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ECOSYSTEMS

Effects of environmental variability on phytoplankton structure, diversity and biomass at the Brazil-Malvinas Confluence (BMC)

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Abstract: The Brazil-Malvinas Confluence (BMC) is a significant biological frontier where distinct currents meet, fostering optimal conditions for phytoplankton development. In this study we tested the hypothesis that eddys promote an increase in phytoplankton biomass at the Brazil-Malvinas Confluence (BMC), altering species diversity. Phytoplankton were collected with Niskin bottles and nutrient concentrations assessed at two depths (Surface and Deep Chlorophyll Maximum Layer – DCML) in areas outside and under the influence of Cold-Core (CCE) and Warm-Core (WCE) Eddies. Environmental variables were determined *in situ* using a CTD profiler. Four regions were separated based on environmental variables and phytoplankton species, namely, the Brazil Current (BC), Malvinas Current (MC), CCE, and WCE. Species diversity was higher in the eddies. The conditions of the WCE were different from those of the CCE, with low temperature and salinity and high cell density values in the latter. The phylum Bacillariophyta was predominant in terms of species richness in all regions and was responsible for the higher cell density in the MC, while dinoflagellates were dominant in the BC and eddies. Therefore, eddy activity alters the structure, diversity and biomass of the phytoplankton community in the BMC.

Key words: Brazil Current, Malvinas (Falkland) Current, Dinoflagellates, Cold-Core Eddy, Warm-Core Eddy.

INTRODUCTION

The Brazil-Malvinas Confluence (BMC) is the encounter of two currents with distinct physical, chemical and biological characteristics, creating appropriate environmental conditions for the development of phytoplankton (Angel-Benavides et al. 2016). The nutrients provided by the Malvinas (Falkland) Current (MC) promote the development of species from the Brazil Current (BC) whose growth is limited by nutrients, and the BC, in turn, provides the physical stability necessary for the accumulation of biomass in the MC through intrusions (Brandini et al. 2000).

The BMC is an important biological frontier for phytoplanktonic organisms (Gayoso & Podestá 1996), with the presence of species of subtropical (e.g. *Thalassiosira delicatula* and *Lauderia annulata* Cleve) and subantarctic [e.g. *Ceratium lineatum* (Ehrenberg) Cleve and *Corethron criophilum* Castracane] origin (Gayoso & Podestá 1996, Gonçalves-Araújo et al. 2012). The region has one of the highest phytoplankton diversity in the Atlantic Ocean, representing a hotspot, especially for diatoms (Cermeño et al. 2008, Barton et al. 2010). This is due to the wide variety of (spatial and temporal) hydrodynamic features, which allow the formation of niches, in addition to the horizontal barriers of water mixing generated by mesoscale eddies (D'ovidio et al. 2010).

The BMC is also one of the most energetic oceanic areas with intensified instability (Chelton et al. 1990) due to eddy-meandering activities reported in several studies (Campagna et al. 2006, Chelton et al. 1990). According to Karabashev & Evdoshenko (2018), mesoscale activity occurs in the region due to the interaction of currents, the influence of the slope, and the effect of oceanic islands on the MC. The region's productivity is further increased by cyclonic eddies (Angel-Benavides et al. 2016) as it does the influence of the Rio de la Plata estuarine plume (Carreto et al. 2016) and the spring season (Odebrecht & Castello 2001).

In general, the biogeochemistry and primary productivity of the oceans are affected by eddy activity (Dai et al. 2020, Zhang et al. 2019, Zhao et al. 2021). In some regions, eddy activity increases local productivity by up to three times (Chen et al. 2007) through the fertilization of nutrient-limited waters, contributing to the development of phytoplankton by increasing their exposure to light (limiting factor) (Karabashev & Evdoshenko 2018). In these cases, eddies interfere with the availability of nutrients that can increase phytoplankton biomass, favoring the dominance of specific groups or species and leading to lower local diversity (Chen et al. 2007). Other studies have demonstrated that depending on the characteristics of the eddies, they may reduce the primary productivity through nutritional reduction within the feature (Thompson et al. 2007).

Studies conducted in the BMC have evaluated the phytoplankton biomass through chlorophyll *a* (Garcia et al. 2004, Angel-Benavides et al. 2016), but studies focusing on carbon biomass in the region are still necessary because they are fundamental for understanding the biological carbon pump in marine ecosystems and for monitoring phytoplankton (Jakobsen et al. 2015).

The present study investigated the distribution, carbon biomass and diversity patterns of the phytoplankton community during the spring in the BMC region and determined the effects of eddies on this community based on the hypothesis that eddys promote an increase of phytoplankton biomass and alter the species diversity in the BMC.

MATERIALS AND METHODS

Area description

In the South Atlantic Ocean, along the western margin of the Argentina basin, the encounter between the BC and the MC forms a strong thermal front called the “Brazil-Malvinas Confluence” (BMC), usually near the latitude of 38° S (Gordon & Greengrove 1986, Gu et al. 2019). The two currents flow in opposite directions and converge with each other; both are then diverted offshore and flow southeastwards in the form of eddies and meanders (Gordon 1989, Chiessi et al. 2007).

