



# Abiotic Changes Driving Microphytoplankton Functional Diversity in Admiralty Bay, King George Island (Antarctica)

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Environmental gradients can provide habitat-specific scenarios for community functional diversity (FD) that determine the composition of populations on both spatial and temporal scales. The western shelf of the Antarctic Peninsula has experiencing increasing air temperatures while the climate is transitioning to a warm-humid sub-Antarctic-type of climate. As a consequence, abiotic changes are leading to alterations in the trophic web. Microphytoplankton FD was analyzed across environmental gradients of sea surface temperature, salinity, meltwater percentage and nutrient availability in Admiralty Bay, South Shetland Islands, Western Antarctic Peninsula. Samples were collected during the austral summer from 2009 to 2011 and from 2013 to 2015, at Admiralty Bay for which FD indices were calculated based on species traits. The amount of meltwater (MW) present in Admiralty Bay groups microphytoplankton into communities according to physiological and ecological tolerances, thus leading to a greater FD. When meltwater dominated the bay (>2.25% MW scenarios iii - 2013-14 and iv - 2014-15), diatoms and dinoflagellates were codominant. An increase in the dinoflagellate fraction of microplankton, notably with auxotrophic and mixotrophic nutrition mode, can be considered a trigger for changes in the structure of the Antarctic food web. Our results suggest using Admiralty Bay as a model for studies on changes in microphytoplankton community composition and FD.

**Keywords:** functional diversity, microphytoplankton, Antarctic, abiotic variation, meltwater

## INTRODUCTION

The climate of the western shelf of the Antarctic Peninsula (WAP) is undergoing a transition from a cold-dry polar-type climate to a warm-humid sub-Antarctic-type climate (Montes-Hugo et al., 2009). Air temperature in WAP has increased in relation to global variation (Abram et al., 2013), making this region one of the most rapidly warming on Earth over the last 50 years, with an increase

of  $0.56^{\circ}\text{C decade}^{-1}$  over the years analyzed (Turner et al., 2005) and a  $2^{\circ}\text{C}$  increase in annual mean temperature (Ducklow et al., 2007). This regional increase has consequences for the dynamics of shelf and sea ice (Moline et al., 2004; Rozema et al., 2017; Aracena et al., 2018).

Since climate change has also consequences for the dynamics of chemical and physical properties of seawater, it can also induce changes in the phytoplankton community structure in WAP (Kopczyńska, 2008; Piquet et al., 2011). Abiotic factors are capable of constraining species establishment or permanence and establishing communities in certain sites (Kraft et al., 2015) by acting as environmental filters. This, in turn, can be reflected throughout all the trophic levels of the regional trophic web (Moline et al., 2004; Schofield et al., 2010; Lange et al., 2014; Saba et al., 2014). Climate change in WAP (e.g., increase in temperature and environmental variables) has driven modifications in phytoplankton size (Barrera-Alba et al., 2012, 2015; Lange et al., 2014; Vanzan et al., 2015), composition, biomass and community structure (Kopczyńska, 2008; Montes-Hugo et al., 2009; Piquet et al., 2011; Lange et al., 2014; Tenório et al., 2015; Mendes et al., 2018; Russo et al., 2018).

The use of classification schemes based on functional groups to determine the ecological dynamics of phytoplankton is a growing theme in environmental sciences (Kruk et al., 2002; Litchman et al., 2010; Moser et al., 2014; Roselli and Basset, 2015; Moser et al., 2017; Roselli et al., 2017). Such schemes can help explain the distribution of species along environmental gradients, as well as phytoplankton diversity and community structure (Litchman et al., 2010; Naselli-Flores et al., 2007). Associations are based on physiological, morphological and ecological attributes of species that potentially and alternatively can dominate or co-dominate the system. A reasonable hypothesis is that all species can potentially grow, but their establishment and development are conditioned by environmental variables and community responses, such as the ability to sustain processes of net population growth loss (Kruk et al., 2002, 2010). Morphological traits of species are essential properties that influence growth rate, resource use efficiency (e.g., nutrients, light) and susceptibility to herbivory under different environmental conditions. They can also predict the effects of climatic variability over time (Padisák et al., 2003; Salmaso, 2003). This means that species-specific strategic adaptations can be selectively favored in certain environments (Reynolds, 1980), since the cell morphology of phytoplankton and their adaptive strategies are under different selection pressures due to the fact that aquatic environments differ in many physical and chemical characteristics (Weithoff et al., 2014).

Traits of phytoplankton can be used to evaluate community functional diversity (FD) using a matrix in which community traits and species are combined and compared (Petchey and Gaston, 2007). Trait-based approaches aids to community ecology can help to explain species distribution along environmental gradients and changes in diversity and community structure (Litchman et al., 2010). Morpho-functional traits include physiological, morphological and phenological characteristics that drive the ecological functions of organisms

(McGill et al., 2006; Violle et al., 2007) and can be used to evaluate FD since trait variation among phytoplankton species expresses FD (Vallina et al., 2017). FD has been identified as a key component of ecosystem functioning and sustainability (Mouillot et al., 2014). Furthermore, loss of biodiversity can be related to functional loss, since the extinction of a species or a community in a system can decrease its resilience or productivity (Mouchet et al., 2008). For all methods based on traits, a high number of diverging lineages reflects higher FD, while converging lineages represent the opposite (Martin, 2002). Morpho-functional trait diversity within communities responds to environmental parameters, which influence specific traits or trait groups, even during different periods (Verberk et al., 2013; Weithoff and Gaedke, 2016).

The present study focuses on microphytoplankton community structure and function during eight sampling campaigns of the austral summer over four different years in five regions of Admiralty Bay (AB), South Shetland Islands, Antarctica. Our goal was to perform a trait-based evaluation of changes to microphytoplankton communities by characterizing functional groups, FD and yearly variation throughout early and late summer in AB. We hypothesized that: (i) environmental gradients are the main drivers of temporal variation in microphytoplankton from year-to-year and from the early- to late-summer; and (ii) FD, characterized by functional evenness (FEve), functional richness (FRic) and functional dispersion (FDis), varies under stressful environmental conditions. The results are expected to provide insight into patterns of microphytoplankton FD in a changing polar environment.

## MATERIALS AND METHODS

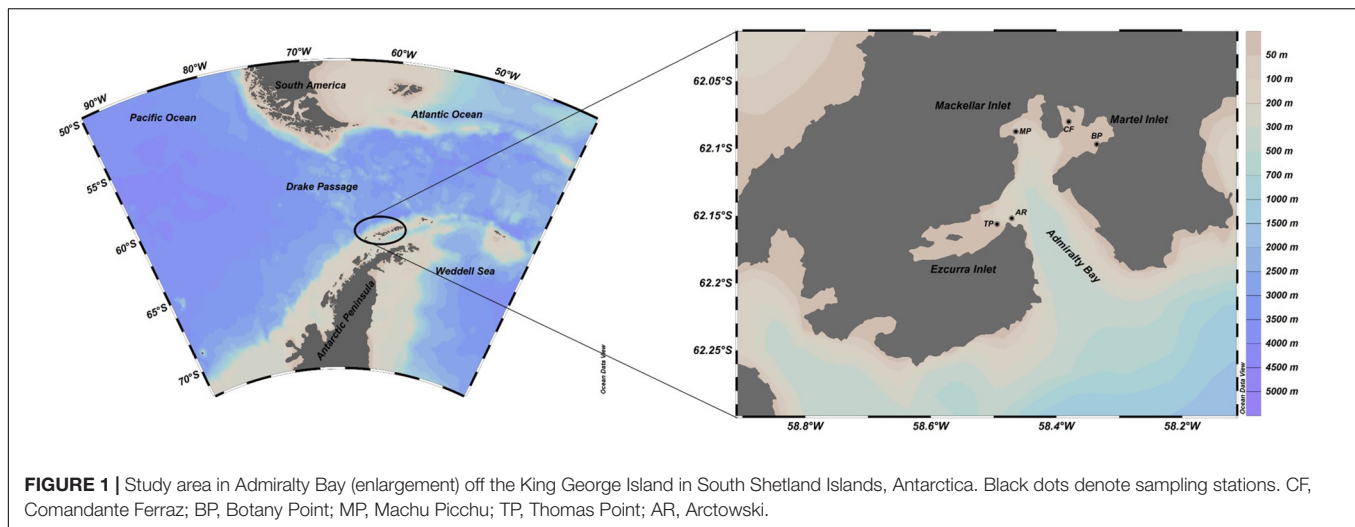
### Study Area

Covering an area of  $122\text{ km}^2$  and reaching approximately 500 m depth (Pruszek, 1980; Rakusa-Suszczewski, 1980), Admiralty Bay (AB) (**Figure 1**) is the largest bay of the South Shetland Islands. Water exchange with the adjacent Bransfield Strait is favored by wind-driven surface currents and tidal exchanges of deep-water masses (Pruszek, 1980). Winds can be an important factor driving the level of horizontal accumulation through advection in semi-enclosed bays like AB, since interactions between physical factors favors significant biomass accumulation in some cases (e.g., phytoplankton blooms in summer) (Schloss et al., 2014).

### Sampling Methods and Analysis

Admiralty Bay was surveyed during eight sampling periods: early and late summer 2009–2010, early and late summer 2010–2011, early and late summer 2013–2014 and early and late summer 2014–2015.

Sampling and data collection were conducted according to sampling period (I and II, early and late summer, respectively) at five stations: Comandante Ferraz (CF), Botany Point (BP), Machu Picchu (MP), Thomas Point (TP), and Arctowski (AR) (**Figure 1**) at three depths [surface (1 m), mid-water (15 m) and bottom (23–30 m)]. Vertical profiles of temperature and salinity were recorded with a Valeport® mini-CTD probe.



