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Phytoplankton dynamics in nearshore regions of the western Antarctic Peninsula in relation to a variable frontal zone in the Gerlache Strait

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The Gerlache Strait is a narrow channel that separates the western coast of the Antarctic Peninsula (WAP) from the Palmer Archipelago. This area is characterized by the presence of interconnected fjords, bays, islands, and channels that serve as a refuge for megafauna during summer. Through the framework of FjordPhyto – a citizen science collaboration with the International Association of Antarctica Tour Operators (IAATO) vessels – we assessed phytoplankton biomass and composition in surface waters of six under-explored nearshore areas connected to the Gerlache Strait (between 64° and 65° S) during three consecutive seasons, from November to March (2016–2019). During the first two seasons, we found significant differences in the phytoplankton community distribution and successional patterns to the north and south of the sampling area; the greatest differences were evidenced mainly in the months of high biomass, December and January. During December, cryptophytes bloomed in the north, while microplanktonic diatoms dominated in the south, and during January, small centric diatoms dominated in the north, while prasinophytes bloomed in the south. This spatial distinction in phytoplankton communities were mainly associated with the occurrence of a surface thermal front in the Gerlache Strait around 64.5° S. The presence of the front separating warm waters to the north and colder waters to the south, during the months of December to February, was confirmed by the analysis of 10 years of remote sensing data. By contrast, during the third season, low biomass prevailed, and no differences in the phytoplankton composition between the north and south areas were observed. The third season was the coldest of the series, with smaller differences in water temperature north and south of the usual front location. This study shows for the first time a complete overview of the phytoplankton composition throughout the entire growth season (November

through March) in the nearshore areas of the WAP between 64° and 65° S. The results of this work contribute to the understanding of the phytoplankton community in relation to small scale physical features during the Antarctic austral summer.

KEYWORDS

thermal front, diatoms, cryptophytes, prasinophytes, phytoplankton succession, Citizen Science

1 Introduction

The Gerlache Strait is a narrow channel about 200 km long that separates the western coast of the Antarctic Peninsula (WAP) from the Palmer Archipelago (between ~63.5° and 65° S). This is a highly productive coastal area with a significant abundance of krill-feeding predators that ultimately rely on phytoplankton (Ducklow et al., 2013). The depth in the Gerlache Strait can reach up to 1,000 m, but it is mainly characterized by the presence of numerous small, interconnected fjords, islands, coves, embayments, and channels (Kerr et al., 2018). The reduced mixing processes characteristic of protected coastal areas favor the development of several phytoplankton blooms of different composition during the spring and summer months (Vernet et al., 1991; Ferrario and Sar, 1992; Rodriguez et al., 2002; Mendes et al., 2018; Costa et al., 2021, among others).

The surface water in the Gerlache Strait is influenced from the south by waters from the Bellingshausen Sea entering the Bismarck Strait and between the islands of the Palmer Archipelago, and by waters from the north by way of the Bransfield Strait – Weddell Sea (García et al., 2002). The main surface circulation pattern within the Gerlache Strait is driven by a current flowing northeastward (Zhou et al., 2002; Su et al., 2022). As a result of air-sea temperature fluxes, including heat advection by currents in the area, a thermal front forms during summer months represented by the 1°C surface isotherm near the Schollaert Channel around 64.5° S (Torres Parra et al., 2020). This front separates colder water to the south from warmer water to the north within the surface mixed layer (Torres Parra op. cit.). Several studies mention these water temperature differences during different years and summer months, December and/or January (Anadón and Estrada, 2002; Rodriguez et al., 2002), and February (Kerr et al., 2018; Mendes et al., 2018; Torres Parra et al., 2020).

Marine fronts are characterized by high biological activity; seabirds and marine mammals tend to congregate and feed in and around the fronts. Frontal regions are also sites of pronounced exchange between deep and surface layers of the ocean (Acha et al., 2015; Chapman et al., 2020). Because the Gerlache Strait front is found during the summer months in the upper mixed layer, it likely has several implications for phytoplankton biology and ecology in the euphotic zone, since phytoplankton are the base of the Antarctic food web. da Cunha et al. (2018) proposed that this front promotes the export of organic carbon produced at the surface to deeper layers, associated with high biological productivity in the area.

Concurrently, Mendes et al. (2018) hypothesized that this front separated different phytoplankton communities during February, with cryptophyte dominance to the north of the front in warmer waters and small diatoms and flagellates in colder southern waters. However, few studies investigate the interannual variability or the seasonal development of the front, needed to understand the role such a front can play in determining phytoplankton distribution.

Large summer phytoplankton blooms have been previously reported in the Gerlache Strait, composed by diatoms (Costa et al., 2020), cryptophytes (Ferrario and Sar, 1992; Mendes et al., 2018), and prasinophytes (*Pyramimonas* sp.) (Bird and Karl, 1991; Rodriguez et al., 2002). However, studies in nearshore environments are scarce and the dynamics between phytoplankton blooms there and the waters of the Strait are poorly understood. A recent study suggests that these coastal areas of central Antarctic Peninsula present blooms of cryptophytes, prasinophytes, and unarmored dinoflagellates, with diatoms being less abundant (Mascioni et al., 2019), however, still dominating the primary production (Mascioni et al., 2021). Diatoms are the main food for Antarctic krill, a key Antarctic species, and any decrease in this group with a replacement by other taxa could represent up to 40%-60% of energy loss in these ecosystems (Moline et al., 2004). Therefore, the study of phytoplankton composition and seasonal dynamics is crucial to understand how the food web in these nearshore areas is sustained as they are important refuge and nesting areas for the megafauna. In order to understand the phytoplankton communities of the nearshore WAP areas and the influence of the surface thermal front of the Gerlache Strait on them, we assessed surface phytoplankton biomass, cell abundance, composition, and succession through the summer months (November to March) of the growth season.

1.2 Brief description of the study area

Sampling opportunities available to FjordPhyto depended on locations visited by the International Association of Antarctica Tour Operators (IAATO) expedition vessels. In this study we present results from stations visited throughout the austral summer, in six nearshore areas of the WAP between 64° and 65° S that generated a time series (Figure 1). We clustered those areas according to the estimated front location (64.5°S by Torres Parra et al., 2020) into northern areas (2 sites): Cierva Cove and

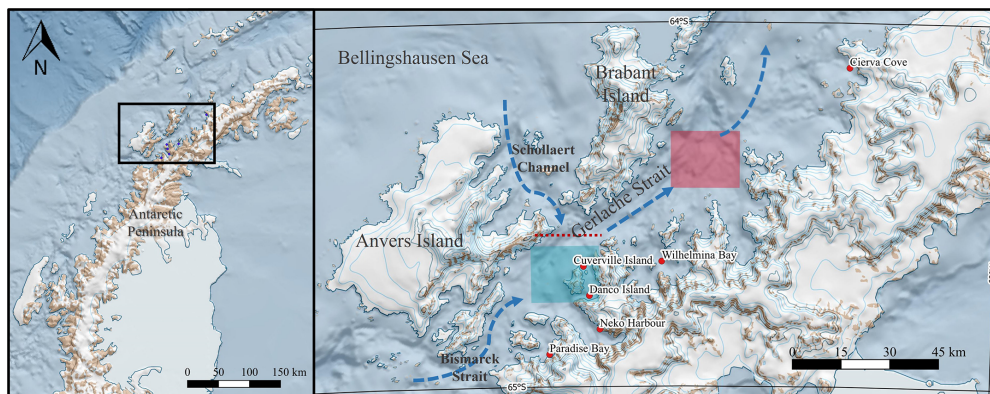


FIGURE 1

Map showing the six sampling sites on the WAP coast between 64° and 65° S. The front is marked with a red dashed line at the location proposed from observations in previous studies (i.e., around 64.5° S, Torres Parra et al., 2020). The areas are clustered to the estimated front location into northern areas (2 sites): Cierva Cove and Wilhelmina Bay; and southern areas (4 sites): Cuverville and Danco Islands, Neko Harbor, and Paradise Bay. The blue arrows show the directions of surface currents. The squares show where satellite data was extracted from the northern region (red) and southern region (light-blue) of the Gerlache Strait.

Wilhelmina Bay; and southern areas (4 sites): Cuverville and Danco Islands, Neko Harbor, and Paradise Bay.

Cierva Cove is an embayment located in the Danco Coast (64° 7.41' S – 60° 56.79' W, Figure 1), connected with the northern Gerlache Strait. It is close to a Specially Protected Antarctic Area, (ASPAN° 134) “Punta Cierva and littoral islands, Danco Coast, Antarctic Peninsula”, proposed and under the conservation of Argentina (Perterra and Hughes, 2013). Numerous bird species nest in this area, and large mammals feed and search for refuge there. On its coast, three glaciers, Sikorsky, Breguet, and Gregory discharge together and are stable according to Seehaus et al. (2018).