The BC has a subtropical origin (Telesca et al. 2018), is formed at 10° S from the bifurcation of the South Equatorial Current and is characterized by a strong thermocline (up to about 500 m deep) (Garzoli & Garraffo 1989) and southward-flowing warm and saline waters with low nutrient and oxygen concentrations (Chiessi et al. 2007, Orúe-Echevarría et al. 2021). This current collides with the MC, which is a northward branch of the Antarctic circumpolar current of cold nutrient-rich waters (Telesca et al. 2018, Orúe-Echevarría et al. 2021) and homogeneous vertical profile (Garzoli & Garraffo 1989).

At this confluence, a complex vertical thermohaline structure is formed by the intercalation of water masses, with distinct temperatures and salinities (Bianchi et al. 2002), promoting large variability in surface temperature (7 to 18 °C) and salinity (33.6 to 36.0) (Gordon 1989). Furthermore, intense eddy activity allied with the nutrient input from the estuary of the Río de la Plata and the Patos Lagoon (Odebrecht & Castello 2001, Garcia et al. 2004) contribute to water fertilization and consequent enhanced local primary productivity (Barlow et al. 2002, Angel-Benavides et al. 2016).

Sampling strategy

This study was conducted aboard the Polar Vessel Almirante Maximiano. Collections were carried out at the BMC (between range 38° S - 45° S) during spring (October 2019). A total of 11 sampling stations (Table I and Figure 1) were established *in situ* in two areas of the BMC, the first outside and the second under the influence of eddies. These locations were determined by observing the daily position of the eddies using remote sensing. (OISST: Optimum Interpolation SST; Altimetria da SSHA: Sea Surface Height Anomalies). Thus, a transect was defined capturing the eddies (Cold and Warm) and the representative stations of BC and MC.

In the first area, samples were taken at 4 stations (BC1, BC2, MC1 and MC2), and in the second area at 7 stations: 3 in a Warm-Core Eddy (WCE) (WCE1, WCE2 and WCE3), and 4 in a Cold-Core Eddy (CCE) (CCE1, CCE2, CCE3 and CCE4). In all stations, sampling was performed at two depths: at the Surface (~2m) and at the Deep Chlorophyll Maximum Layer (DCML).

Environmental variables

Vertical profiles of temperature (°C), salinity, conductivity (ms cm^{-1}) and dissolved oxygen (mL L^{-1}) were determined using a CTD. The transparency of the water was verified *in situ* through the disappearance of the Secchi disk. Water samples collected with Niskin bottles were used for nutrient and dissolved oxygen analyses (mg L^{-1}). Nitrite values were obtained by the method of Strickland & Parsons (1972) and phosphate concentrations by the standard colorimetric method of Grasshoff (1983).

Table I. Environmental parameters (Latitude, Longitude, Temperature, Salinity, Dissolved Oxygen, Phosphate and Nitrite) evaluated at each depth (SURF = Surface and DCML= Deep Chlorophyll Maximum Layer) of the stations analyzed in the Brazilian Current (BC1 and BC2), Malvinas Current (MC1 and MC2), Cold Core Eddy (CCE1, CCE2, CCE3 and CCE4) and Warm Core Eddy (WCE1, WCE2 and WCE3).

Spring period - October 2019																					
Region	**Brazil Current (BC)**				**Malvines Current (MC)**				**Cold Core Eddy (CCE)**								**Warm Core Eddy (WCE)**				
Sampling Points	**BC1**		**BC2**		**MC1**		**MC2**		**CCE1**		**CCE2**		**CCE3**		**CCE4**		**WCE1**		**WCE2**		**WCE3**
Depth	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**
Latitude	38°13”436’ S		38°27”436’ S		39°32”877’ S		39°58”973’ S		43°26”491’ S		44°52”707’ S		45°04”060’ S		45°12”869’ S		43°58”114’ S		44°15”917’ S		44°37”312’ S
Longitude	52°34”361’ W		52°53”460’ W		54°23”460’ W		54°59”702’ W		53°36”732’ W		51°46”273 W		51°28”846’ W		51°09”030’ W		53°08”806’ W		52°42”270’ W		52°09”394’ W
Temperature (°c)	16.83	15.64	15.66	15.51	6.67	6.11	6.79	5.9	9.71	9.48	9.71	9.49	8.02	7.77	9.94	10.28	14.19	14.19	14.11	14.11	11.77
Salinity	33.25	35.59	35.59	35.56	34.09	34.08	34.07	34.08	34.11	34.14	34.62	34.63	34.26	34.28	34.72	34.81	35.67	35.67	35.64	35.64	34.72
Dissolved Oxygen (ml.L^{-1})	5.54	5.59	5.59	5.6	6.85	6.94	6.83	6.97	6.39	6.42	6.37	6.4	6.63	6.67	6.33	6.28	5.75	5.75	5.76	5.76	6.08
Phosphate (μmol L^{-1})	0.3	0.63	0.64	0.18	1.13	0.95	1.16	1.16	0.73	0.85	0.93	1.37	0.98	0	0.67	0.76	0.17	0.7	0.68	0.73	0.67
Nitrite (μmol L^{-1})	0.28	0.23	0.5	0.29	0.25	0.26	0.22	0.32	0.25	0.2	0.32	0.48	0.28	0.4	0.3	0.32	0.22	0.25	0.2	0.15	0.23