**FIGURE 1** | Study area in Admiralty Bay (enlargement) off the King George Island in South Shetland Islands, Antarctica. Black dots denote sampling stations. CF, Comandante Ferraz; BP, Botany Point; MP, Machu Picchu; TP, Thomas Point; AR, Arctowski.

Water samples were collected with 3-L Niskin bottles for laboratory analysis of phytoplankton biomass and composition and dissolved macronutrients.

To evaluate dissolved inorganic macronutrients, 0.7  $\mu\text{m}$  aliquots of filtered water were preserved at  $-20^{\circ}\text{C}$  until laboratory analysis according to the methods described at Aminot and Chaussepied (1983) and Grasshoff et al. (1983).

To evaluate possible impacts of sea ice melting on phytoplankton community structure, meltwater percentage (% MW) was calculated from the difference between salinity values at the surface ( $S_{surf}$ ) and the bottom ( $S_{btm}$ ), assuming 6 to be the average salinity value of marine ice (Ackley et al., 1979) (See Equation 1). To classify the environment according to %MW (Mendes et al., 2018), two scenarios were proposed: (i) stations under influence of melting sea ice ( $>2.25\%$  MW); and (ii) stations not under the influence of melting sea ice ( $<2.25\%$  MW).

$$\%MW = \left(1 - \frac{S_{surf} - 6}{S_{btm} - 6}\right) \times 100 \quad (1)$$

## Laboratory Methods for Phytoplankton

Chlorophyll *a* was determined by the spectrofluorometric method (Varian Cary Eclipse®) described in Neveux and Lantoiné (1993) and modified by Tenório et al. (2005).

Phytoplankton classification and counts were performed on samples fixed in 2% formaldehyde solution following the Utermöhl method (Lund et al., 1958; Utermöhl, 1958; Rott, 1981). Phytoplankton were analyzed under an inverted microscope (Nikon® Eclipse TS 100) at 200 $\times$  magnification. Phytoplankton taxa were classified according to keys edited by Hustedt (1930), Cupp (1943), Medlin and Priddle (1990), Round et al. (1990), Hasle and Syvertsen (1996), Tenenbaum et al. (2004), and Scott and Marchant (2005).

Functional traits of the most frequent and abundant taxa (criteria described in Lobo and Leighton, 1986) were selected considering the proposal of Litchman et al. (2010), microscopic observations and the literature. Functional traits used to evaluate

the functionality of the phytoplankton community included morphological, physiological, behavioral and life-cycle traits. Morphological traits included greatest axial linear dimension (GALD), which is considered a master trait, and was obtained by measuring between 20 and 40 cells of each taxa with relative frequency above 10%. According to Litchman et al. (2010), classification of GALD as  $<35 \mu\text{m}$  and  $>35 \mu\text{m}$  reflects predation pressure. Other morphological traits (i) determined from microscopic analyses were surface to volume ratio ( $s/v$ ), presence of large vacuoles, presence of silica structure (use of silica in the constitution of frustules and other structures), coloniality or chain formation, and presence of raphe. Physiological traits (ii) included the capacity for forming harmful algal bloom (HABs) (Moestrup et al., 2009) and nutrition mode – autotrophy, heterotrophy or mixotrophy were evaluated through the literature. The behavioral trait (iii) considered was mobility, which was determined by the presence of flagella during microscopic observation and *a priori* knowledge, while the life-cycle trait (iv) considered was resting stages, was also determined through the literature. For plastic traits, such as colony and chain formation, HAB formation capacity, mixotrophy and resting stages, trait values refer to a potential function, and not whether it was expressed in any particular community.

## Data Analysis

### Testing Environmental Patterns

Biotic and abiotic data were submitted to analysis of variation (ANOVA) and Tukey's pairwise test (Software Paleontological Statistical 3 – PAST, Hammer et al., 2001). Comparisons were made among each survey year, early and late summer and sampling stations.

### Calculating Functional Diversity Indices

Functional diversity indices aim to describe how much of the multifunctional space is filled and how the abundance of a community is distributed within this functional space. These indices have positive values, with higher values representing greater FD of the component they scale (Villéger et al., 2008).

Functional richness (FRic) represents a multidimensional measure of amount the of community-filled functional space and corresponds to the volume of a convex hull in the functional space (Cornwell et al., 2006; Villéger et al., 2008). There is no limit as it quantifies an absolute filled volume (Villéger et al., 2008). Functional equitativity (FEve) describes the evenness of the distribution of abundance in the space of functional traits, that is, it corresponds to a measure of regularity the space between species along the gradient of functional traits and regularity in the weighted distribution of their abundance. This measure decreases when abundance is less evenly distributed among species or when functional distances between species are not consistent. It is restricted to values between 0 and 1 (Villéger et al., 2008). FDis is the weighted mean, in the multidimensional space of traits, of the distance that each species is to the centroid of all species within a community. This index considers both traits and abundance of each species, where weights correspond to the relative abundance of each species, and there is no upper limit to its value (Laliberté and Legendre, 2010).

Functional groups were tested by applying a cluster analysis (Euclidian Distance combined with Unweighted Pair-Groups Method - UPGMA), to a data matrix (binary data: absence 0 and presence 1) (**Supplementary Table 1**) of selected traits described in Section “Microphytoplankton Response to Environmental Gradients.” Difference among groups were tested by applying ANOSIM to the resulting distance matrix, with *p*-values lower than 0.05 indicating significant differences. All these procedures were performed using the Vegan package of R software (version 3.5.1 – R Core Team, 2018) (Oksanen et al., 2017).

The functional traits matrix (binary data) and species abundances were used to evaluate community functional diversity (FD) in the resulting groups, using multidimensional indices based on Euclidian distance and non-parametric multidimensional scaling (NMDS) of traits to measure different aspects of diversity, FRic, FEve, and FDis. These metrics were calculated using dbFD function of FD package (Laliberté and Legendre, 2010) (R software, version 3.5.1 – R Core Team, 2018).

### Relationships Between Species and Environment

To determine which environmental variables are correlated with phytoplankton assemblages, a Canonical Correspondence Analysis (CCA) was applied to log-transformed matrices of species abundance and environmental variables (temperature, salinity, nitrogen, phosphate, N:P ratio, silicate and chlorophyll *a*). Normality was tested by the Shapiro–Wilk test (Software Paleontological Statistical 3 – PAST, Hammer et al., 2001), while the significance of canonical axes was tested by a Monte Carlo permutation test.

### Relationships Between Functional Indices and Environment

In order to correlate functional and environmental variables and assess which variables drive variation in FD, a Pearson Correlation Test was applied to a matrix containing the resulting indices and the environmental variables (temperature, salinity, meltwater, nitrogen, phosphate, N:P ratio, silicate and

chlorophyll *a*) (Software Paleontological Statistical 3 – PAST, Hammer et al., 2001). Correlations with *p* values lower than 0.05 were considered significant.

### Identification of Functional Groups

Functional groups were identified by considering species that grouped together in the following steps: cluster analysis, NMDS and CCA, as well as by analysis of functional indices.

## RESULTS

### Environmental Patterns

#### Spatial Variation

The abiotic variables and chlorophyll *a* (**Table 1**) differed among sampling stations, although not significantly (ANOVA – Tukey Test *p* > 0.05), indicating that the spatial distribution of abiotic variables does not influence the response of the microphytoplankton community with regard to biomass (chlorophyll *a*).

The sampling stations influenced by meltwater (% MW; **Figure 2**) were BP during early summer of 2010–2011 (2.66%), all stations during early summer in 2013–2014 (maximum of 20.73% for BP), and CF, MP and TP during late summer 2014–2015 (maximum of 10.08% for TP).

#### Temporal Variation

Temperature varied significantly among sampling periods (ANOVA – Tukey Test *p* < 0.05), with the highest averages being for 2010–2011 (1.66°C) and 2014–2015 (1.24°C), both at the end of summer, and the minimum averages being for 2009–2010 (−0.18°C) and 2014–2015 (−0.61°C) in early summer (**Table 1**).

The highest salinity was observed during early summer 2013–2014 (mean 34.61), while the lowest occurred during late summer, 2014–2015 (mean 33.73). However, salinity was the only variable that did not differ significantly (ANOVA – Tukey Test *p* > 0.05) among sampling periods.

Nitrogen compounds, phosphate and silicate varied widely (**Table 1**). The concentrations of dissolved nutrients were sufficient to support phytoplankton biomass for all the surveys, with the end of summer 2010–2011 having sufficient nitrate and silicate to support an abundance of large diatoms. The maximum concentrations of nitrogen compounds occurred during both early and late summer 2014–2015 (29.01 and 25.11  $\mu\text{mol.L}^{-1}$ , respectively; ANOVA – Tukey Test *p* < 0.05). High phosphate concentrations occurred throughout 2009–2010 (2.98  $\mu\text{mol.L}^{-1}$ ) and 2010–2011 (2.15  $\mu\text{mol.L}^{-1}$ ), the first years of sampling, both in late summer (ANOVA – Tukey Test *p* < 0.05). Regarding N:P ratio, high ratios (ANOVA – Tukey Test *p* < 0.05) were observed during early summer 2010–2011 (maximum of 23.61) and late summer 2013–2014 (maximum of 22.48) (**Table 1**). The highest concentrations for silicate (ANOVA – Tukey Test *p* < 0.05) occurred in early summer in 2010–2011 (76.65  $\mu\text{mol.L}^{-1}$ ) and late summer 2014–2015 (69.86  $\mu\text{mol.L}^{-1}$ ).