Wilhelmina Bay is a large embayment with an area of ~600 km² placed in the Danco Coast (64° 39.41' S – 62° 8.14' W, Figure 1). The mean depth of the channel is ~300 m while the deepest depth is over 600 m (Espinasse et al., 2012). Nine glaciers discharge from its coast (Woodbury, Montgolfier, Rozier, Blanchard, DGC25, Leonardo, DGC23, Bayly, and DGC31), and according to Seehaus et al. (2018) more than 60% of them are in retreat.

Both Danco and Cuverville Islands are located within the Errera Channel, that separates the Rongé Island from the west coast of the Antarctic Peninsula (Figure 1). Danco Island is at the southern side of the channel (64° 45.03' S – 62° 36.19' W) while Cuverville island is at the northern side of the channel (64° 40.2' S – 62° 38.4' W). In the summer, the islands serve as a refuge for the largest colony of gentoo penguin in the WAP (Lynch et al., 2010). These areas only have three glaciers nearby without any direct glacial discharge in the area (Dewille, Orel Ice Fringe, and Wheatstone glaciers, Ferrigno et al., 2006)

Neko Harbor is located in the northeast coast of Andvord Bay (64° 50.57' S – 62° 33.22' W, Figure 1). Five glaciers discharge in this fjord (Bagshawe, Grubb, Arago, Moser, and Rudolph), and none of them are currently retreating (Seehaus et al., 2018; Lundsgaard et al., 2020).

Paradise Bay is a wide embayment behind Lemaire and Bryde Islands (64° 54.66' S – 62° 51.94' W, Figure 1). It has six glaciers discharging from its coast (Toro Mazote, Vivallos, Astudillo, Avalanche, Petzval or Suárez, and Miethe), there is no recent study that assesses their current state of these glaciers.

2 Materials and methods

2.1 Sampling

Phytoplankton sampling was conducted according to protocols established for the Citizen Science project, FjordPhyto (www.fjordphyto.org, Cusick et al., 2020) and explained in this section. Sampling took place from November through March in 2016-2017 (from now on season 1 or S1), 2017-2018 (season 2 or S2), and 2018-2019 (season 3 or S3) aboard multiple tour expedition vessels in the six nearshore areas depicted in Figure 1 (for more information see Supplementary Table 1). Surface samples were collected aboard small inflatable boats by submerging 120-mL bottles in the water by hand to approximately 25 cm depth, to avoid sampling the superficial layer. Subsequently, samples were fixed with Lugol's solution at 4% (Edler and Elbrächter, 2010) and kept in a cool dark location. Expedition ship staff (i.e., polar expedition guides) received in-person training from FjordPhyto project researchers on appropriate sampling methods before the start of each season (Cusick et al., 2020). At the end of the season, samples were sent to the lab at División Ficología in Facultad de Ciencias Naturales y Museo (Universidad Nacional de La Plata, Argentina) for analysis.

2.2 Microscopy analysis

A total of 143 samples from the six areas were analyzed, from three consecutive austral summers: 2016-2017 (n = 31, included in Mascioni et al., 2019), 2017-2018 (n = 51), and 2018-2019 (n = 61). Cell counts were performed according to Utermöhl (1958) using an inverted optical microscope Leica DMIL LED and an Iroscope SI-PH. Subsamples of 50 mL were left to settle for 24 h in a composite sedimentation chamber. At least 100 cells of the dominant taxa were counted at the maximum amplification (400X) (Lund et al., 1958). The whole chamber bottom was also scanned at 200X to count large and sparse species. Five main phytoplankton groups were considered:

cryptophytes, prasinophytes, small unidentified flagellates < 5 μm (referred herein as small flagellates), diatoms, and autotrophic dinoflagellates (dinoflagellates herein). The differentiation between autotrophic and heterotrophic dinoflagellate taxa was made by observation of chloroplasts, although in cases where these could not be observed, the literature was consulted to determine the feeding type of the different taxa.

Biomass (carbon content) of cells was also estimated following Menden-Deur and Lessard (2000), calculating cell biovolumes by approximation to the nearest geometric shapes as proposed by Hillebrand et al. (1999) and Sun and Liu (2003). The size, shape, biovolume, and cell biomass of the main taxa included in this study can be found in Supplementary Table 2.

2.3 Satellite data

MODIS-Aqua level 3 remotely sensed Sea Surface Temperature (SST) data from 2011 to 2021 were retrieved from the NASA Ocean Biology Distributed Active Archive Center (DOI: 10.5067/AQUA/MODIS/L3M/RRS/2018); more detailed analyses focused on 2016-2017, 2017-2018, and 2018-2019. Satellite SST data was extracted from two places north and south of the estimated front location (64.5°S, Figure 1) in order to confirm temperature differences (satellite SST data can be found in Supplementary Table 3). Data were analyzed with geemap (Wu, 2020), a Python package for interactive mapping with Google Earth Engine (GEE). MODIS-Aqua level 3 SST dataset was compiled and visualized in GEE using its NASA/OCEANDATA/MODIS-Aqua/L3SMI image collection (DOI: 10.5067/AQUA/MODIS/L3M/RRS/2018).

2.4 Statistical analysis

In order to assess differences between the northern and southern areas of the Strait, we performed a non-metric multidimensional scaling analysis (NMDS). NMDS was calculated on Bray-Curtis dissimilarities retrieved from the relative biomass of phytoplankton taxa per station using *vegan* package (Oksanen, 2015). Samples from December, January, and February were considered for this analysis ($n = 114$), because these were the months when we observed the thermal gradient (see Results). Difference among NMDS groups were tested by applying ANOSIM (ANalysis Of SIMilarities) to the resulting dissimilarity matrix using *vegan* package. All the statistical analyses were performed in R and Rstudio (R Core Team, 2021).

3 Results

3.1 A thermal gradient in the Gerlache Strait

Through an analysis of 10 years of remote sensing data, we detected a consistent North-South temperature gradient during mid-summer (December - February) with warm waters to the north and

colder waters to the south (Figure 2A). Although the transition line of the thermal front is diffuse and hardly detectable with these images, the observed thermal gradient is attributed to the presence of a frontal zone, previously identified by field measurements (Torres Parra et al., 2020). The thermal gradient was evident during the three seasons included in our study (Figures 2B–D). In addition to the temperature gradient observed, a cooling pattern can be observed within the three seasons sampled (Figures 2B–D), where S1 (Figure 2B) is the warmest and S3 (Figure 2D) the coldest.