Phytoplankton community

The phytoplankton community was collected at each sampled depth (Surface and DCML) with the aid of Niskin bottles attached to rosettes. After sampling, two liters of seawater were concentrated using 5μm membranes (without using a pump to avoid phytoplankton cells damage), put in dark bottles (60 mL) with filtered water (0.45 μm), and fixed in lugol (2%). In the laboratory, the samples were identified using specialized literature (Cupp 1943, Hustedt 1966, Sournia 1978, Balech 1988, Chrétiennot-Dinet et al. 1990, Silva-Cunha & Eskinazi-Leça 1990, Tomas 1997, Bérard-Therriault et al. 1999, Hoppenrath et al. 2009, Moura-Falcão et al. 2022) and cell density (Cel.L^{-1}) (Ferrario et al. 1995) was determined according to the Utermöhl method (Utermöhl 1958), by counting a transect in 50-mL sedimentation chambers on an Axiovert 40 C Carl Zeiss inverted microscope at 450 x (Hasle 1978, Edler 1979).

Richness corresponded to the number of taxa per sample. According to the relative abundance estimated for phytoplanktonic organisms, the species were classified as Dominant, Abundant, and Rare (Lobo & Leighton 1986). The frequency of occurrence of organisms was categorized into: VF - Very Frequent (> 70%), F - Frequent (70 - 40%), I - Infrequent (40 - 20%), and S - Sporadic (< 20%). The Equitability (J') and Specific Diversity Index (H') were calculated according to Pielou (1967) and Shannon (1948),

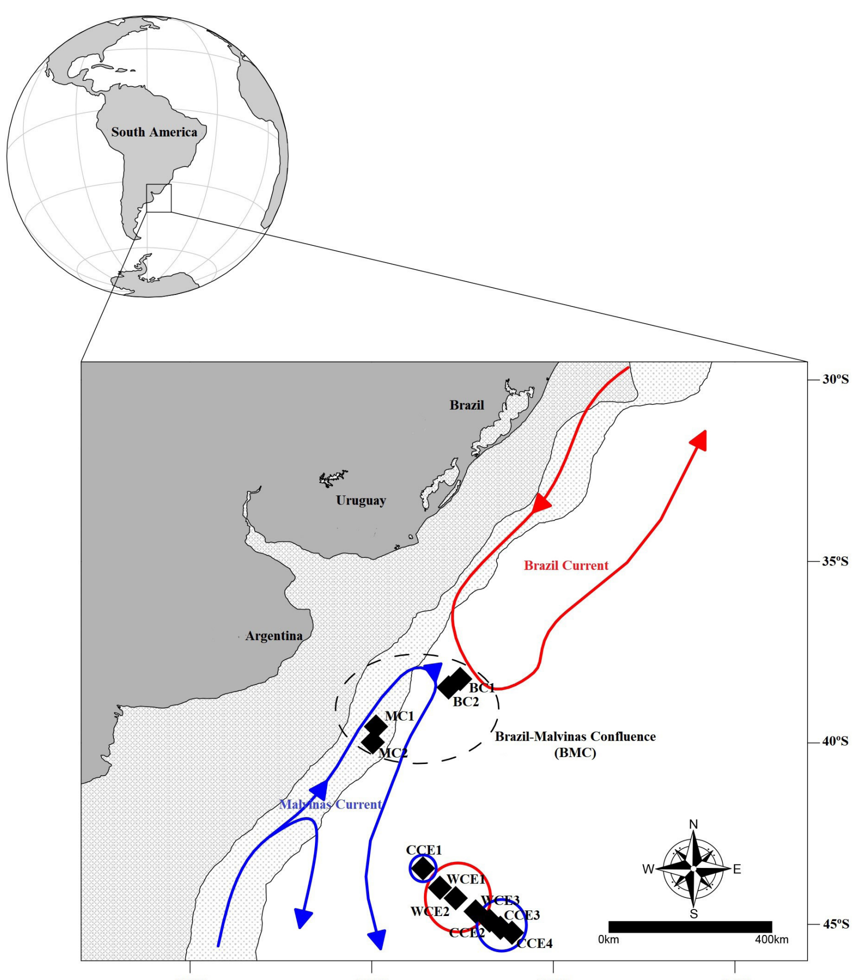

Figure 1. Distribution of sampling points in the Brazil Current (BC1 and BC2), Malvinas Current (MC1 and MC2), Cold-Core Eddy (CCE1, CCE2, CCE3 and CCE4) and Warm-Core Eddy (WCE1, WCE2, WCE3).

respectively. Finally, the sample points were classified as presenting High (5 - 2.5 bits.cel^{-1}), Low (2.5 - 1bits.cel^{-1}), and Very Low (< bits.cel^{-1}) diversity (Margalef 1958).