Chlorophyll *a* concentration varied between 0.28 and 5.69  $\text{mg.m}^{-3}$  (ANOVA – Tukey Test *p* < 0.05), with higher



**TABLE 1** | Chemical and biological characteristics from Admiralty Bay (Mean, minimum and maximum values).

	2009–2010			2010–2011			2013–2014			2014–2015		
	ES	LS	ES	ES	LS	ES	ES	LS	ES	LS	ES	LS
Temperature (°C)	Mean	0.86	0.29	1.66	–0.05	0.65	–0.61	1.24	–0.70 to –0.48	0.85 to 1.41	–0.70 to –0.48	0.85 to 1.41
	Minimum – Maximum	–0.28 to –0.13	0.80 to 1.04	0.18 to 0.42	1.60 to 1.70	–0.10 to 0.02	0.47 to 0.78	–0.70 to –0.48	0.47 to 0.78	–0.70 to –0.48	0.47 to 0.78	–0.70 to –0.48
Salinity (ppt)	Mean	34.22	34.13	34.18	34.10	34.61	34.28	33.73	34.61	34.19	34.28	33.73
	Minimum – Maximum	34.16 to 34.31	34.03 to 34.23	34.11 to 34.25	33.88 to 34.20	31.02 to 37.97	34.18 to 34.33	33.09 to 34.02	31.02 to 37.97	34.03 to 34.26	34.18 to 34.33	33.09 to 34.02
Nitrogen – NO <sub>2</sub> + NO <sub>3</sub> (μmol.L <sup>-1</sup> )	Mean	15.39	16.67	20.43	13.82	15.52	26.89	20.90	15.52	18.78	26.89	20.90
	Minimum – Maximum	14.52 to 15.88	15.07 to 19.35	18.31 to 22.29	11.62 to 16.35	13.79 to 17.50	24.87 to 29.01	12.49 to 25.11	13.79 to 17.50	13.53 to 22.48	24.87 to 29.01	12.49 to 25.11
Phosphate – PO <sub>4</sub> (μmol.L <sup>-1</sup> )	Mean	1.88	1.65	1.24	1.92	1.36	1.86	1.57	1.36	1.45	1.86	1.57
	Minimum – Maximum	1.54 to 2.05	1.07 to 2.98	1.02 to 1.54	1.68 to 2.15	1.14 to 1.60	1.64 to 2.03	1.41 to 1.74	1.14 to 1.60	1.11 to 1.79	1.64 to 2.03	1.41 to 1.74
N:P Ratio	Mean	8.48	11.71	17.67	7.55	12.20	14.54	13.52	12.20	18.78	14.54	13.52
	Minimum – Maximum	7.47 to 10.42	6.55 to 15.86	14.43 to 23.61	6.75 to 8.60	9.69 to 17.12	12.23 to 17.03	7.18 to 15.93	9.69 to 17.12	13.53 to 22.48	12.23 to 17.03	7.18 to 15.93
Silicate – SiO <sub>4</sub> (μmol.L <sup>-1</sup> )	Mean	41.59	41.32	69.35	40.18	48.07	63.13	63.11	48.07	57.45	63.13	63.11
	Minimum – Maximum	40.53 to 42.13	39.83 to 42.03	60.63 to 76.65	35.92 to 44.66	37.68 to 53.69	60.26 to 66.17	56.16 to 69.86	37.68 to 53.69	50.78 to 62.74	60.26 to 66.17	56.16 to 69.86
Chlorophyll <i>a</i> (mg.m <sup>-3</sup> )	Mean	0.38	0.76	0.54	4.07	1.52	0.35	0.67	1.52	1.32	0.35	0.67
	Minimum – Maximum	0.36 to 0.41	0.28 to 1.40	0.45 to 0.70	2.32 to 5.69	0.68 to 1.92	0.30 to 0.39	0.42 to 0.97	0.68 to 1.92	1.15 to 1.48	0.30 to 0.39	0.42 to 0.97

ES, Early Summer; LS, Late Summer; Min, Minimum value recorded; Max, Maximum value recorded.

concentrations being found in late summer 2010–2011 (mean 4.07 mg.m<sup>-3</sup>), followed by early summer 2013–2014 (mean of 1.52 mg.m<sup>-3</sup>) with a maximum of 1.92 mg.m<sup>-3</sup> (Table 1).

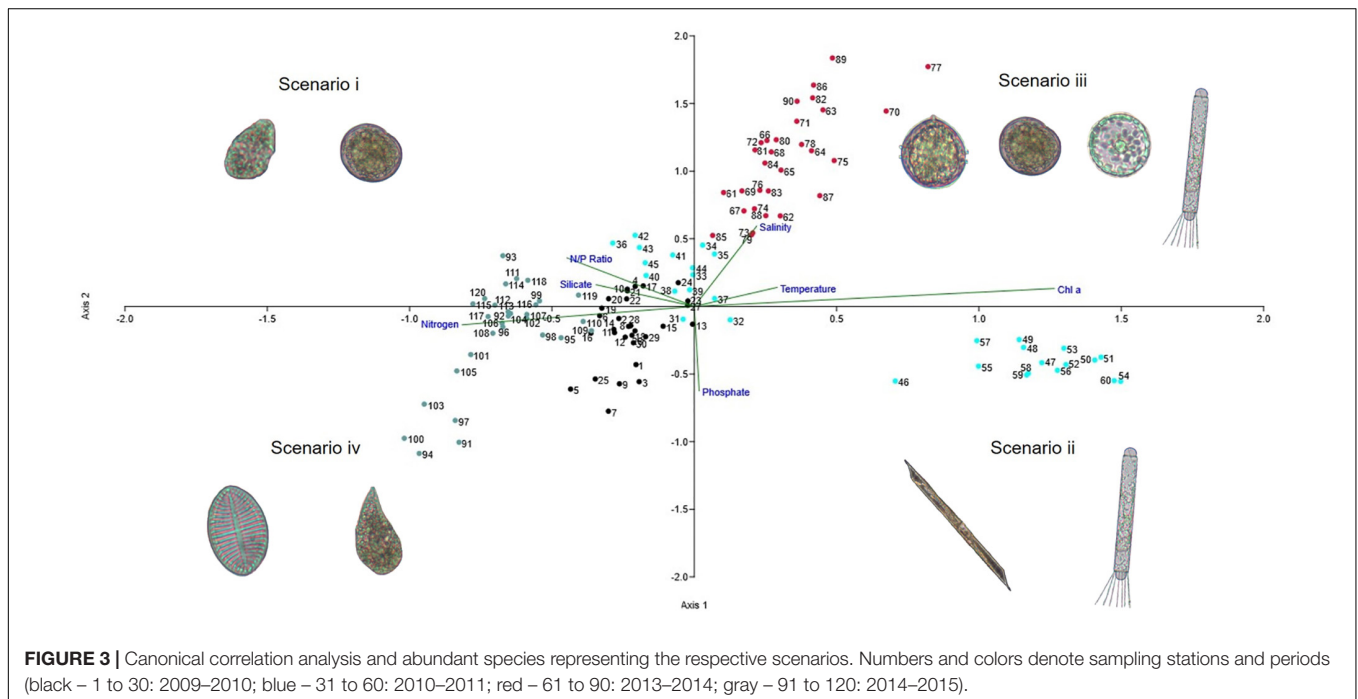
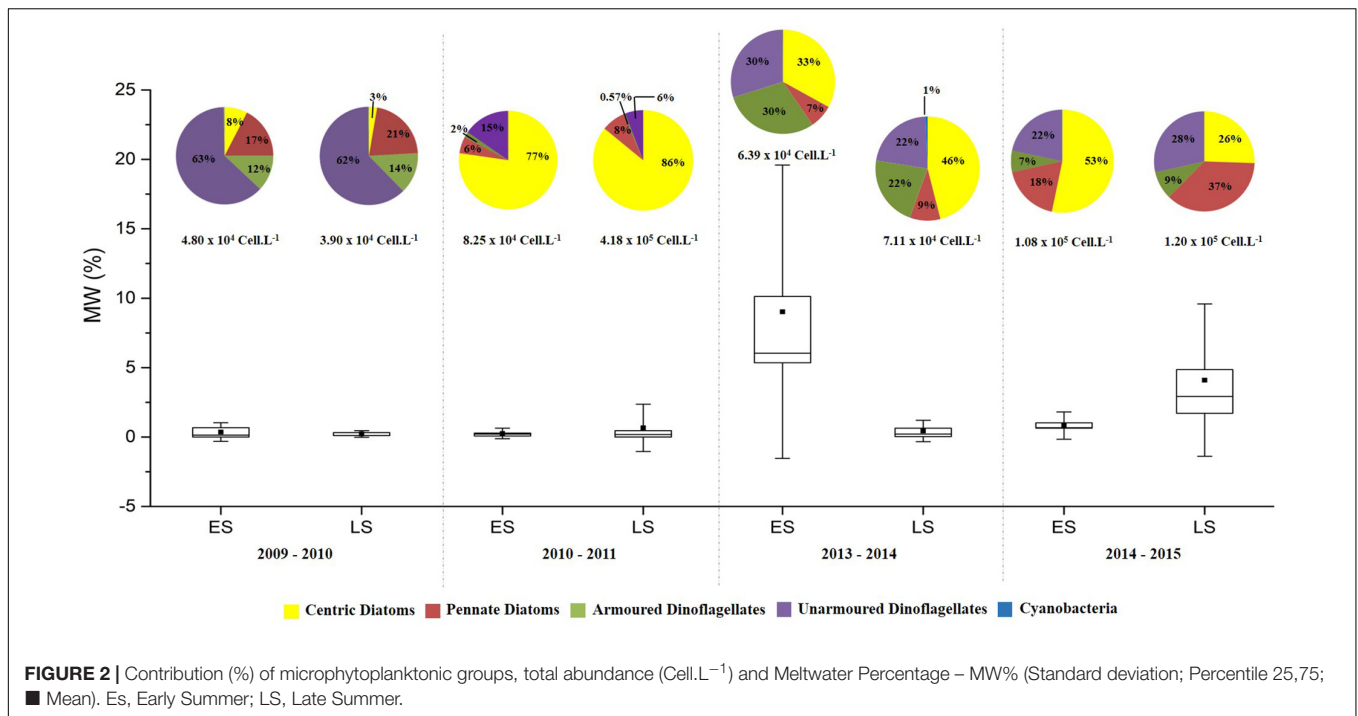
The % MW (Figure 2 and Supplementary Table 2) indicated that the last 2 years of sampling (early summer 2013–2014 and late summer 2014–2015) were influenced by melting sea ice ( $p < 0.05$ ). All stations had MW values  $> 2.25\%$  in early summer 2013–2014 with a maximum of 20.73% in BP, along with low salinity (31.02) for the same station. The average temperature during this period was  $-0.05^{\circ}\text{C}$ . During late summer 2014–2015, three points (CF, MP, and TP) had MW values  $> 2.25\%$ , with a maximum of 10.08% in TP. During this period melting was associated with the lowest salinity values observed (varying from 33.09 to 34.02) and an average temperature of  $1.24^{\circ}\text{C}$ . It is worth mentioning that during late summer 2010–2011, BP had a MW value of 2.25%; however, because it was only a punctual record, the sampling was not classified as under the influence of melting sea ice.