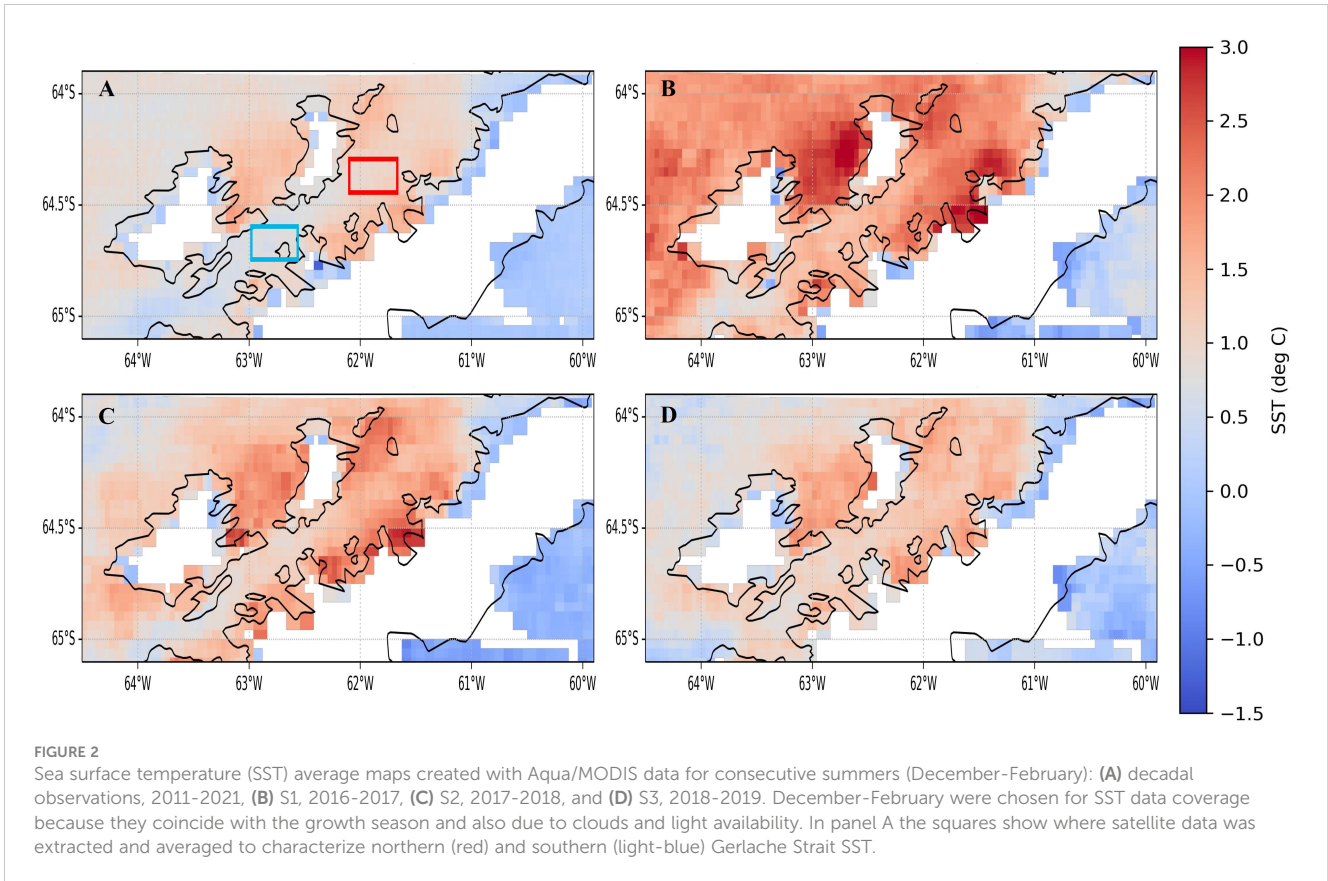
In order to verify the presence of a front, we extracted SST from remote sensing in northern and southern Gerlache Strait (see position in Figures 1, 2A). When plotted these data for the spring-summer months (November to March) for the three sampled seasons, we observed differences in the average temperatures in northern and southern Gerlache Strait, which differ by up to 1°C during January but are lower in November and March (Figure 3). During S3, differences in temperature averages were smaller than in previous years, particularly in December when no difference was detected (Figure 3). During this season a delay in the front development was observed, with differences still greater than 0.5°C in January and February (Figure 3), as defined by Torres Parra et al. (2020).

3.2 Phytoplankton variability in the Gerlache Strait nearshore region

3.2.1 Interannual and spatial variability in phytoplankton biomass and cell abundance

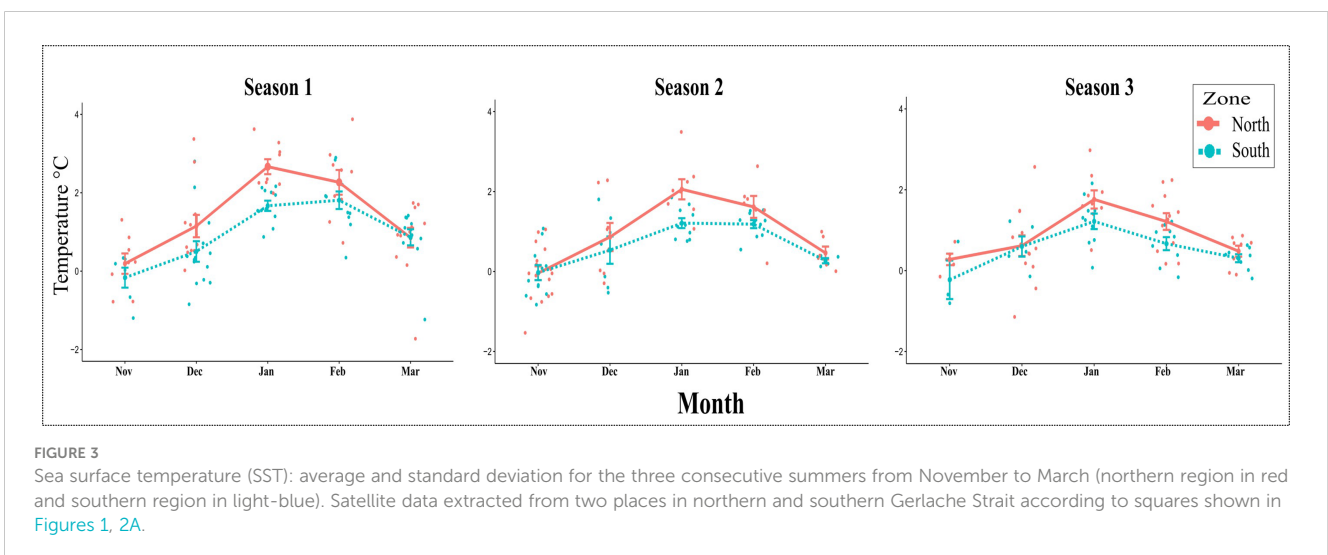
Biomass and cell abundance showed high interannual variability with different patterns between zones (i.e., north vs south, Figure 4). During the first two seasons, total biomass for the northern and southern zones were similar in the months of low abundance (i.e., November and February), but were notably higher in the southern zone during the summer months (i.e., December and January). In the northern zone, maximum biomass was found in December (113.5 $\mu\text{gC L}^{-1}$ in S1 and 16.8 $\mu\text{gC L}^{-1}$ in S2) with biomass in January similar to the ones in December (up to 79.8 $\mu\text{gC L}^{-1}$ in S1 and 15.3 $\mu\text{gC L}^{-1}$ in S2). In the southern zone, phytoplankton biomass increased (>50 $\mu\text{gC L}^{-1}$) during December and January, with peaks up to 1,687 $\mu\text{gC L}^{-1}$ and 800 $\mu\text{gC L}^{-1}$ during S1 and S2, respectively (the first value is off scale and not shown in Figure 4) with a marked decrease in February, and a slight increase in cell abundance in March (Figure 4). During S3, the average cell abundance and biomass to the north and south of the front were quite similar and did not resemble those of previous years, with biomass markedly low overall. The seasonal progression was maintained, with minimum values in November, a slight increase in December and January, followed by a maximum peak of abundance in February, and a final decrease in March (in the southern zone).

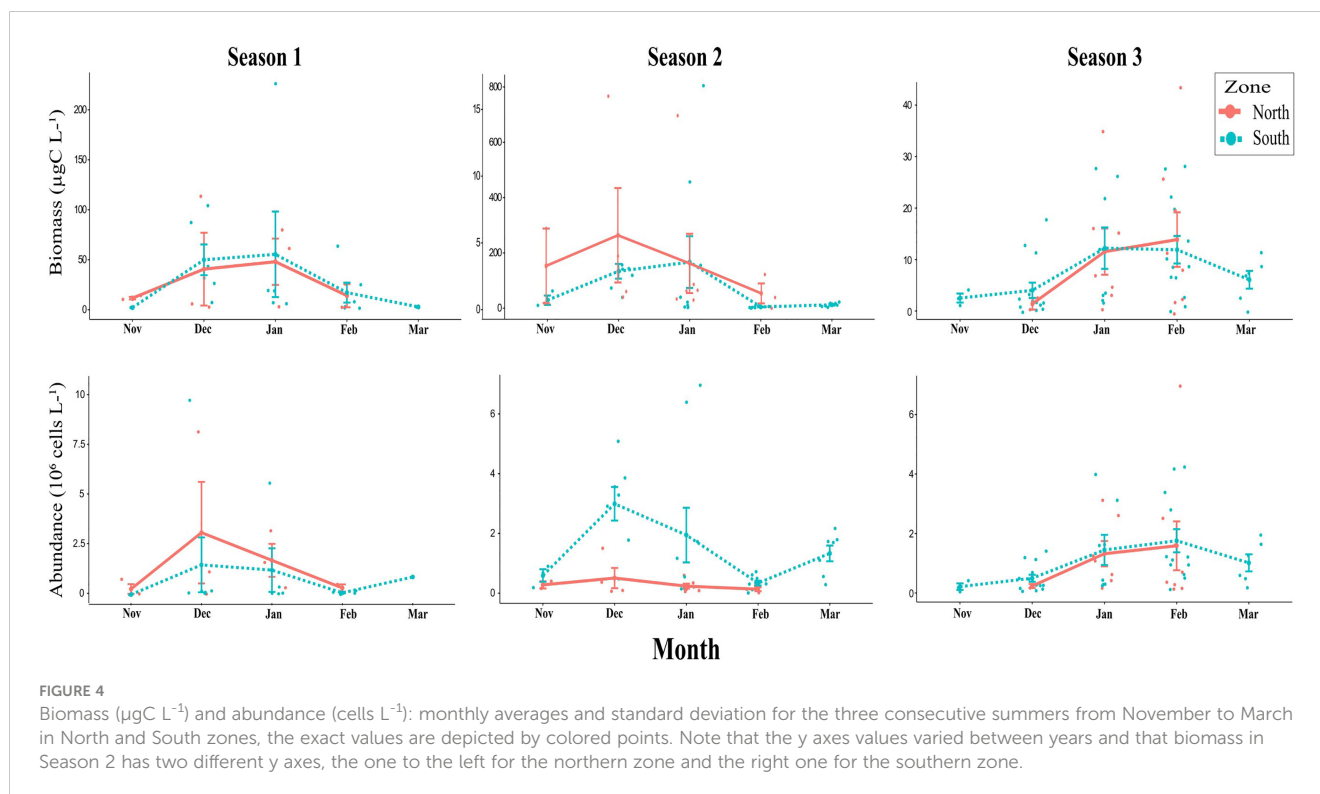
We found a close relationship between total biomass and phytoplankton composition. In the northern sites sampled, consistently over the three seasons, small flagellates and cryptophytes were the most important groups in term of cell