The six most representative species in terms of relative abundance (Dominant and Abundant species) and frequency (Very Frequent and Frequent) not forming colonies were used for the calculation of cell biovolume (mm^3.L^{-1}), according to the specific formulas for each geometric form and based on the linear dimensions (microscopic measurements) of the phytoplankton species (Hillebrand et al. 1999, Sun & Liu 2003, Vadrucci et al. 2007) and subsequently converted into carbon biomass (pgC.L^{-1}). Twenty cells of each species in the Brazil Current (BC), Malvinas Current (MC), and the Cold-Core Eddy (CCE) were measured to obtain the average cell biovolume (mm^3.L^{-1}) and biomass. This criterion was used to obtain consistent values for statistical analysis.

Data analysis

Phytoplankton abundance, carbon biomass and environmental variables were tested for normality and homocedasticity in the software Sigmaplot (Version: 14). To assess the variability between sampling areas a one-factor ANOVA was applied to test differences in temperature, salinity, dissolved oxygen, phosphate, nitrite, density and carbon biomass values. To test groupings of the phytoplankton community within the sampling areas fourth root transformed species abundance values were used to calculate the Bray-Curtis similarity between samples. This matrix was then subjected to a cluster analysis (average linkage) in the PRIMER 6 statistical program (Version 6.1.6).

Indicator value analysis (IndVal) was performed to select the indicator species (depths and regions), and a Canonical Analysis of Principal Coordinates (CAP) was generated to analyze the patterns of distribution of the dominant and abundant species (occurrence greater than the average value of the individuals sampled) related to environmental variables (temperature, salinity, dissolved oxygen, phosphate, nitrite) in each area. The ANOVA and CAP analyses were performed in R using the Vegan package (Version: 2.5-7) (R Core Team 2019) and PRIMER 6, respectively.

RESULTS

Abiotic factors

The BC was characterized by high temperature values and salinity levels (mean values of 15.91 °C and 35.00) and low dissolved oxygen concentration (5.54 to 5.60 ml.L^{-1}) (Table I). In contrast, the MC had the lowest temperature (6.37 °C) and salinity (34.08) values and high dissolved oxygen concentration (6.83 to 6.97 ml.L^{-1}) (Table I). The MC also presented higher phosphate contents (above 0.95 µmol L^{-1}) compared to the warm regions (BC and WCE) (ANOVA; $p > 0.05$), especially on the surface. High nitrite levels (0.26 and 0.32 µmol L^{-1}) were also recorded in the DCML of the MC (Table I).

The mean temperature, salinity and dissolved oxygen values in the WCE were 13.68 °C, 35.48 and 5.82 ml.L^{-1}, respectively (Table I). Toward the center of the feature, there was an increase in phosphate concentration between 0.68 µmol L^{-1} (WCE2-SURF) and 0.73 µmol L^{-1} (WCE2- DCML) and a reduction in nitrite concentration between 0.20 µmol L^{-1} (WCE2-SURF) and 0.15 µmol L^{-1} (WCE2- DCML) (Table I). In turn, the CCE exhibited mean temperature and salinity values of 9.30 °C and 34.45, respectively. Dissolved oxygen concentrations within this eddy varied between 6.28 and 6.67 ml.L^{-1}, similar to the concentrations in the MC (Table I).

Finally, temperature, dissolved oxygen and phosphate concentration values in the BC differed from those in the MC and the CCE, as well as values in the WCE differed from those in the MC (ANOVA; $p < 0.05$). Salinity was different only between the BC and MC, while nitrite values were not significantly different among regions (ANOVA; $p > 0.05$).

Phytoplankton community

Sixty-two taxa were identified. Bacillariophyta (32 spp. = 52%) stood out among the phyla, followed by Miozoa (25 spp. = 40%), Ochrophyta (3 spp. = 5%), and Haptophyta (2 spp. = 3%) (Table II). Among the identified species, only 13% were very frequent (VF): the pennate diatoms *Fragilariopsis kerguelensis* (O'Meara) Hustedt, *Nitzschia longissima* (Brébisson) Ralfs, and *Thalassionema nitzschioides* (Grunow) Mereschkowsky; the centric diatom *Minidiscus* sp.; and the dinoflagellates *Azadinium* sp., *Karlodinium* sp., *Prorocentrum dentatum* F.Stein, and *Oxytoxum gracile* Schiller (Table II and Figure 2). The community also had frequent (16%), infrequent (39%), and sporadic (32%) species.

Based on the Bray-Curtis similarity matrix, samples clustered in relatively good agreement with the four groups previously defined by physical parameters (BC, MC, WCE, and CCE; Figure 3). In terms of species richness, the MC differed from the BC (ANOVA; $p = 0.008$) and WCE (ANOVA; $p = 0.010$) regions. No differences were found between the BC and the WCE (ANOVA; $p = 0.986$), between the MC and the CCE (ANOVA; $p = 0.113$), and between the WCE and CCE (ANOVA; $p = 0.366$). In the indicator value analysis (IndVal), nineteen indicator species of either the DCML, BC, MC, WCE or cold regions (MC and CCE) were identified (Table III).