## Microphytoplankton Response to Environmental Gradients

The CCA highlighted the response of the microphytoplankton community to %MW and the environmental variables (Figure 3). Interannual variation was represented by four scenarios with different communities: (i) flagellates during 2009–10 and early summer 2010–2011; (ii) large diatoms during late summer 2010–2011; and two scenarios influenced by meltwater ( $> 2.25\%$  MW), both with co-dominance between dinoflagellates and diatoms: (iii) centric diatoms and armored dinoflagellates during 2013–2014; and (iv) pennate diatoms and unarmored dinoflagellates during 2014–2015.

Axis 1 of the CCA explained 45% of environmental variation, with the availability of nitrogen compounds, N:P ratio and silicate being associated with scenario i. As well as with greater species richness with a predominance of dinoflagellates ( $5.80 \times 10^4$  cell.L<sup>-1</sup>; 76% of total cell numbers in 2009–2010), particularly *Prorocentrum* spp. (*P. cf. compressum*), *Protoperdinium* spp. (*P. cf. defectum*, *P. cf. nanum*), *Amphidinium* spp. (*A. hadai*), *Gymnodinium* spp. (*G. soyai*), and *Gyrodinium* spp. (*G. glaciale*) and diatoms ( $6.83 \times 10^4$  cell.L<sup>-1</sup>; 83% of total cell numbers in early summer 2010–2011), such as *Corethron pennatum* and *Thalassiosira* spp. Scenario ii, on the other hand, was characterized by decreases in the concentration of silicate and nitrogen concentrations and by the predominance of diatoms ( $3.59 \times 10^5$  cell.L<sup>-1</sup>; 86% of total cell numbers), with large organisms such as *Corethron pennatum*, *Rhizosolenia* spp. (*R. hebetata*, *R. setigera*) and *Odontella* spp. (*O. litigious*, *O. weissflogi*) (Figure 2 and Supplementary Table 3).

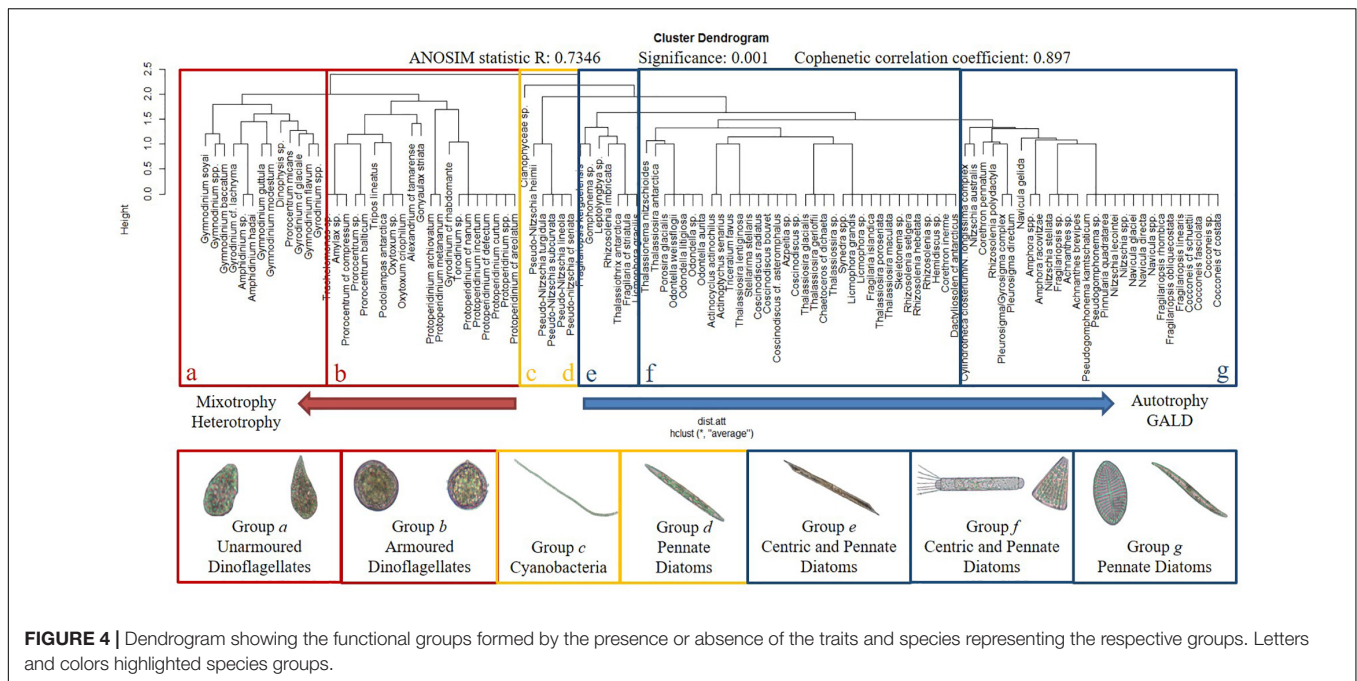
Axis 2 explained 22% of environmental variation, with salinity, a variable related to melting sea ice, being associated with scenarios iii and iv, with differences in each context. In scenario iii, there was co-dominance between dinoflagellates ( $6.92 \times 10^4$  cell.L<sup>-1</sup>; 52%), represented mainly by species of the genus *Protoperdinium* spp. (*P. curtum* and *P. cf. areolatum*) and *Prorocentrum* spp., and centric diatoms ( $6.53 \times 10^4$  cell.L<sup>-1</sup>; 48%), mostly *Corethron pennatum* and *Thalassiosira*



*cf. antarctica*. Scenario iv was characterized by the predominance of diatoms ( $1.52 \times 10^5 \text{ cell.L}^{-1}$  – 67%), with emphasis on pennate and raphid tycho planktonic diatoms, such as *Cocconeis* spp. (*C. costata* and *C. fasciolata*), and a great contribution of unarmored dinoflagellates ( $5.74 \times 10^4 \text{ cell.L}^{-1}$ ; 25%), especially *Gyrodinium* spp. (*G. glaciale* and *G. lachryma*) and *Gymnodinium* spp. (*G. soyai* and *G. guttula*) (Figure 2 and Supplementary Table 3).

## Functional Groups and Functional Diversity

Cluster analysis (Figure 4) revealed seven groups formed by organisms with distinct functional traits (ANOSIM:  $0.734 - p < 0.05$ ; cophenetic correlation coefficient: 0.897). Groups *a* and *b* were mainly comprised of dinoflagellates: group *a* mostly by unarmored dinoflagellates (*Gyrodinium* sp. and *Gymnodinium* sp.) and group *b* by armored dinoflagellates



**FIGURE 4 |** Dendrogram showing the functional groups formed by the presence or absence of the traits and species representing the respective groups. Letters and colors highlighted species groups.

(*Protoperdinium* spp. and *Prorocentrum* spp.). Group *c* comprised filament-forming Cyanophyceae; group *d* raphid and chain-forming pennate diatoms (e.g., *Pseudo-nitzschia* spp.); groups *e* and *f* centric and pennate diatoms; and group *g* essentially large-sized pennate diatoms (*Pseudogomphonema* spp., *Fragilaria* spp. and *Nitzschia* spp.).

Non-parametric multidimensional scaling (NMDS) (Figure 5) revealed relationships between species groups and three sets of functional traits. Groups *a* and *b*, both comprising dinoflagellates, were associated with set one: trophic traits (mixotrophy and heterotrophy), resting stage, vacuole presence, flagella presence, and potential for forming harmful algal bloom. Groups *c* and *d* were associated with set two: coloniality/chain formation, the presence of raphe and high  $s/v$  ratio. Groups *e*, *f* and *g* were associated with set three: GALD ( $> 35 \mu\text{m}$ ), autotrophy and the presence of silica.