abundance, representing on average 44.7%–58.0% and 26.3%–42.2% of total phytoplankton respectively (Table 1). In terms of biomass, cryptophytes and diatoms were equally important, representing on average 31.6%–49.6% and 26.9%–49.0% of total phytoplankton biomass, respectively (Table 1). Each summer, cryptophytes dominated the blooms, which were repeatedly observed in Wilhelmina Bay, in December during S1 (6.4×10^6 cells L^{-1} and $97.5 \mu g C L^{-1}$), in December during S2 (1.5×10^6 cells L^{-1} and $16.8 \mu g C L^{-1}$), and in February during S3 (7×10^6 cells L^{-1} and $42.3 \mu g C L^{-1}$).

In the southern sites, phytoplankton composition differed among seasons (Table 1). During S1, dinoflagellates, and small flagellates were the most important groups in term of abundance, representing on average 51.7% and 31.7% of the total phytoplankton abundance, respectively. In terms of biomass, dinoflagellates, and diatoms were the most important contributors, representing on average 74.9% and 18% of total phytoplankton biomass, respectively. The highest abundance and biomass values during this summer were observed during December during S1 in Danco Island when an unarmored





dinoflagellate bloom reached $10.4 \times 10^6 \text{ cells L}^{-1}$ and $1686.9 \mu\text{gC L}^{-1}$. During S2, small flagellates and diatoms were the most important groups in term of abundance, representing on average 42.5% and 33.6% of total phytoplankton abundance, respectively. In terms of biomass, prasinophytes and diatoms were the most important contributors, representing on average 54.3% and 36.7% of the total phytoplankton biomass, respectively. The highest peak of cell abundance and biomass was found in January during S2 in Paradise Bay when a *Pyramimonas* sp. (prasinophyte) bloom reached $7 \times 10^6 \text{ cells L}^{-1}$ and $804.6 \mu\text{gC L}^{-1}$. During S2, a *Chaetoceros* spp. bloom (diatom) took place in December, the highest peak was registered in Cuverville at $3.9 \times 10^6 \text{ cells L}^{-1}$ and $146 \mu\text{gC L}^{-1}$. During S3, small flagellates, diatoms, and cryptophytes were the most important groups, representing on average 55.8%, 21.7% and 20.5% of total phytoplankton abundance, respectively. In terms of biomass, cryptophytes and diatoms were the most important contributors, representing on average 39.5% and 27.9% of the total phytoplankton biomass, respectively. The highest peak, similar to the patterns identified in the northern area, occurred in February during S3 in Cuverville Island when cryptophytes reached $4.2 \times 10^6 \text{ cells L}^{-1}$ and $27.8 \mu\text{gC L}^{-1}$.

In order to statistically assess the differences in the composition of phytoplankton between the northern and southern areas, we performed an NMDS analysis based on the Bray-Curtis dissimilarity in the relative biomass from December to February. This analysis showed two clearly differentiated groups (tested by ANOSIM): (Group A) represents the southern sites in December and January during S1 and S2 and February during S1; and (Group B) represents the northern sites in December, January, and

February during S1 and S2, southern sites in February during S2, and every sample during S3 (Figure 5).

The two groups were differentiated by their specific composition. The samples in group A were mainly dominated by large microplanktonic diatoms ($>20 \mu\text{m}$) such as *Eucampia antarctica*, *Odontella weissflogii*, *Proboscia* spp., large centric diatoms from the genus *Coscinodiscus*; other medium-size centric diatoms ($20\text{--}60 \mu\text{m}$) that form chains such as *Porosira* spp., *Thalassiosira* spp., *Shionodiscus* spp. that were grouped according to their size as centrics $\sim 25\mu\text{m}$, centrics $\sim 35\mu\text{m}$, and centrics $\sim 55\mu\text{m}$; *Chaetoceros* spp., and flagellates from the genus *Pyramimonas*. Samples in group B were characterized by the predominance of small flagellates $<5 \mu\text{m}$, cryptophytes, nanoplanktonic diatoms (between $2\text{--}20 \mu\text{m}$) such as *Fragilariopsis* spp., small centrics ($10\text{--}15 \mu\text{m}$) from the genus *Thalassiosira* and *Shionodiscus*; and the large diatom *Corethron pennatum*.

3.2.2 Phytoplankton successional patterns north and south of the Gerlache Strait

In order to describe the successional patterns of phytoplankton in the surface waters of the coastal areas of the Gerlache Strait, we explore in detail how the specific composition of the species (or taxa) varied along the spring-summer months (November to March) in northern and southern Gerlache Strait during the three studied seasons (Figure 6).

The phytoplankton composition during November was similar in both areas during the first two years, represented mainly by the diatoms *Corethron pennatum*, centrics between 20 and $60 \mu\text{m}$ (mostly *Thalassiosira* spp. and *Shionodiscus* spp.), small centrics $<15 \mu\text{m}$, and *Chaetoceros* spp. (Figure 6).

TABLE 1 Abundance and biomass average values and relative percentages of major phytoplankton groups during three consecutive summer seasons.

	Abundance (10^4 cells L^{-1})						Biomass ($\mu gC L^{-1}$)					
	Season 1	%	Season 2	%	Season 3	%	Season 1	%	Season 2	%	Season 3	%
Total Phytoplankton												
Northern	158.1 ± 257.8	100	29.1 ± 37.1	100	131.8 ± 173.9	100	29.9 ± 37.8	100	3.8 ± 5.2	100	11.9 ± 12.3	100
Southern	99 ± 257.8	100	147.8 ± 177.3	100	109.3 ± 115.4	100	118.6 ± 373	100	74 ± 155.5	100	8.6 ± 8.2	100
Cryptophytes												
Northern	66.7 ± 191.4	42.2	8.2 ± 19.8	26.3	38.7 ± 58.8	29.3	10.2 ± 29.1	34.0	1.2 ± 2.9	31.6	5.9 ± 8.9	49.6
Southern	8.6 ± 32.2	8.7	12.4 ± 21.2	8.4	22.4 ± 31	20.5	1.3 ± 4.9	1.1	1.8 ± 3.2	2.4	3.4 ± 4.7	39.5
Prasinophytes												
Northern	0.6 ± 1.3	0.4	0.3 ± 0.5	1.0	0.9 ± 1.2	0.7	0.4 ± 0.6	1.3	0.1 ± 0.2	2.6	0.3 ± 0.5	2.5
Southern	3 ± 7.9	3.0	18 ± 60.2	12.1	0.3 ± 0.4	0.3	6.3 ± 18.1	5.3	40.1 ± 138.7	54.3	0.1 ± 0.2	1.2
Small flagellates												
Northern	70.6 ± 88.1	44.7	18.1 ± 17.1	58.0	75.7 ± 122.2	57.3	1.8 ± 2.3	6.0	0.5 ± 0.4	13.2	2 ± 3.2	16.8
Southern	31.4 ± 83	31.7	63 ± 84.3	42.5	61 ± 61.8	55.8	0.8 ± 2.2	0.7	1.6 ± 2.2	2.2	1.6 ± 1.6	18.6
Dinoflagellates												
Northern	2.4 ± 3.6	1.5	1 ± 1.5	3.2	0.9 ± 1.2	0.7	2.9 ± 5	9.7	0.5 ± 0.8	13.2	0.5 ± 0.7	4.2
Southern	51.2 ± 215.9	51.7	5 ± 12	3.4	1.9 ± 4.1	1.7	88.8 ± 365.4	74.9	3.3 ± 7.3	4.5	1.1 ± 2.4	12.8
Diatoms												
Northern	17.8 ± 25.9	11.3	3.6 ± 3.7	11.5	15.8 ± 32.6	12.0	14.7 ± 22.7	49.0	1.5 ± 2.1	39.5	3.2 ± 3	26.9
Southern	4.9 ± 7	4.9	49.8 ± 84.4	33.6	23.7 ± 58.4	21.7	21.3 ± 28.6	18.0	27.1 ± 51.4	36.7	2.4 ± 3.2	27.9

Average ± standard deviation of cell abundance (10^4 cells L^{-1}) and biomass ($\mu gC L^{-1}$). The areas are clustered to the estimated front location into northern areas (2 sites): Cierva Cove and Wilhelmina Bay; and southern areas (4 sites): Cuverville and Danco Islands, Neko Harbor, and Paradise Bay.