Species diversity was classified as low in the BC (between 1.69 and 2.08 bits.cel^{-1}) and MC (between 1.87 and 2.45 bits.cel^{-1}). However, higher diversity values were observed within the eddies, with the exception of some points distributed at the edges of the features (Table II).

Cell density, relative abundance and carbon biomass

Cell density in the studied area ranged from 928 x 10^5 cel.L $^{-1}$ (WCE) to 93,213 x 10^5 cel.L $^{-1}$ (CCE). Regarding the density values of each phylum by depth, dinoflagellates were more representative in the BC and in eddies (Surface and DCML), and diatoms in the MC (Surface and DCML) (Figure 4). The phylum Ochrophyta occurred in the DCML of the WCE and the phylum Haptophyta occurred exclusively in the DCML of the MC. The density of the organisms was significantly reduced in the WCE compared to the BMC (BC and MC) (ANOVA; $p < 0.02$) (Figure 4), and the CCE presented the highest density values, but no significant differences were observed (ANOVA; $p > 0.05$). No significant differences between the surface and DCML regions studied were observed either (ANOVA; $p > 0.05$).

In the BC, higher density values were found for *Karlodinium* sp. (17,377 x 10^5 cel.L $^{-1}$), *P. dentatum* (7,065 x 10^5 ccel.L $^{-1}$), *P. minimum* (2,137 x 10^5 cel.L $^{-1}$), *Azadinium* sp. (2,108 x 10^5 cel.L $^{-1}$), *O. graciles* (1,886 x 10^5 cel.L $^{-1}$), and *Minidiscus* sp. (1,694 x 10^5 cel.L $^{-1}$). In the MC, the higher values were observed for the diatoms *Minidiscus* sp. (29,630 x 10^5 cel.L $^{-1}$), *Pseudo-nitzschia* cf. *pungens* (Grunow ex Cleve) Hasle (21,765 x 10^5 cel.L $^{-1}$), *F. kerguelensis* (4,293 x 10^5 cel.L $^{-1}$), and *Porosira glacialis* (Grunow) Jørgensen (1,405 x 10^5 cel.L $^{-1}$), and the haptophyta *Phaeocystis* cf. *globosa* Scherffel (1,001 x 10^5 cel/L).

In the CCE, *Minidiscus* sp. (14,170 x 10^5 cel.L $^{-1}$), *Azadinium* sp. (13,246 x 10^5 cel/L), *O. graciles* (10,704 x 10^5 cel.L $^{-1}$), *P. minimum* (8,962 x 10^5 cel.L $^{-1}$), and *Karlodinium* sp. (1,78 x 10^8 cel.L $^{-1}$) were the species with the highest cell density values, while *Minidiscus* sp. (4,938 x 10^5 cel.L $^{-1}$) and *Karlodinium* sp. (1,366 x 10^5 cel.L $^{-1}$) were the most representative in the WCE.

Compared to the BMC (BC and MC), the individual density of the species was altered by

Table II. List of identified phytoplanktonic species based on frequency of occurrence (F.O) and relative abundance. Species richness by sampling point: Brazilian Current (BC1 and BC2), Malvinas Current (MC1 and MC2), Cold Core Eddy (CCE1, CCE2, CCE3 and CCE4) and Warm Core Eddy (WCE1, WCE2 and WCE3) and depth (SUP and DCML), Equitability (J') and Diversity (H' LOG2). Note: VF - Very Frequent, F - Frequent, I - Infrequent, and S - Sporadic.

