank two anonymous reviewers for their valuable comments and contributions to the improvement of this work.

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SUPPLEMENTARY MATERIAL

Table SI-SII.

How to cite

PETTI MAV, GHELLER PF, BROMBERG S, PAIVA PC, MAHIQUES MM & CORBISIER TN. 2023. Glacier retreat effects on the distribution of benthic assemblages in Martel Inlet (Admiralty Bay, Antarctica). An Acad Bras Cienc 95: e20210622. DOI 10.1590/0001-3765202320210622.

Manuscript received on April 20, 2021;
accepted for publication on May 10, 2022

MONICA A.V. PETTI[1]
https://orcid.org/0000-0002-6730-3503

PAULA F. GHELLER[1]
https://orcid.org/0000-0002-1455-1271

SANDRA BROMBERG[1]
https://orcid.org/0000-0003-2159-5683

PAULO C. PAIVA[2]
https://orcid.org/0000-0003-1061-6549

MICHEL M. MAHIQUES[3]
https://orcid.org/0000-0002-5249-5610

THAIS N. CORBISIER[1]
https://orcid.org/0000-0001-7686-0654

[1]USP, Departamento de Oceanografia Biológica, Instituto Oceanográfico, Praça do Oceanográfico, 191, 05508-120 São Paulo, SP, Brazil

[2]UFRJ, Departamento de Zoologia, Instituto de Biologia, Av. Brig. Trompowski, s/n, CCS Bloco A, 21941-590 Rio de Janeiro, RJ, Brazil

[3]USP, Departamento de Oceanografia Física, Química e Geológica, Instituto Oceanográfico, Praça do Oceanográfico, 191, 05508-120 São Paulo, SP, Brazil

Correspondence to: **Monica Angelica Varella Petti**
E-mail: mapetti@usp.br

Author contributions

MAVP, SB collected the data. PFG conducted the sample processing. PCP, MMM, MAVP conceived and designed the analysis. PCP performed the statistical analysis, prepared the tables and figures. MMM contributed with historical data and maps. MAVP, PFG, TNC drafted the initial manuscript. TNC coordinated the project. All authors actively participate in result discussions, writing, and contributing to the final version of the manuscript.