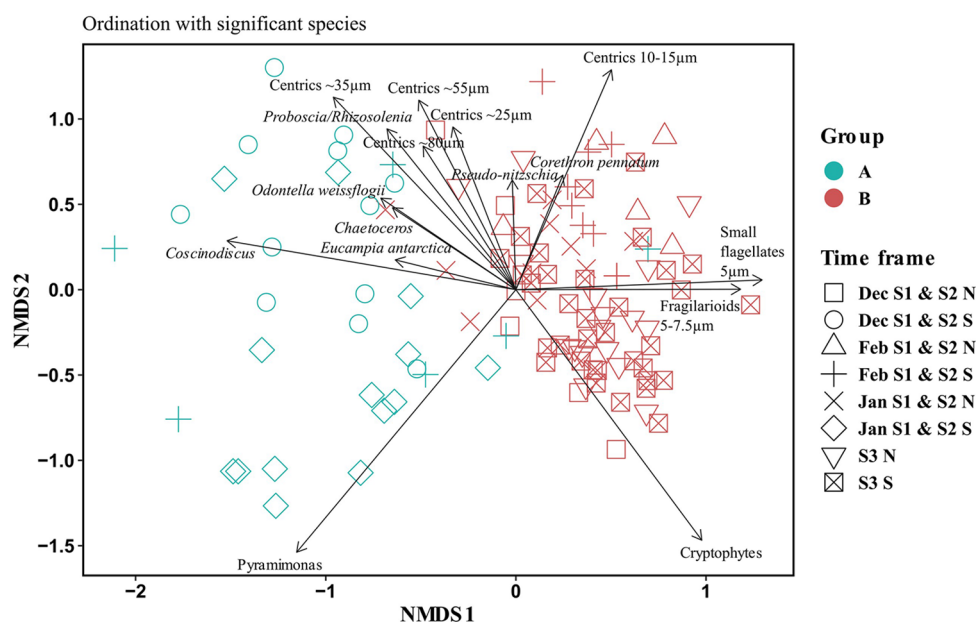


FIGURE 5 Non-metric multidimensional scale analysis (NMDS) based on the Bray-Curtis dissimilarities of the phytoplankton community composition (each taxa represented by their relative contribution to total biomass). The samples are colored according to group (A, light-blue or B, red) and labeled by time frame: Month (if applicable, Dec, Jan, Feb), Season (S1, S2, S3), and area (N, North or S, South). The black arrows show the main taxa that were significant in the statistical analysis. ANOSIM $R = 0.7$, $p < 0.001$.

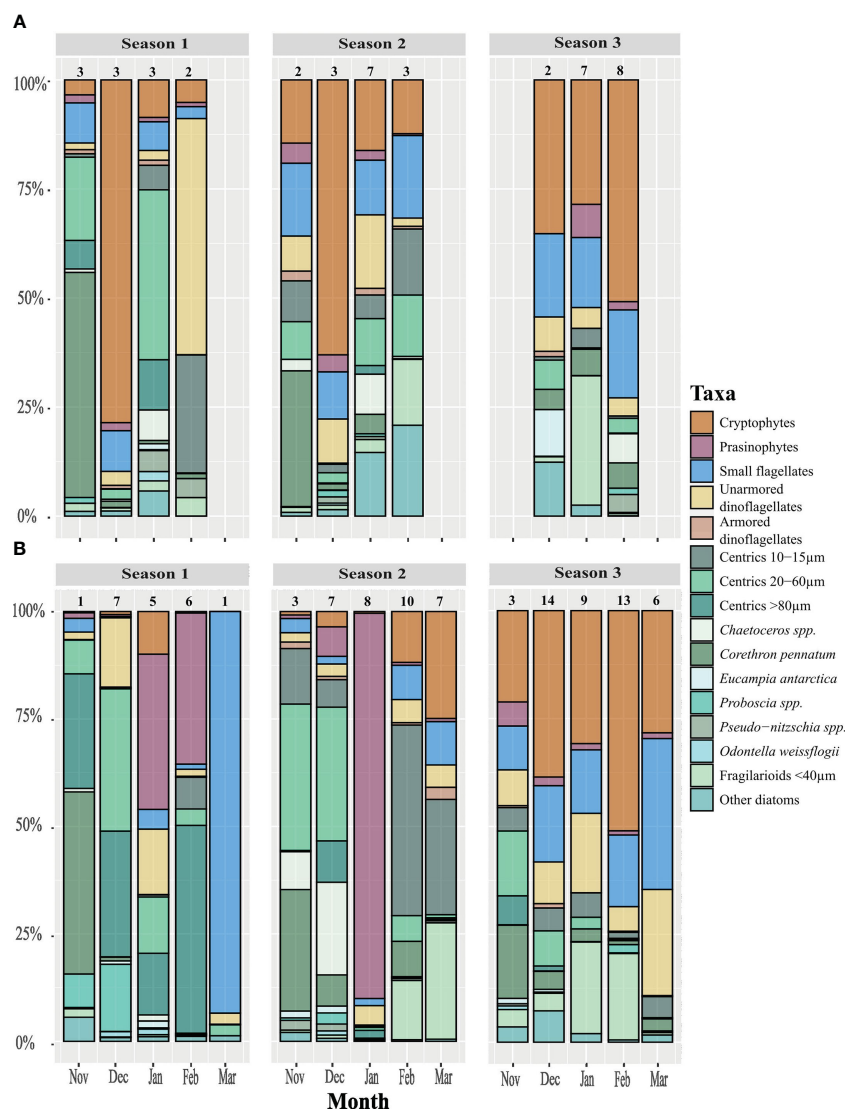


FIGURE 6
 Bar plot of relative biomass specific composition of representative taxa in (A) North and (B) South zones of the Gerlache Strait from November to March 2016–2017, 2017–2018, and 2018–2019. This graph was constructed by averaging the samples obtained in each zone during that month and season, the n of the averaged samples can be seen above each bar. Note that this is a percentage graph and that the changes in biomass are relative. All diatoms are colored in shades of green.

Between December and February during S1 and S2, phytoplankton composition differed to the north and south of the thermal front in the Gerlache Strait (Figure 6). In the northern sites during December, the phytoplankton community was dominated by cryptophytes (Figure 6). During January, the diatoms were the most important group, in particular, centrics between 20 and 60 μm (e.g., *Actinocyclus actinochilus*, *Thalassiosira* spp., *Porosira* spp.), and *Chaetoceros* spp. During February, small diatoms dominated, small centrics (*Thalassiosira* spp.) and small fragilarioids (e.g., *Fragilariopsis nana*), and particularly during S2 small naked dinoflagellates were also important.

In the southern areas, during December the phytoplankton community was dominated by diatoms. Centric diatoms between 20 and 60 μm dominated both years, followed by large centrics (>80 μm, *Coscinodiscus* spp.), *Proboscia* sp., and *Odontella weissflogii*

during S1, and *Chaetoceros* spp. on S2. During January, prasinophytes from the genus *Pyramimonas* dominated. In February during S1, prasinophytes were also accompanied by large centric diatoms, however during S2 the composition was similar to the northern areas' composition, there was an absence of prasinophytes with a dominance of small fragilarioid and small centric diatoms. During March, the phytoplankton community was similar during the three seasons, dominated by small flagellates, followed by cryptophytes, small centric diatoms <15 μm, fragilarioid diatoms <40 μm, and small naked dinoflagellates (Figure 6).

S3 showed a different successional pattern than previous seasons since phytoplankton composition was similar between both areas and months (Figure 6). Cryptophytes dominated during the entire period, followed by small fragilarioid and small

centric diatoms (10–15 μm), *Chaetoceros* spp., *Corethron pennatum*, and small flagellates.