Region		BRAZIL CURRENT (BC)				MALVINAS CURRENT (MC)				COLD CORE EDDY (CCE)								WARM CORE EDDY (WCE)				
Species	**F.O**	**BC1**		**BC2**		**MC1**		**MC2**		**CCE1**		**CCE2**		**CCE3**		**CCE4**		**WCE1**		**WCE2**		**WCE3**
BACILLARIOPHYTA		**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**	**DCML**	**SURF**
Asterolampra marylandica	**S**	-	-	-	-	-	-	0.07	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-
Asteromphalus sarcophagus	**I**	-	3.01	0.25	0.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cerataulina pelagica	**S**	-	0.11	-	0.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetoceros dichaeta	**I**	-	-	-	-	0.28	1.91	1.04	1.12	-	-	-	0.09	-	-	-	0.69	-	-	-	-	-
Chaetoceros peruvianus	**I**	-	-	-	-	0.28	0.16	-	0.09	-	-	-	-	-	0.05	-	-	-	-	-	-	-
Corethron pennatum	**F**	-	-	-	-	0.70	0.96	0.35	0.35	0.25	0.33	0.15	0.09	0.06	-	0.19	-	-	-	2.63	-	-
Coscinodiscus sp.	**I**	-	0.11	-	-	0.28	-	0.21	0.04	-	-	0.07	-	-	-	-	-	-	0.62	-	-	-
Coscinodiscus marginatus	**I**	-	-	0.13	-	-	-	-	-	-	0.16	-	-	-	-	-	-	11.32	-	-	2.60	-
Coscinodiscus radiatus	**I**	-	-	-	-	-	0.04	-	-	-	-	0.15	-	0.12	-	-	-	-	-	-	-	-
Ditylum brightwellii	**S**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.31	-	1.30	-
Eucampia antarctica	**S**	-	-	-	-	-	-	0.42	0.22	-	-	-	-	-	-	-	-	-	-	-	-	-
Fragilariopsis kerguelensis	**VF**	-	0.89	-	-	6.01	3.82	8.21	8.16	-	0.66	5.38	6.17	5.75	13.86	2.95	0.83	11.32	4.01	-	6.49	2.11
Hemiaulus sinensis	**S**	1.15	-	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptocylindrus minimus	**I**	-	-	-	-	-	0.40	0.28	0.13	-	-	-	-	-	-	-	-	-	0.62	-	1.30	-
Membraneis cf. *challengeri*	**I**	-	-	-	-	0.14	0.08	0.28	0.22	-	-	-	-	-	-	-	-	-	-	-	-	-
Minidiscus sp.	**VF**	2.87	1.00	8.25	5.81	46.37	14.97	70.24	58.72	94.99	94.57	10.47	18.71	0.75	1.62	4.16	6.60	52.83	7.10	44.74	25.97	89.85
Navicula sp.	**I**	-	-	-	-	-	0.08	1.46	0.91	-	-	-	-	-	-	-	-	-	-	-	-	-
Nitzschia longissima	**VF**	-	-	0.13	0.06	1.68	1.35	2.92	3.32	-	-	0.37	0.28	0.12	0.05	1.01	0.28	1.89	0.62	-	1.30	-
Nitzschia sp.	**I**	1.15	2.23	1.00	2.30	-	-	-	-	-	0.49	-	-	-	-	-	-	-	0.93	-	1.30	-
Planktoniella sol	**I**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.55	1.23	-	2.60	-
Podosira sp.	**F**	-	-	-	-	0.14	-	-	-	-	-	0.15	1.59	0.06	0.27	0.05	0.55	-	0.93	-	1.30	-
Porosira glacialis	**F**	-	-	-	-	5.31	2.79	-	1.64	-	0.16	0.74	0.19	0.12	0.32	0.43	0.28	-	-	-	-	-
Proboscia alata	**S**	-	-	-	-	-	0.12	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-
Pseudo-nitzschia cf. *punges*	**I**	-	-	-	-	31.01	57.64	6.95	21.20	-	-	-	0.19	-	-	-	0.83	-	0.62	-	1.30	-
Pseudo-nitzschia cf. *delicatissima*	**F**	0.57	1.34	-	-	-	-	1.53	0.39	-	-	0.15	0.19	0.19	0.27	0.24	0.55	-	-	-	-	-
Rhizosolenia hebetata f. semispina	**S**	-	-	-	-	-	-	-	-	0.50	-	-	-	-	-	-	-	-	-	5.26	-	-
Rhizosolenia imbricata var. minuta	**I**	-	-	-	-	-	0.24	-	0.13	0.50	-	-	-	0.31	0.05	0.05	-	-	-	5.26	-	-
Rhizosolenia setigera	**I**	-	-	-	-	0.14	0.12	-	-	-	-	0.07	-	0.31	-	0.05	-	-	-	-	-	-
Thalassionema frauenfeldii	**I**	-	-	-	-	-	0.16	0.90	0.39	-	-	-	-	-	-	-	-	-	-	-	-	-
Thalassionema nitzschioides	**VF**	-	-	-	0.12	0.56	0.32	0.56	0.09	0.50	0.16	0.74	0.75	0.19	-	0.43	0.41	-	-	5.26	1.30	0.42
Thalassiosia eccentrica	**S**	-	0.11	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-
Thalassiosira gravida	**F**	-	-	-	-	-	0.56	1.18	0.91	0.50	0.16	1.84	1.78	-	1.08	1.30	3.85	-	3.70	5.26	5.19	-
Total		5.75	8.81	10.00	8.83	92.88	85.71	96.59	98.10	97.24	96.71	20.28	30.03	8.00	17.64	10.87	14.86	84.91	20.68	68.42	51.95	92.39

Table II. Continuation.