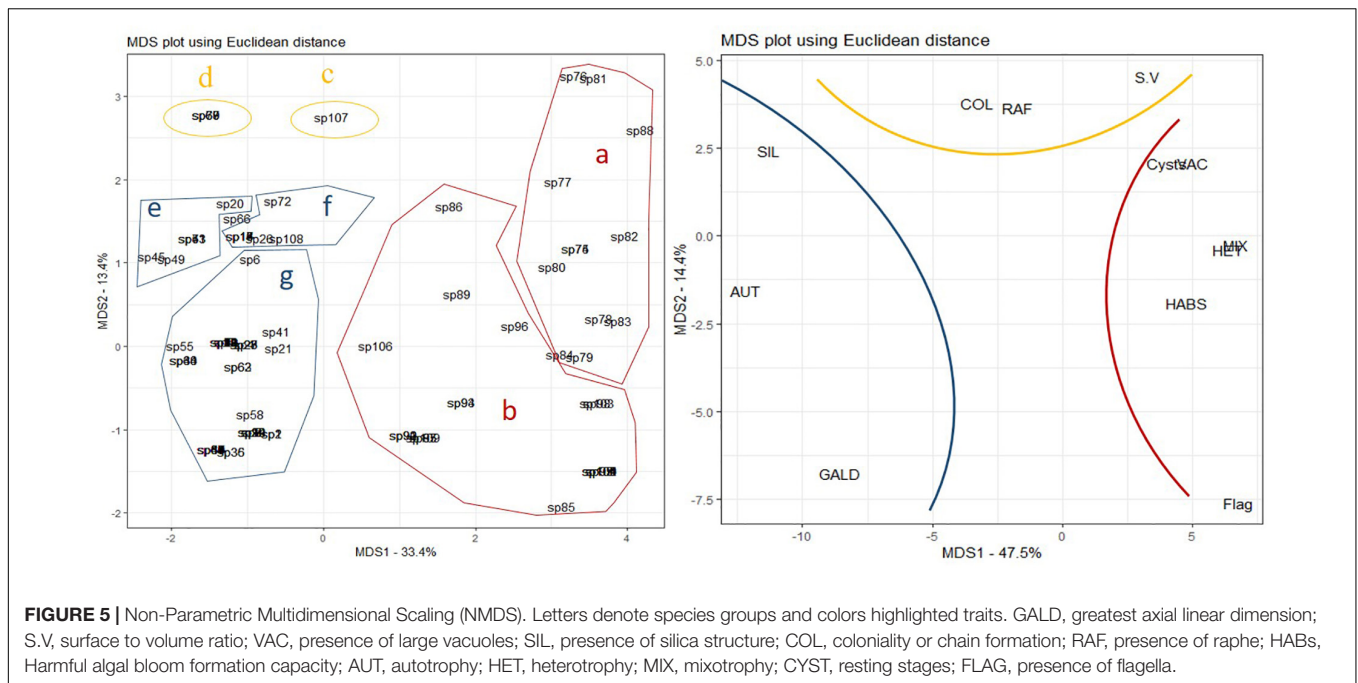
These groups related to the three sets of traits (Figure 5) were also observed in the CCA analysis as correlated with environmental variables/scenarios (Figure 3): scenario i – groups *a* and *b* correlated with N:P and silica; group *c* and *d* correlated with phosphate; scenario iii – groups *e* and some species of groups *f* and *b* correlated with temperature and salinity; scenario ii groups *g* and some species of group *f* correlated with chlorophyll *a*; scenario iv – some species of group *g* and some species of group *a*. As revealed above, variation in salinity and the amount of meltwater favor the codominance of dinoflagellate and diatom species.

Species of groups *a* and *b*, *c* and *d* and *e*, *f* and *g* grouped together (95% of the species) in the Cluster, NMDS and CCA analyses, comprising different sets of traits, thus they were considered functional groups. A Pearson Correlation Test was performed to correlate environmental scenarios/functional groups and with FD indices (Supplementary Table 4).

Higher FEve was observed in scenarios iii and iv (Table 2). FDis ranged from 0.10 (scenario ii) to 0.28 (scenarios i, iii, and iv) while FRic was higher in scenario i. According to the values of these indices, scenarios iii and iv had high FD.

Pearson linear correlation revealed FDis to be negatively correlated with temperature ( $-0.999$ ,  $p < 0.05$ ) and chlorophyll *a* ( $-0.968$ ,  $p < 0.05$ ) and positively correlated with N/P ratio (0.940,  $p < 0.05$ ) (Table 4 from Supplementary Material). According to the CCA analysis, scenario ii (without MW influence) shows the correlation between vectors for temperature and chlorophyll *a* on axis 1 and the highest relative abundance of diatom species (groups *d* to *g*); precisely in this scenario there is a reduction in FDis values (Table 2 - functional indices). The highest functional richness index (FRic) was for scenario i associated with the greater availability of nitrogen compounds and silicate, as revealed by the CCA (Figure 3). In fact, the NMDS revealed a lower number of traits associated with autotrophy (e.g., presence of silica and GALD  $> 35 \mu\text{m}$ ), with the high relative abundance of species presenting these traits decreasing the distance to the centroid, thus decreasing values for FDis (Figure 5 - MDS).

Increases in nitrogen and N:P ratio favored dinoflagellates, as represented in scenario i in the negative portion of the CCA (Figure 3). It is noteworthy that although the trait mixotrophy had a higher weight for relative abundance, there was greater distribution and abundance weight for the other traits (presence of vacuoles, cysts, presence of flagella, HABs) in relation to the centroid and, thus, greater FDis. FEve was positively correlated (Pearson correlation) with MW (0.957,  $p < 0.05$ ) and negatively ( $-0.905$ ,  $p < 0.05$ ) correlated with FRic. According to the CCA analysis, scenario iii (with the influence of MW) shows greater FEve, reflecting codominance of diatom and dinoflagellate species and, therefore, in the trophic traits of autotrophy and myxotrophy, respectively. These trophic functional traits had the



highest scores on axis 1 of the NMDS. The relative abundance of species with autotrophy and mixotrophy was functionally more equitative in the scenarios under the influence of MW.

Functional richness was not significantly correlated with any environmental variable. Autotrophic and mixotrophic organisms occurred in all scenarios, and the area in the multidimensional space of traits was similar (Figure 5). However, there was a negative correlation between trait richness and FEve ( $-0.905$ ,  $p < 0.05$ ), due to the higher relative abundance associated with autotrophy or mixotrophy, as in scenarios i and ii (without the influence of MW).

## DISCUSSION

### Environmental Patterns in Admiralty Bay in the Context of the Western Antarctic Peninsula

Hydrographic conditions in southern Ocean coastal systems are influenced by seasonal reductions in sea ice cover, the melting of glaciers and the breaking of ice shelves (Aracena et al., 2018). These coastal ecosystems are extremely sensitive to climatic variation due to the seasonality of ice (Ducklow et al., 2007);

fluctuations in meltwater can affect biological production due to increased flow of freshwater in surface waters (Aracena et al., 2018; Kim et al., 2018). These conditions have become more prevalent due to the warming tendency in the region (Dierssen et al., 2002; Moline et al., 2004; Rozema et al., 2017). Over the last 30 years, the warming of water in the northern region of WAP, including the Bransfield Strait, has resulted in increased cloud cover and wind speed and reduced extent of ice cover (Montes-Hugo et al., 2009).