4 Discussion

4.1 Gerlache Strait physical oceanographic features influence on the nearshore waters' phytoplankton community

During the summer months in surface waters of the Gerlache Strait a thermal gradient is usually established, with warmer waters to the north and cold waters to the south, towards Bismarck Strait. When analyzing satellite data from summers in a decade (2011–2021), we found that the temperature gradient was noticeable during the summer months from December to February, with the greatest temperature differences in January, reaching up to 1°C. We consider this gradient to be the manifestation of a thermal front previously reported in the Gerlache Strait around 64.5° S (García et al., 2002; Kerr et al., 2018; Torres Parra et al., 2020). SST in the sites of phytoplankton sampling, measured *in situ* (see Supplementary Table 1 and Supplementary Figure 1) also showed a temperature gradient between northern and southern sites, where the temperature in the nearshore sites was related to the SST detected by satellites in the Gerlache Strait (Supplementary Table 3). During the three seasons sampled, differences were also detected in our SST observations from month to month, suggesting an interannual variation in the moment of establishment of the gradient. Likewise, Torres Parra et al. (2020) found two different scenarios (February 2015 and February 2017), a first year with a more defined front, and a second year when it was less defined. However, in both scenarios they found differences greater than ~0.5°C in northern and southern Gerlache Strait. The differences in temperatures to the north and south found in our study were always greater than 0.5°C from December to February, except for December 2018 (S3), suggesting that the front might have been established later in that summer.

Analysis of the satellite data also detected a cooling pattern during the three summers studied that would be related to an extreme El Niño event in 2015. The anomalous temperatures recorded during the 2016–2017 summer were probably given by a strong El Niño that started in April/May 2015, lasted until May 2016 and followed by a weak La Niña (Stuecker et al., 2017). Locally, in the Gerlache Sound, Torres Parra et al. (2020) suggested that the elevated temperatures observed during 2016–2017 were probably caused by the inflow of warm water from the north, resulting from northeasterly surface winds around the northern Antarctic Peninsula, forced by a negative phase of the Southern Annular Mode (SAM) that came after the 2015 El Niño from October 2016 to March 2017. Several studies have highlighted the effects of this extraordinary El Niño event during 2015 in Antarctica on water temperature, winds, sea ice retreat, among other factors, ultimately affecting phytoplankton (Costa et al., 2021; Meredith et al., 2021; Trifoglio et al., 2022). While the long-term effects of this event are still being understood, this event would likely explain the high temperatures recorded in the study area in our first summer.

The results of this work suggest that the close relationship of adjacent nearshore areas may be due to processes occurring in the open waters of the Gerlache Strait. Although we were not able to sample in the Strait, the high similarity in phytoplankton composition found in adjacent nearshore areas that may be up to 40 km apart suggests a high connection of the surrounding surface waters and the main Strait. The waters of the Gerlache Strait are characterized by long residence times that can range from weeks to months and it is estimated that within coastal areas this residence time may be longer (Zhou et al., 2002), which may explain this interconnectedness between coastal areas and the long persistence of phytoplankton assemblages. Studies from Andvord Bay can explain the interconnectedness between the Strait and the coastal areas affecting inshore phytoplankton assemblages (Ekern, 2017; Lundesgaard et al., 2019; Hahn-Woernle et al., 2020; Lundesgaard et al., 2020; Ziegler et al., 2020; Forsch et al., 2021). Modeling by Hahn-Woernle et al. (2020) found a significant exchange of surface waters between Andvord Bay and the Gerlache Strait, which causes the fjord to lose or gain heat, mainly driven by winds. In addition, both planktonic organisms (larvae), chlorophyll *a*, and macro- and micronutrients originating within the fjords can be exported to the Gerlache Strait within a month, an exchange strongly enhanced by recurrent katabatic winds (Ekern, 2017; Ziegler et al., 2020; Forsch et al., 2021). Similar processes have been reported for Arthur Harbor in Anvers Island and Southeast Greenland, suggesting wind-driven exchange of surface waters is a common process in high-latitude nearshore areas (Moline and Prezelin, 1996; Spall et al., 2017). As winds affect primarily surface waters, analysis of surface waters can be considered the most sensitive way to detect the effect of the thermal front in phytoplankton composition. In this way, results from this study provide more in-depth information on the exchange of phytoplankton between surface waters of the fjords and embayments and the Gerlache Strait, which are still poorly understood (Ferreira et al., 2020).

Our results suggest that there is a relationship between the phytoplankton composition and the establishment of the thermal gradient in the Gerlache Strait, as we found that summer phytoplankton composition differed between the sites in the northern and southern Gerlache Strait during S1 and S2. Particularly during December and January, when the highest SST differences and the highest phytoplankton biomass values were observed, the composition were markedly dissimilar north and south. Furthermore, our records can be related to *in situ* SST data in the Gerlache Strait— in February 2017, there was a predominance of prasinophytes in the southern zone, while in the northern zone dinoflagellates dominated, and there is evidence that the front was present during that time (Torres Parra et al., 2020). During other months, as in November, the lack of compositional difference in the northern and southern sites (i.e., the same phytoplankton assemblage was found in both zones), is consistent with similar temperature averages north and south of the Strait (Figures 2, 6). The lack of difference in the third summer in phytoplankton assemblages could be related to the delay in the front's formation during December probably combined with overall lower temperatures. Although with lower temperatures we could have expected the southern assemblage to be dominated by diatoms and

Pyramimonas, other factors, beyond SST and the presence of the front in the Gerlache Strait, not measured in this study, are expected to have influenced the phytoplankton composition during S3.

Spatial variability in phytoplankton composition of the Gerlache Strait has been recorded over 30 years ago. Vernet (1992) found that during December 1991–January 1992, there were two different assemblages north and south of the Gerlache Strait – with cryptophytes dominating to the north, and diatoms and *Pyramimonas*-like cells to the south – although this author did not relate these differences to any physical phenomenon. During December 1995 and January 1996, Rodriguez et al. (2002) found two different assemblages north and south of the Gerlache Strait, also probably affected by the surface front (Anadón and Estrada, 2002). Mendes et al. (2018) found that different phytoplankton assemblages were found north and south of the Strait during February 2013, 2014, and 2015, agreeing with the February results in our study for the nearshore areas (see following section). These previous records also demonstrate that, despite the complexity and seasonal variability of the area, the patterns of spatial phytoplankton distribution seem to occur often, or to be stable and recurrent, summer after summer, suggesting that the observations during S3 are more of an anomaly. The results from this study add to previous records in the literature and are consistent with the concept of frontal zones co-occurring with changes in biological community composition (Acha et al., 2015). Furthermore, this work extends the influence of physical features in coastal embayments and fjords. In addition, Giraldo et al. (2019) found two different copepod

assemblages in the northern and southern Gerlache Strait, meaning the frontal area may have several implications for the rest of the food web.

4.2 Summer phytoplankton succession in northern vs southern coastal areas

Our analysis of three consecutive seasons from November to March allowed us to assess the phytoplankton succession during late spring through the duration of the austral summer in surface waters. Like other studies that have evaluated the phytoplankton composition for several consecutive years in coastal areas of the WAP, we found a high interannual variability (Garibotti et al., 2005; Rozema et al., 2017; Kim et al., 2018). Nevertheless, we observed a consistent pattern in phytoplankton community succession between the first two seasons. Based on results from the first two seasons, we propose two different successional patterns in the surface waters of the nearshore areas in northern and southern Gerlache Strait (Figure 7).

Underlying any successional patterns observed in the seasons, months, and locations sampled, there is a basic assemblage composed by small unidentified flagellates, cryptophytes, small naked dinoflagellates, small prasinophytes, haptophytes, and small fragilarioid and naviculoid diatoms (Figure 7, in brown). These phytoplankton taxa were repeatedly found in low abundance in all the samples analyzed, accompanying the dominant taxa, if present.