Region		BRAZIL CURRENT (BC)				MALVINAS CURRENT (MC)				COLD CORE EDDY (CCE)								WARM CORE EDDY (WCE)				
Species	**F.O**	**BC1**		**BC2**		**MC1**		**MC2**		**CCE1**		**CCE2**		**CCE3**		**CCE4**		**WCE1**		**WCE2**		**WCE3**
MIOZOA		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphisolenia globifera	**S**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.31	-	-	-
Azadinium sp.	**VF**	5.17	-	3.00	11.25	-	2.23	-	-	1.00	0.66	12.83	18.15	14.74	14.56	14.11	27.79	3.77	16.36	10.53	9.09	2.96
Corythodinium tessellatum	**S**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.31	-	-	-
Gymnodinium sp.	**S**	-	-	-	-	-	0.40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gonyaulax scrippsae	**F**	-	-	-	-	0.14	0.16	0.21	0.13	-	-	0.29	0.19	0.87	1.08	0.14	1.24	-	-	-	-	-
Karlodinium sp.	**VF**	69.54	48.83	41.75	54.93	-	3.58	-	-	0.50	0.33	45.13	23.76	53.34	10.57	66.31	20.36	-	40.74	5.26	10.39	-
Oxytoxum graciles	**VF**	0.57	21.07	0.75	-	1.26	1.11	-	-	-	-	8.26	10.48	5.87	35.06	3.48	9.90	5.66	12.65	-	2.60	1.90
Oxytoxum laticeps	**F**	5.17	-	0.13	-	1.26	0.08	-	-	-	-	3.39	3.37	6.50	4.21	0.58	6.05	-	-	-	-	-
Phalacroma rotundatum	**I**	-	-	-	-	-	-	0.21	0.04	-	-	-	-	-	-	-	0.14	-	-	-	-	-
Prorocentrum dentatum	**VF**	10.34	20.51	37.75	13.91	-	-	-	-	0.50	0.16	0.15	0.84	0.19	0.05	0.24	0.96	5.66	0.62	7.89	3.90	0.21
Prorocentrum minimum	**F**	3.45	-	6.50	9.92	-	1.04	-	-	-	1.81	9.59	12.54	9.62	15.86	3.87	17.61	-	0.93	-	5.19	2.11
Protoperidinium bipes	**I**	-	-	0.13	0.30	-	-	1.53	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-
Protoperidinium brevipes	**S**	-	-	-	-	-	-	-	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-
Protoperidinium divergens	**S**	-	-	-	-	-	-	0.14	-	-	-	-	0.09	-	-	-	-	-	-	-	-	-
Protoperidnium mite	**S**	-	-	-	-	-	0.04	-	0.09	-	-	-	-	-	-	-	-	-	-	-	-	-
Protoperidinium oceanicum	**S**	-	-	-	-	-	-	0.07	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-
Protoperidinium sp.	**F**	-	0.45	-	0.06	1.96	0.64	-	0.47	-	-	-	0.09	0.37	0.05	0.19	0.28	-	1.54	-	1.30	-
Protoperidinium steinii	**S**	-	-	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-
Protoperidinium subinerme	**S**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.28	-	-	-	-	-
Scrippsiella trochoidea	**I**	-	0.11	-	0.36	1.26	-	-	0.47	-	-	-	-	-	-	-	-	-	-	-	-	-
Tripos fusus	**I**	-	-	-	-	0.14	-	-	-	-	-	-	-	-	-	0.05	0.14	-	-	-	-	-
Tripos horridum	**I**	-	-	-	-	-	-	-	-	0.25	0.16	0.07	-	-	-	-	-	-	-	2.63	-	0.42
Tripos lineatus	**I**	-	-	-	-	1.12	0.16	0.70	0.04	-	-	-	-	-	-	-	-	-	0.62	-	1.30	-
Tripos minutus	**I**	-	-	-	-	-	-	-	-	-	-	-	-	0.44	0.92	0.10	0.14	-	-	-	-	-
Tripos muelleri	**S**	-	-	-	-	-	-	-	-	-	-	-	0.19	-	-	-	-	-	-	-	-	-
Total		94.25	90.97	90.00	90.74	7.12	9.43	2.85	1.47	2.26	3.29	79.72	69.69	91.94	82.36	89.08	84.87	15.09	74.07	26.32	33.77	7.61
HAPTOPHYTA		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Emiliania huxleyi	**S**	-	-	-	-	-	-	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-
Phaeocystis antarctica	**I**	-	-	-	-	-	3.98	-	0.17	-	-	-	-	-	-	-	-	-	-	-	1.30	-
Total		0.00	0.00	0.00	0.00	0.00	3.98	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.30	0.00
OCHROPHYTA		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dictyocha fíbula	**F**	-	0.11	-	0.24	-	0.48	0.07	-	0.25	-	-	0.09	0.06	-	0.05	0.28	-	4.94	2.63	11.69	-
Octactis speculum	**I**	-	-	-	0.18	-	0.40	0.49	0.09	0.25	-	-	0.19	-	-	-	-	-	-	2.63	1.30	-
Octacys octonária	**S**	-	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.31	-	-	-
Total		0	0.22	0	0.42	0	0.88	0.56	0.09	0.50	0	0	0.28	0.06	0	0.05	0.28	0	5.25	5.26	12.99	0
Species richness (S)		10	15	13	15	20	31	24	32	12	14	20	23	21	19	22	23	8	22	12	22	8
Species richness (S) each region		24				45				38								30				
Equitability (J')		0.5	0.52	0.53	0.53	0.52	0.49	0.4	0.4	0.12	0.12	0.6	0.66	0.52	0.63	0.41	0.66	0.74	0.65	0.78	0.83	0.23
Diversity: H'(LOG2)		1.69	2.03	1.97	2.08	2.25	2.45	1.87	2.02	0.45	0.47	2.61	3	2.28	2.69	1.86	3.01	2.23	2.91	2.82	3.7	0.71

eddy activity. The conditions in the CCE promoted the highest cell densities of *Azadinium* sp., *F. kerguelensis*, *Gonyaulax scrippsae* Kofoid, *O. laticeps*, *T. nitzschioides, Thalassiosira gravida* Cleve, *O. graciles*, and *P. minimum*, whereas the conditions in the WCE were favorable for *Azadinium* sp. and *Dictyocha fibula* Ehrenberg (Table IV).