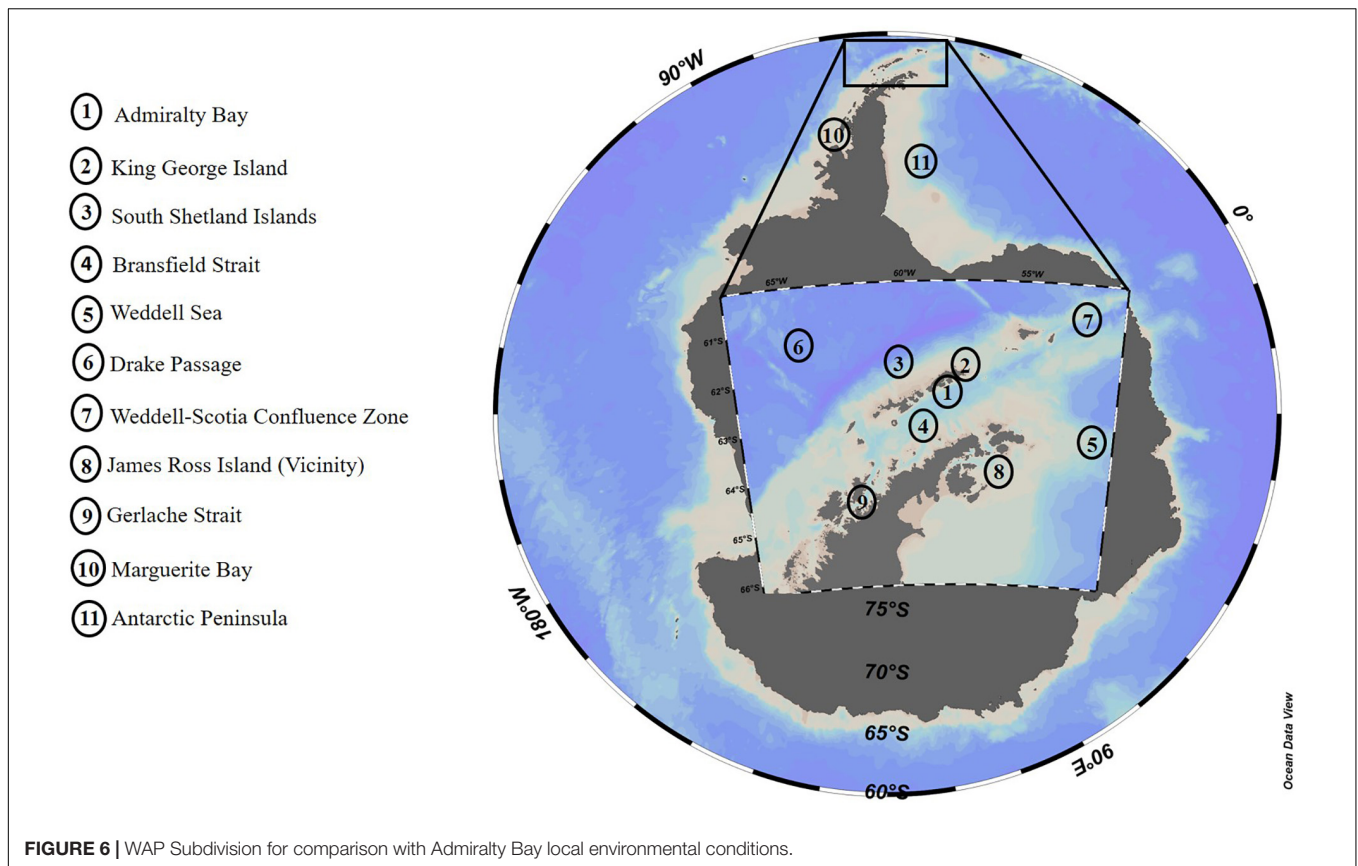
Seawater temperature has increased around King George Island (Clarke et al., 2005; Schloss et al., 2014), which supports the hypothesis of regional heating and potential threat to the local biota (Gutt et al., 2011). Considering the variation of environmental variables (e.g., temperature, salinity, ice cover) among the different areas of the Antarctic Peninsula, we subdivided WAP into 11 regions for comparison with the local environmental conditions of Admiralty Bay (Figure 6): Sector 1 – Admiralty Bay; Sector 2 – King George Island; Sector 3 – South Shetland Islands; Sector 4 – Bransfield Strait; Sector 5 – Weddell Sea; Sector 6 – Drake Passage; Sector 7 – Weddel-Scotia Confluence Zone; Sector 8 – Near James Ross Island; Sector 9 – Strait of Gerlache; Sector 10 – Marguerite Bay; and Sector 11 – Antarctic Peninsula.

Average temperature values above  $1^{\circ}\text{C}$  were observed in all WAP sectors (Table 3), especially sector 2, King George Island (Figure 6), with a minimum of  $-2.0^{\circ}\text{C}$  and a maximum of  $3.0^{\circ}\text{C}$  (Lange et al., 2018), as observed in the present study (Table 1). Interannual differences were also observed, with higher temperatures at the end of the summer. Salinity exhibited little variation, with values higher than 34.0, except at the end of summer 2014–2015 when average values were lower, as observed in the literature both for AB (sector 1) and King George Island (sector 2) (Lange et al., 2018). Lange et al. (2014) observed higher

**TABLE 2 |** Functional diversity indices.

Scenarios	Functional diversity			
	i	ii	iii	iv
Functional Richness	0.81	0.49	0.38	0.55
Functional Evenness	0.31	0.36	0.45	0.38
Functional Dispersion	0.28	0.10	0.28	0.28





salinities during the beginning than at the end of the summer, while Tenenbaum et al. (2010) reported reduced salinity for neritic regions, possibly due to the presence of glaciers in the region. In this context, Mendes et al. (2018) found lower values for salinity (mean 33.68) in areas near ice-covered regions and higher values (mean 34.14) in regions with little or no influence of ice cover seasonality for sector 7 (Weddel-Scotia Confluence Zone), thus correlating low salinity with water column stability. Additionally, Wasilowska et al. (2015) associated low salinities (<34) with increased water column stability and a shallow (<2 m) mixture layer in sector 1. Similarly, Mendes et al. (2017) related high values of salinity with reduced water column stability and, consequently, the presence of a deeper mixing layer in sector 9 (Gerlache Strait).

Sampling under greater influence of meltwater occurred in early summer 2013–2014 (scenario iii) and late summer 2014–2015 (scenario iv), as also observed by Mendes et al. (2018) in Weddell-Scotia Confluence Zone in 2013 (sector 7). Despite the high water temperatures recorded in 2010–2011 (average 1.66°C during late summer) only one station, Botany Point, exhibited an influence from meltwater. Vanzan et al. (2015) suggested an increase in the effect of glacial melt in sector 1, near Botany Point, due to high water temperatures and low salinity values in surface waters during summer.

Another factor controlling the phytoplankton community is the availability of dissolved inorganic nutrients, which seems not to be limiting phytoplankton growth in WAP (this study,

Lange et al., 2014; Schloss et al., 2014; Kim et al., 2016; Arrigo et al., 2017). In AB, temporal variation in inorganic macronutrients is correlated with biogeochemical and physical processes, such as terrigenous contribution, luminous incidence, marine and glacial melting water, influx of oceanic water masses and water column instability (Nedzarek and Rakusa-Suszczewski, 2004; Lange et al., 2007; Kim et al., 2016).

The temporal variation in average nutrient concentrations recorded in Admiralty Bay (present study) follows an increasing trend over recent years. The lowest N:P (<10) ratios were associated with higher phosphate concentrations in early summer (1.92  $\mu\text{mol.L}^{-1}$ ), while higher ratios (N:P > 10) were associated with increased supply of nitrogenous compounds during late summer (maximum of 26.89  $\mu\text{mol.L}^{-1}$ ) (Table 1). Lange et al. (2007) also documented differences in N:P ratios related to increased inorganic nitrogen and low phosphate concentrations at the end of the summer in the same sector. However, even with differences in the N:P ratio of 16:1 (Redfield, 1958), the elemental composition of phytoplankton was not constant due to the taxonomic variety (Falkowski, 2000; Geider and La Roche, 2002; Tenenbaum et al., 2015) that essentially occurs in coastal regions (Clarke et al., 2008; Henley et al., 2017; Kim et al., 2016). The same pattern of temporal increase was also observed for silicate concentrations, with high values related to a greater influence (%) of meltwater (scenarios iii and iv). Extensive variation in the concentration of dissolved nutrients was observed in the present study, as was reported in the literature for all sectors

**TABLE 3** | WAP Subdivision for comparison with Admiralty Bay local environmental conditions.

Sectors	Sampling period (Year)	Temperature (°C)	Salinity (ppt)	Nitrate ( $\mu\text{mol.L}^{-1}$ )	Phosphate ( $\mu\text{mol.L}^{-1}$ )	Silicate ( $\mu\text{mol.L}^{-1}$ )	Density (* Cells.L <sup>-1</sup> )	Chlorophyll a (mg.m <sup>-3</sup> )	References
1	2009 – 2011/2013 – 2015	–0.61 to 1.66	33.73 – 34.61	13.82 – 26.89	1.24 – 1.92	40.18 – 69.35	10 <sup>5</sup>	0.35 – 4.07	This Study
	1994 – 1995	0.16 to 1.71	–	–	–	–	10 <sup>6</sup>	–	Kopczyńska, 1996
	1996 – 1998/2003 – 2005	0.98 to 1.38	33.9 – 34.6	26.27 – 39.76	1.84 – 2.52	16.43 – 34.20	10 <sup>6</sup>	–	Kopczyńska, 2008
	2002 – 2003	–0.4 to 1.5	33.9 – 34.6	33.5 – 35.0	2.6 – 4.5	66.0 – 67.2	10 <sup>4</sup>	0.4 – 0.5	Lange et al., 2007
	2002 – 2003/2008 – 2009	–0.2 to 1.6	33.8 – 34.6	11.18 – 29.55	1.40 – 4.47	32.07 – 71.12	10 <sup>4</sup>	0.13 – 0.45	Lange et al., 2014
	2007/2009 – 2010	0.0 to 1.32	33.93 – 34.37	14.23 – 24.33	0.17 – 2.83	59.55 – 102.0	10 <sup>6</sup>	0.28 – 9.01	Wasiłowska et al., 2015
2	1980 – 2013 (Review)	–2.0 to 3.4	30.7 – 35.8	4.4 – 46.9	0.2 – 9.9	20.8 – 102.0	>10 <sup>4</sup>	0.15 – 17.9	Lange et al., 2018
	2010	0.73 to 0.77	34.09 – 34.11	16.0 – 26.0	2.40 – 4.40	–	10 <sup>5</sup>	<1.0 – 23.5	Schloss et al., 2014
3	2013	–1.1 to 1.8	33.9 – 34.4	5.34 – 25.51	0.63 – 3.30	16.43 – 84.52	–	0.16 – 7.06	Aracena et al., 2018
4	2008 – 2009	–	–	–	–	–	–	0.55 – 0.92	Mendes et al., 2012
	2008 – 2010	0.16 to 1.08	33.93 – 34.26	16.6 – 47.8	0.3 – 3.4	23.1 – 79.9	–	0.52 – 1.07	Mendes et al., 2013
	2013	–0.03 to 1.11	34.03 – 34.25	23.88 – 28.51	1.68 – 2.08	34.46 – 38.10	10 <sup>6</sup>	0.65 – 1.58	Russo et al., 2018
5	2008 – 2009	–	–	–	–	–	–	0.15 – 0.27	Mendes et al., 2012
6	2008 – 2009	–	–	–	–	–	–	0.39†	Mendes et al., 2012
7	2013 – 2014	–0.90 to 0.31	33.68 – 34.14	25.94 – 28.48	1.37 – 1.92	29.30 – 42.64	–	0.53 – 1.37	Mendes et al., 2018
8	2008 – 2009	–	–	–	–	–	–	1.76 – 3.73	Mendes et al., 2012
9	2013	1.32	33.39	7.25	1.60	40.38	10 <sup>6</sup>	1.22	Russo et al., 2018
	2013 – 2015	1.12 to 1.32	33.62 – 33.93	19.62 – 30.45	0.64 – 1.65	30.49 – 75.09	–	1.01 – 1.54	Mendes et al., 2017
10	1997 – 2012	–	–	–	–	–	–	8.53 <sup>x</sup>	Rozema et al., 2017
11	1998 – 2016	–1.58 to 2.03	–	36.0	2.43	–	–	0.2 – 2.3	Arrigo et al., 2017