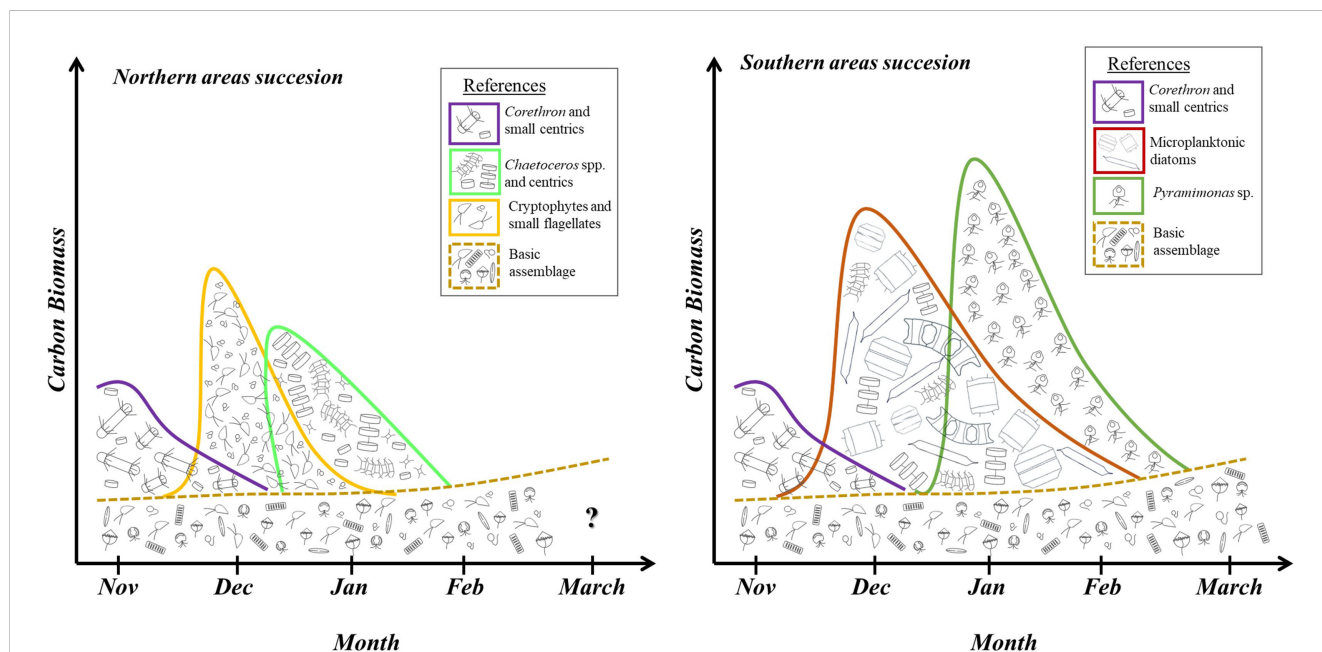


FIGURE 7

Conceptual model diagram illustrating the phytoplankton summer succession from November to March in northern and southern areas of the Gerlache Strait during seasons 1 and 2, constructed from the average of the biomass data found in the northern and southern areas for each season. The main assemblages described here are: 1) an assemblage composed of *Corethron pennatum* and small centric diatoms < 15 μm (in violet); 2) an assemblage of medium-size centric diatoms between 20 and 60 μm (e.g. *Actinocyclus actinochilus*, *Thalassiosira* spp., *Porosira* spp.) and *Chaetoceros* spp. (in light green); 3) an assemblage dominated by cryptophytes and small flagellates (in orange); 4) a basic assemblage composed by small unidentified flagellates, cryptophytes, small naked dinoflagellates, small prasinophytes, haptophytes, and small fragilarioid and naviculoid diatoms (in brown); 5) an assemblage composed of large microplanktonic diatoms (e.g. *Odontella weissflogii*; *Proboscia* spp., *Eucampia antarctica*, *Coscinodiscus bouveti*) (in red); 6) an assemblage dominated by prasinophytes from the genus *Pyramimonas* (in green).

This 'basic' assemblage forms the background in which different assemblages are immersed and transition over time. The basic composition is observed during periods of low biomass, like November and March. This concept agrees with several studies in the WAP that mention the nanoplankton dominates the basic phytoplankton composition, particularly evidenced during autumn and winter months (Garibotti et al., 2005; Clarke et al., 2008; Annett et al., 2010; Rozema et al., 2017; Mascioni et al., 2021). In addition, previous studies in one of the sampled sites, in a WAP fjord (Neko Harbor in Andvord Bay) describe a similar assemblage during a period with low productivity during autumn, but also present during late spring (Mascioni et al., 2019; Pan et al., 2020; Mascioni et al., 2021).

In accordance with the results from three seasons, the phytoplankton community at the end of November, both in northern and southern Gerlache Strait, is mainly represented by a mix of *Corethron pennatum* and small centric diatoms < 15 μm (Figure 7, in violet), together with the basic assemblage. This coincides with other studies that record *Corethron pennatum* as an important diatom at the beginning of the season, e.g., in King George Island's embayment at the northern Antarctic Peninsula (Lange et al., 2018); however, in WAP coastal southern areas near Marguerite Bay, *C. pennatum* seems to be an uncommon species during spring months (Annett et al., 2010). This species, apart from dominating the November assemblage in the nearshore waters of the Gerlache Strait, is a well-known component of the phytoplankton community throughout the summer on the WAP continental shelf (Garibotti et al., 2005).

After November, the successional patterns to the north and south of the thermal front differ (Figure 7). In the northern areas during December, there is an assemblage dominated by cryptophytes and small flagellates (orange). Then, during January, there is an assemblage dominated by *Chaetoceros* spp. and centric diatoms < 50 μm (light green, Figure 7). Towards the end of the summer season, during the month of February, the composition is similar to January but there is a clear decrease in total carbon biomass. By contrast, in the southern areas, during December, the phytoplankton assemblage is dominated by microplanktonic diatoms, such as *Odontella weissfloggii*, *Proboscia* spp., *Eucampia antarctica*, *Coscinodiscus* spp., *Thalassiosira* spp., *Porosira* spp., and *Chaetoceros* spp. among others (Figure 7 in red). During mid-summer season, in January develops an assemblage dominated by *Pyramimonas* sp. that stays until late February. In late summer/early autumn, around March, the basic assemblage is dominant (Figure 7, in brown) and enriched in small fragilarioid and naviculoid diatoms, with low biomass. We were not able to sample during March in the northern areas, however, as the thermal gradient is not present during March (Figure 3), we predict a similar assemblage may be present in the northern areas as well as a biomass decline due to the reduction of light availability (Vernet et al., 2012).

Studies evaluating phytoplankton succession in this area are scarce. Pan et al. (2020) suggested a phytoplankton succession for Andvord Bay, a fjord located in the southern Gerlache Strait, in relation to glacial meltwater and nutrient supply. The succession

pattern we propose for the southern areas is similar, although the authors suggested that the diatom bloom would occur in January-February, and we observed it earlier, during December-January. In these WAP coastal areas, assemblages can be sustained for extended periods of time, so an incipient diatom assemblage during the month of December could well have spread and remained stable until February, having a peak in January (Costa et al., 2020; Mascioni et al., 2021). Pan et al. (2020) also found low prasinophyte abundance during January-February, likely due to *Pyramimonas* appearing only in late February that summer (Mascioni et al., 2019), probably delayed by the substantial diatom bloom that took place in the area during January-February (Costa et al., 2020).

The lack of other studies on successional patterns for the area highlights the importance of this first description that can be considered foundational to future studies. Further studies relating the phytoplankton composition with environmental variables, in consecutive years, and even in other coastal areas related to the Gerlache Strait, would help to better understand the patterns here described. The collection of data from IAATO vessels preclude any complex filtration or storage system, limiting the type and number of variables that can be collected, as well as the depths sampled. This limitation is balanced by the ability to generate a time series during the phytoplankton growth season (Cusick et al., 2020). Future studies involving sampling throughout the euphotic zone could test whether the models presented in Figure 7 for surface waters apply to the rest of the water column. There is evidence that in nearshore waters of the WAP the upper layer is well mixed due to the recurrent presence of katabatic winds (Supplementary Figure 1; Vernet et al., 2012; Christensen, 2017; Ekern, 2017; Höfer et al., 2019; Pan et al., 2019; Pan et al., 2020). Moreover, in one of the sampled fjords, Mascioni et al. (2021) demonstrated that the phytoplankton composition was similar throughout the euphotic zone. In this context, our results could be potentially applicable to the upper mixed layer.

Our conceptual model has little or no overlap with other successional patterns that have been suggested in the literature. To the southernmost region of the WAP, van Leeuwe et al. (2020) suggested a phytoplankton succession for Rothera station by evaluating five consecutive years of sampling. Here, microplanktonic diatoms play a key role forming two diatom blooms, one when the sea ice breaks up in November-December, and one in late summer, February-March. Garibotti et al. (2005) suggested a successional pattern for the WAP continental shelf extending from southern Anvers Island to Marguerite Bay but did not include nearshore areas. These authors suggested that the successional patterns were closely related to sea ice retreat and that the variability in the timing of sea ice retreat influenced the interannual differences observed. At the beginning of the season, they found a diatom bloom associated with the sea ice edge together with *Phaeocystis*, followed by assemblages enriched with cryptophytes, and at the end of the season an assemblage dominated by unidentified phytoflagellates and small-sized diatoms. In comparison with our pattern, we did not find diatom blooms at the beginning of the season in the three years sampled, and although cryptophytes were important north of

the Gerlache Strait, they were less important to the south where prasinophytes dominated.

In addition to the successional patterns, in the WAP some studies have also evaluated what happens in high vs low biomass summers. Garibotti et al. (2005) suggested that low biomass summers, with sampling constraint to January, are dominated by cryptophytes and high biomass summers are dominated by diatoms. In Marguerite Bay, Rozema et al. (2017) similarly suggested that low biomass summers are dominated by cryptophytes and chlorophytes and high and medium biomass summers are dominated by diatoms. We also observed biomass variability during our sampling period, with high biomass during the first two seasons (maximum of 1.7×10^4 cells L^{-1} and $804.6 \mu g C L^{-1}$ respectively) and a S3 with low biomass (maximum of $42.3 \mu g C L^{-1}$). In this study, high biomass was associated with a clear successional pattern, while the third season, with low biomass, did not present a successional pattern and was dominated by a nanoflagellate- and small diatoms-assemblage. However, the dominance by diatoms in the sampled nearshore areas was not as clear as in those other studies; moreover, in the northern zone, cryptophytes dominated most of the time with the exception of January. Therefore, we consider that our conceptual model explains the phytoplankton succession in surface waters of the coastal areas of the Gerlache Strait between 64° and 65° S during years with high biomass, when microplanktonic diatoms are more abundant in the southern part of the Strait.

4.3 Diatoms vs nanoflagellates in coastal ecosystems

Our results suggest that the surface waters of the coastal areas of the Gerlache Strait are dominated by nanoflagellates, and diatoms, although present and ubiquitous, not always dominate. Different nanoflagellate taxa form important blooms during the summer months, making large contributions to carbon biomass. Further south, in Marguerite Bay Rozema et al. (2017) observed that, on average, 75% of the chlorophyll-*a* (Chl *a*) stock was comprised to the microphytoplankton fraction of the assemblage sampled. This contrasts markedly with our results, where even in the southern part of the Gerlache Strait – where more diatoms were observed during December to February in our samples – microphytoplankton represented on average only 46% of the total biomass. Although we cannot know what happened in the rest of the water column, the records in the literature of diatom blooms in the Gerlache Strait are rather scarce, with only two large diatom blooms recorded in the last 30 years (Holm-Hansen and Vernet, 1990; and Costa et al., 2020, see Mascioni et al., 2019 Table 3). Costa et al. (2021) mention these blooms would be more the exception than the rule and probably become more and more rare in the upcoming years.

As suggested by Costa et al. (2021) the low sea ice conditions could be a major deterrent of large diatom blooms in WAP, which is consistent with our observations in the field between 2016 and 2019. The marked decrease in sea ice extent in the WAP in the last three decades has been more noticeable in the central and northern WAP

(Stammerjohn et al., 2008; Meredith et al., 2021). If this trend of sea ice retreat continues, we might expect diatom blooms to become increasingly infrequent (Costa et al., 2021a) and blooms of other flagellates such as cryptophytes to remain recurrent. However, there is not enough evidence that the recurrence of the flagellate blooms are increasing. Our observations show that a large bloom of cryptophytes -that can last several days/weeks- repeatedly occurs in surface waters during summer related to higher temperatures north of the Gerlache Strait, a phenomenon that has been commonly observed in the area for the last 30 years (Vernet, 1992; Rodriguez et al., 2002; Mendes et al., 2013; Mascioni et al., 2019; Mascioni et al., 2021). It has recently been proposed that the cryptophytes that form these blooms would be a novel species endemic of WAP waters (Hamilton et al., 2021).

Alongside cryptophytes, prasinophytes blooms seem to be a persistent phenomenon in the southern part of the Gerlache Strait (Vernet, 1992; Rodriguez et al., 2002; Mascioni et al., 2019). Prasinophytes made important contribution to the phytoplankton biomass during January-March in the surface waters of the southern part of the Gerlache Strait. Particularly, in January S2, a bloom of *Pyramimonas* sp. (Prasinophyte) took place in the southern area, with the highest peak of abundance and biomass in Paradise Bay. The first known record of a *Pyramimonas* bloom was north of the Gerlache Strait in 1987 (Bird and Karl, 1991); however, in 1996 (10 years later), Rodriguez et al. (2002) found it south of the Gerlache, as in this study and in 2015 (Mascioni et al., 2019). We have no record of these prasinophytes at northern stations, suggesting that these flagellates may be adapted to lower temperatures, although *Pyramimonas* do not seem to be important south of the WAP (Garibotti et al., 2003; Rozema et al., 2017; Mascioni et al., 2019; van Leeuwe et al., 2020). It is also noteworthy that the bloom forming *Pyramimonas* species is still unknown, and although it is suggested that it could be *Pyramimonas* cf. *gelidicola* its morphological characteristics do not agree with that species and its distribution suggests something rather endemic, although more studies in the subject would be necessary (Mascioni et al., 2019).

Diatoms are an important component in the surface waters of the southern area of the Gerlache Strait, but they do not reach high biomass values. During S2, as happened in S1, we did not find a large microplanktonic diatom bloom. However, we did find a *Chaetoceros* spp. bloom during December 2017 S2 in Neko Harbor (up to 3.9×10^6 cells L^{-1} and $146 \mu g C L^{-1}$), although the biomass in this bloom did not reach previous values recorded for WAP diatom blooms, e.g., 2.1×10^6 cells L^{-1} and $1,563 \mu g C L^{-1}$ (Garibotti et al., 2003); the lower biomass values are explained due to the small size of the *Chaetoceros* spp. found ($\sim 10 \mu m$, Supplementary Table 2). Garibotti et al. (2005) found that *Chaetoceros socialis* was the characteristic species of the coastal region between Anvers Island and Marguerite Bay, contributing between 29% - 62% of the diatom abundance during 1996, 1997, and 1999 summers. However, due to the small size of this species, it contributed less than 17% of diatom biomass during those summers. Concurrently with our sampling, Höfer et al. (2019) recorded a diatom bloom in a nearby coastal area south of Anvers Island in the South Bay during February 2017. No such bloom was found in our study area during S1 because the surface waters

surrounding Anvers Island do not enter the Gerlache Strait (Zhou et al., 2002).

Despite the absence of large microplanktonic diatom blooms, the Gerlache is a highly productive area. It has already been seen that microplanktonic diatom assemblages in the Gerlache Strait are highly productive with high growth rates (Mandelli and Burkholder, 1966; Isla et al., 2004; Mascioni et al., 2021). Mascioni et al. (2021) recently demonstrated that the diatom assemblage that dominates in the southern Strait is highly productive despite not reaching high biomass values. This assemblage persists in the area for a month (Figure 7) suggesting a highly productive region in the surface waters south of the Gerlache Strait front. The waters of the Gerlache are also important as seed the major blooms in the Bransfield Strait (Basterretxea and Arístegui, 1999). There is a high krill recruitment in the Gerlache Strait, yet krill aggregations are even greater within the nearshore waters than in the Strait (Nowacek et al., 2011; Espinasse et al., 2012; Cleary et al., 2016; Cleary et al., 2018). As krill graze selectively on microplanktonic diatoms, large aggregations of krill could exert high grazing pressure on the microplanktonic diatom assemblages, controlling diatom proliferation and favoring the development of small flagellates' blooms (Cavan et al., 2019).

5 Conclusion

This is the first study to assess phytoplankton composition throughout the entire growth season (November through March) in the surface waters of nearshore areas of the WAP between 64° and 65° S, that based on previous studies are considered representative of communities in the upper mixed layer and the majority of the euphotic zone. Overall, our results suggest that phytoplankton composition and carbon biomass within the surface waters of the nearshore areas of the WAP can be closely related with mesoscale features created by physical oceanographic characteristics, such as a surface thermal front. Winds are suggested by the literature as major players in the surface water exchange between the nearshore areas and the Gerlache Strait. Although we consider the thermal gradient can be a major determinant of the phytoplankton composition in the nearshore areas connected to the Gerlache Strait, there are other known factors that control the phytoplankton community that we did not analyze, such as glacial and sea ice meltwater. Continuing to monitor these areas with the FjordPhyto project, by combining biological and physical measurements in consecutive years is needed to further understand the complex dynamics of the Antarctic phytoplankton community in nearshore areas. These coastal areas are important locations for phytoplankton biomass accumulation during the summer months, especially during December and January in the southern areas of the Gerlache Strait where microplanktonic diatoms and prasinophytes dominate in surface waters. Alongside, cryptophytes form important blooms during the summer months, making large contributions to carbon biomass in surface waters of the region north of the thermal front.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

MM performed all the microscopy analyses. BJP provided the satellite data. AC performed part of the field sampling and trained the polar tour guides to carry on the citizen science project in Antarctica. MM and GA performed all the data analysis. MM, BJP, and MV performed the satellite data analysis. MM, GA, and MV conceptualized the manuscript. All authors contributed to the article 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.2023.1139293/full#supplementary-material>

SUPPLEMENTARY TABLE 1

FjordPhyto phytoplankton sampling stations during seasons 2016–2017, 2017–2018, and 2018–2019.

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