Data from this study and literature, based on different methods of analysis and measurements in Antarctic waters: Abiotic data, cell density and biomass (Average - Variation between sampling years). <sup>x</sup>Average between summers in all years; <sup>\*</sup>Maximum value; <sup>†</sup>Average in 2008; NO<sub>2</sub> + NO<sub>3</sub>.

of WAP (Table 3). The lowest average concentrations of silicate ( $40.18 \mu\text{mol.L}^{-1}$ ) and nitrogen compounds ( $13.82 \mu\text{mol.L}^{-1}$ ), and lowest N:P ratio (7.55), were observed in association with higher diatom densities (94% relative abundance, chlorophyll concentration at  $4.07 \text{ mg.m}^{-3}$ ) during periods of low MW% (scenario ii). When lower macronutrient concentrations were observed in WAP, phytoplanktonic cell densities increased, revealing no limitation to the densities of autotrophic organisms.

In the last century, polar regions have exhibited a tendency for decreased chlorophyll *a* (Boyce et al., 2010). Marguerite Bay (sector 10) experienced a significant decrease in total biomass over the past 15 years (Rozema et al., 2017), due to increases in temperature (Boyce et al., 2010; Schloss et al., 2014). The chlorophyll *a* data of the present study follow this trend for some regions of WAP (Table 3), with values around  $0.5\text{--}2.0 \text{ mg.m}^{-3}$  (Lange et al., 2007; Wasilowska et al., 2015). Exceptions were in cases of blooms (e.g., Wasilowska et al., 2015 sector 1; Schloss et al., 2014 sector 2; Lange et al., 2018 sector 2; Aracena et al., 2018 sector 3; Table 3). Great variation was found for other sectors of WAP, including 4 (Bransfield Strait), 5 (Weddell Sea), 6 (Drake Passage) and 8 (James Ross Island), in association with water column stratification (e.g., seasonal heating of the sea water) (Mendes et al., 2012, 2018).

Since the life cycles of the main polar organisms are directly related to sea ice seasonality, the changes observed in WAP food webs are driven by increased water temperature and the consequent decline in ice cover (Moline et al., 2004; Montes-Hugo et al., 2009; Deppeler and Davidson, 2017; Rozema et al., 2017; and the present study). Changes in ice-free areas and micronutrient inputs generate environmental gradients of temperature, salinity and water column stability at WAP (Mendes et al., 2012), which lead to succession of the phytoplankton community, with consequences to the structure of the entire food web.

## The Relationship Between Microphytoplankton Community Structure, Meltwater and Resuspension

Considering the observed abiotic environment and variation in phytoplanktonic biomass discussed in the previous section, WAP bays can be considered natural experiments for studying aquatic productivity in response to the effects of local climate and seasonal melting of sea ice, as also discussed by Aracena et al. (2018). Interannual changes in environmental conditions were observed in Admiralty Bay (sector 1). Furthermore, spatial and seasonal variation in meltwater percentage (Mendes et al., 2013; Arrigo et al., 2017; Mendes et al., 2018) lead to changes in both composition and density ( $10^3 \text{ cell.L}^{-1}$  to  $10^6 \text{ cell.L}^{-1}$  – Table 3) of phytoplankton communities.

The present study documented a dominance of dinoflagellates or diatoms in the periods without influence from ice melt, represented by scenarios i and ii, respectively, and the codominance of these groups during periods with influence from ice melt (scenarios iii and iv). Such differences in taxonomic composition have been described for several sectors of the Antarctic Peninsula, such as Weddell-Scotia Confluence

(sector 7 – Mendes et al., 2018) and Gerlache Strait (sector 9 – Mendes et al., 2017; Russo et al., 2018), but not for Admiralty Bay (sector 1). In AB (sector 1), the predominance of diatoms in the microphytoplankton community during summer is frequent (Lange et al., 2007; Kopczyńska, 2008; Barrera-Alba et al., 2012, 2015). In particular, the region is influenced by microphytobenthic species derived from the resuspension of sediments or the contribution of meltwater (Lange et al., 2007; Kopczyńska, 2008), as also observed in the present study. This dominance was also recorded in other sectors of WAP under the influence of sea ice melt (Schloss et al., 2014; Lange et al., 2018 – sector 2; Aracena et al., 2018 – sector 3; Mendes et al., 2012 – sectors 4, 5, 6, and 8; Rozema et al., 2017 – sector 10; Arrigo et al., 2017 – sector 11).

The decrease in cell size of microphytoplanktonic organisms in relation to hydrological conditions is noteworthy (e.g., Tenenbaum et al., 2010; Barrera-Alba et al., 2015), and associated with changes in dominance of taxonomic groups of phytoplankton from diatoms to dinoflagellates (Tenenbaum et al., 2010; Lange et al., 2014). This was seen in scenarios iii and iv, periods under the influence of meltwater, when there was codominance between diatoms (e.g., *Corethron pennatum*, *Thalassiosira* cf. *antarctica*, *Cocconeis* spp.) and dinoflagellates (*Prorocentrum* spp., *Protoperidinium* spp., *Amphidinium* spp., *Gyrodinium* spp., *Gymnodinium* spp.). The high species richness, especially for the diatom both planktonic and benthic, contribution, observed in sector 1 (Lange et al., 2018 – review; this study), has previously been recorded in the water column and correlated with the resuspension and/or sea ice melting hypothesis (Tenenbaum et al., 2011).

According to Lange et al. (2007), alternation in dominance of centric and pennate diatoms suggests an influence from temporal variation in sea ice cover and phytoplankton communities. In this sense, the remarkable contribution of benthic diatoms in scenarios iii and iv, periods under the influence of meltwater, represented mainly by *Cocconeis* spp. (*C. costata* and *C. fasciolata*), eponymous diatoms such as *Fragilariopsis* spp. (e.g., *F. rhombica*), and chain-forming diatoms, mainly *Pseudo-nitzschia* spp. (e.g., *Pseudo-nitzschia subcurvata*), reinforce the influence that sea ice melting has on the microphytoplankton community of AB. Ticopelagic diatoms in the water column can be associated with advection processes of water masses driven by continental ice melting (Pichlmaier et al., 2004) and/or coastal upwelling events generate by winds (Schloss et al., 2002; Schloss et al., 2014). Otherwise, centric diatoms (*Thalassiosira* spp. and *Corethron pennatum*) observed in scenario ii, without sea ice melt, were possibly transported by currents from Bransfield strait (Kopczyńska, 2008; Wasilowska et al., 2015).

It should be noted that although the phytoplankton community and events of Antarctic blooms are commonly dominated by diatoms, other taxa are also important components of the trophic web (Henley et al., 2019). Increases in cryptophytes and other flagellates have previously been reported (e.g., *Phaeocystis antarctica* and *Gymnodinales*),

as well as the substitution of diatoms for these flagellates in WAP, due to the influence of sea ice melt (Moline et al., 2004; Mendes et al., 2013; Lange et al., 2014; Mendes et al., 2017), as observed in the WAP sectors of the present study (**Figure 3**): sector 1 (Wasiłowska et al., 2015), sector 4 (Mendes et al., 2012, 2013), oceanic regions of sectors 5 (Mar de Weddell) and 6 (Passagem de Drake) (Mendes et al., 2012), as well as sectors 7 (Mendes et al., 2018), 9 (Gerlache Strait) (Mendes et al., 2017; Russo et al., 2018) and 11 (Arrigo et al., 2017).

Another important consequence of sea ice melting is an increase in turbidity due to suspension of bottom sediments (Pichlmaier et al., 2004). Thus, conditions of high turbidity may have favored the increase in dinoflagellates, and consequently the codominance observed in the scenarios under the influence of meltwater, since the mixotrophy of the majority of these organisms allow them to grow in low light conditions.

Since phytoplankton support the marine trophic web and play a key role in the resilience of marine ecosystems of the Antarctic Peninsula, changes in the abundance and composition of phytoplankton groups can affect interactions in trophic levels and generate a direct effect throughout the regional ecosystem (Haberman et al., 2003; Mendes et al., 2013; Schofield et al., 2017; Mendes et al., 2018). In this context, Antarctic krill (e.g., *Euphausia superba*), which are an important link in the trophic web of the region (Corbisier et al., 2004; Saba et al., 2014), assimilate diatoms more efficiently than cryptophytes (Haberman et al., 2003) and dinoflagellates, with benthic diatoms accounting for 46% of their diet in coastal zones, as well as in Admiralty Bay, sector 1 (Ligowski, 2000).

Small microalgae, such as cryptophytes and other flagellates, including dinoflagellates, are preferred by salps and other suspensivores, as they are not palatable to herbivores such as krill (Moline et al., 2004; Montes-Hugo et al., 2009). In addition, these nannoplanktonic microalgae are generally less efficient in the assimilation and exportation of carbon, when compared to a community dominated by diatoms (Schloss et al., 2007; Weston et al., 2013; Schofield et al., 2017; Da Cunha et al., 2018). Therefore, a decrease in the size of phytoplankton can cause a significant change in the local trophic web and in biogeochemical cycles (Rozema et al., 2017; Aracena et al., 2018; Da Cunha et al., 2018). It is possible that changes in the phytoplankton community and the seasonality of krill lead to population decreases in penguins (Sander et al., 2007), changes in the benthic community (Montes-Hugo et al., 2009) and variation in the period and frequency of migratory movements of humpback whales (Johnston et al., 2012; Andrews-Goff et al., 2018).

The observed increase in the dinoflagellate contribution (e.g., *Gymnodinium* spp., *Protoperidinium* spp. and *Prorocentrum* spp.) (Kopczyńska, 2008; Tenenbaum et al., 2010; Lange et al., 2014, 2018; this study) indicates a change in phytoplankton species composition (Lange et al., 2018). This supports the findings of other studies in AB (Sector 1) and King George Island (sector 2), that highlighted shifts in biota due to environmental changes (increase in solar radiation and temperature, thus increasing the sea ice melting) (Kopczyńska, 2008; Schloss et al., 2012; Campos et al., 2013; Mendes et al., 2013, 2018;

Saba et al., 2014; Schofield et al., 2017). These observations were not restricted to coastal areas in WAP. Changes in phytoplankton and the consequences to the trophic web in oceanic areas (Bransfield Strait – sector 4; Drake Passage – sector 6) were previously reported in the literature (Kopczyńska, 2008; Mendes et al., 2012; Lange et al., 2014).

## Sea Ice Melt Drives Changes in Microphytoplankton Functional Groups and Functional Diversity

Cell morphology and adaptive strategies of phytoplankton are under different selective pressures due to the physico-chemical environmental characteristics to which they are subjected (Litchman et al., 2009; Weithoff et al., 2014). The influence of sea ice melting in WAP promoted environmental gradients, which can function as filters and restrict diversity, or create niches and promote competition among species, through selecting traits (Lebrija-Trejos et al., 2010; Roselli and Basset, 2015; Weithoff and Gaedke, 2016). Three sets of functional traits were classified in the present study, which varied from scenario i to scenario iv along an environmental gradient of % MW.

The first set of functional traits, composed of dinoflagellates (groups *a* and *b*), was selected by trophic traits (heterotrophy and mixotrophy); resistance stages; presence of vacuoles and flagella; and potential HABs formation. Heterotrophy and mixotrophy confer advantages to dinoflagellates under conditions of low nutrient concentrations (Litchman and Klausmeier, 2008) and, associated with the motility of these organisms, represent unique strategies for competing in stratified environments (Bellinger and Sigee, 2011; Klais et al., 2016; Roselli et al., 2017). When compared to heterotrophic competitors, mixotrophy confers the ability to compete and overcome both strictly autotrophic and heterotrophic organisms by using nutrients more efficiently (Leles et al., 2018). In addition, the presence of vacuoles, associated mainly with mixotrophic dinoflagellates, may be indicative of a digestive function for these organelles and the consequent occurrence of phagotrophy by these organisms (Onuma and Horiguchi, 2013; Almada et al., 2017). Another selected trait was the production of resistance stages, which is a survival strategy among dinoflagellates that favors the reintroduction of species into the water column and eventually HAB formation (McQuoid et al., 2002; Ellegaard and Ribeiro, 2018).

It is worth noting that no HAB events were reported for the studied region; however, HAB forming algae exhibit trait plasticity, which may favor the development of these species in different environmental conditions (Litchman et al., 2010). Most harmful events reduce diversity and threaten the fitness of local ecosystems; such effects can be intensified under a climate change scenario (Paerl and Huisman, 2009).

The second set of traits was composed of filamentous cyanobacteria (group *c*) and pennate diatoms with raphe (group *d*). Coloniality (trait that includes a group of cells forming colonies, filaments and chains) was the trait that characterized these groups. Coloniality in both cyanobacteria and diatoms confers ecological advantages to these organisms because it



modifies their effective size by altering their interaction with the environment and possible predators (Thingstad et al., 2005; Barton et al., 2013), reduces losses by processes of sedimentation (Brasil and Huszar, 2011), and regulates buoyancy allowing migration to depths of optimal irradiance and/or nutrient availability (Brookes and Ganf, 2001; Tamulonis et al., 2011). Besides coloniality, diatoms of group *d* also possess higher *s/v* ratios and the presence of raphe. An additional function of diatom chains is to keep cells together in order to prevent dispersion in turbulent environments (Crawford and Sims, 2008; Wadt et al., 2017), such as the case with *Pseudo-nitzschia* spp., a dominant genus of group *d*. Since higher *s/v* ratios allow nutrients to be absorbed more effectively, they favor diatoms in light-limiting conditions (Roselli et al., 2017).

The third set of traits mostly combined centric large-sized diatoms (groups *e*, *f*, and *g*) selected by autotrophy, GALD and silica presence. The observed diatoms are strictly autotrophic and characterized in the literature as having high photosynthetic efficiency (e.g., Roberts et al., 2007), which confers a competitive advantage in environments with high light and nutrient availability (Litchman et al., 2009). Large-sized cells (e.g., GALD > 35  $\mu\text{m}$ ; Litchman et al., 2010), such as those observed in this set, can store nutrients, even in conditions of high availability or in environments with fluctuations in the availability of this resource (Thingstad et al., 2005; Litchman et al., 2009). Another advantage of large diatoms (GALD > 35  $\mu\text{m}$ ) is their reduced palatability (Kruk and Segura, 2012), which is reflected in high predation pressure on small sized fractions (<35  $\mu\text{m}$ ) (Litchman et al., 2010). Additionally, the presence of silica in their constitution is one of the main traits of this group, while the presence of ornaments and processes on the frustule also confer advantages against certain types of predation (Hamm et al., 2003; Barton et al., 2013).

This diversity of traits discussed above translated into the higher FD indices observed in the periods influenced by meltwater, namely scenarios iii and iv, in which the codominance between diatoms and dinoflagellates was recorded. The high contribution of sea ice melt in 2013–2014 and 2014–2015 (scenarios iii and iv) can be considered an intermediate disturbance, which allowed the coexistence of several morphotypes with different traits and/or strategies, thereby potentializing functional niche diversity (Weithoff et al., 2014). Competition for resources may be a key process for shaping phytoplankton community structure by characterizing and clustering organisms in their niche, and thus directing ecosystem functioning, resulting in species coexistence (Mayfield and Levine, 2010; Segura et al., 2013). It is probable that competition among functional groups selected species/types that differed most from each other in the use of resources, resulting in the codominance observed during periods of meltwater, scenarios iii and iv, since competition entails ecological differentiation of coexisting species (Cornwell et al., 2006). Abiotic factors of scenarios iii and iv, associated with % MW, did not act as environmental filters because the organisms exhibited tolerance to this disturbance, which was reflected in greater diversity of the phytoplanktonic community.

The greatest FRic with no influence of meltwater was observed in early summer 2009–2010 and 2010–2011 (scenario i), and was not accompanied by greater expression of FD in the analyzed indices. An increase in taxonomic diversity and lower values of FD may indicate that, although richness is greater, the functional traits that allowed the species to be successful were selected and the community is composed of only functionally similar species, since the taxonomic diversity does not always reflect FD (Weithoff et al., 2014). Thus, FD is lower because different phytoplanktonic species can be functionally neutral (Roselli et al., 2017), that is ecologically equivalent, and so there is no distribution in trait based factorial plan (Vallina et al., 2017), which is evidenced by the dominance of dinoflagellates in this scenario.

While scenarios iii and iv (2013–2014, 2014–2015), characterized by high %MW, had lower FRic than scenario i (2009–2010, 2010–2011), they had high trait diversity, with emphasis on functional equitability (e.g., Villéger et al., 2008; Cardoso et al., 2017). It is likely that the use of contrasting ecological strategies, directed by biotic and abiotic processes as a trade-off between form and size, key features for the selection and interaction of organisms, allowed the coexistence of species (Roselli et al., 2017). This in turn determined changes in the dynamics and functioning of phytoplankton communities (Pomati et al., 2013), and was expressed in the highest values of FD among the scenarios influenced by meltwater.

## CONCLUSION

The hydrographic conditions, as well as the nutrient availability and variation in phytoplankton biomass, observed in this study resemble the gradients and variation reported in the literature for WAP at various temporal scales. The influence of meltwater associated with increasing water temperatures has been highlighted by recent studies as the main environmental stressor for microphytoplankton biomass. The functional groups of the present study reflect different adaptive strategies produced by the divergence of traits. These different adaptive strategies are responsible for the codominance of diatoms and dinoflagellates and the structuring of the microphytoplankton community and FD in scenarios dominated by meltwater. FD increased in relation to a gradient of %MW from summer 2009–2010 to summer 2014–2015. The increased contribution of dinoflagellates in scenarios of meltwater may be a trigger for changes in the structure of the Antarctic trophic web reported in literature. In this sense, we suggest that Admiralty Bay be used as a model for studies on changes to microphytoplankton community composition and FD, since they are relevant descriptors for evaluating potential changes to the local ecosystem at different scales.

## DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the manuscript/**Supplementary Files**.

## AUTHOR CONTRIBUTIONS

GM, JB-A, and DL conceived the experimental design. DT and JB-A organized the database. DL, MC, MT, and TC performed the sample analysis. DL, GM, FP, and LD performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to the manuscript revision, read and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00638/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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