The relative abundance followed the same pattern as density, with greater abundance of dinoflagellates in the BC, CCE and the DCML of the WCE, and of diatoms in the MC (Figure 4). However, despite the high densities of dinoflagellates on the surface of the WCE, diatoms were abundant in this region, particularly due to the dominance of *Minidiscus* sp. (40×10^5 cel.L^{-1}= 89.85%) at the edge of the eddy.

The carbon biomass of the most representative species in the WCE was estimated based on the biovolume of the BC, since these regions were similar according to the Bray-Curtis similarity cluster analysis. Also, the biomass of the BMC (BC and MC) was used as a standard of comparison for the effects of eddies. The analyses revealed that the WCE presented the lowest biomass of organisms, with significant differences only for *Azadinium* sp. (2,691 pgC.L^{-1}) and *Prorocentrum dentatum* (7,920 pgC.L^{-1}) (ANOVA; $p < 0.05$). The conditions in the CCE favored changes, leading to higher biomass values for the species *O. graciles* (120,270 pgC.L^{-1}), *P. minimum* (926,039 pgC.L^{-1}), *Karlodinium* sp. (639,008 pgC.L^{-1}), with significant results for *Azadinium* sp. (100,304 pgC.L^{-1}) (ANOVA; $p < 0.05$), and lower values for *Minidiscus* sp. (ANOVA; $p > 0.05$) and *P. dentatum* (ANOVA; $p < 0.05$). Thus, the carbon biomass of *Azadinium* sp. and *P. dentatum* was significantly influenced by the eddies (Figure 5).

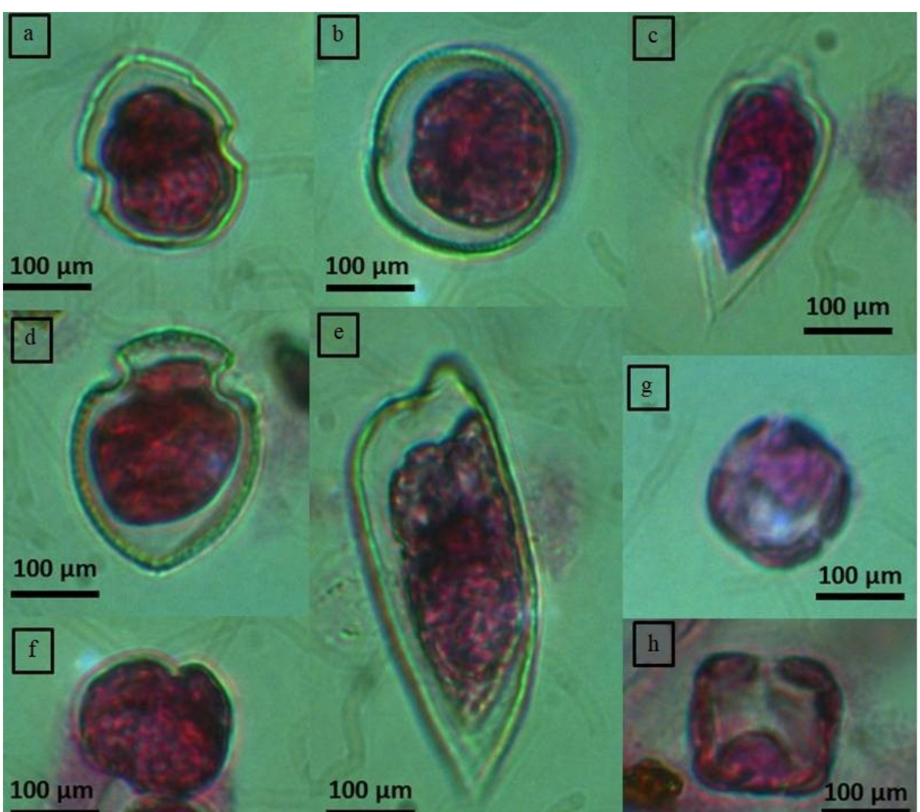

Figure 2. Very frequent and Frequent species in the studied areas. a - *Azadinium* sp., b - *Prorocentrum minimum* (Pavillard) J.Schiller, c - *Oxytoxum gracilis* Schiller, d - *Oxytoxum laticeps* J.Schiller, e - *Prorocentrum dentatum* F.Stein, f - *Karlodinium* sp., g and h - *Minidiscus* sp.

Effect of environmental variables on phytoplankton

Based on the results of the CAP analysis, both the phytoplankton community and the abiotic factors contributed to differentiating the sampling regions. In the CAP plot relating to the phytoplankton community, it is possible to identify four well-defined groups, each representing the Brazil and Malvinas currents and the two eddies (CCE and WCE) (Figure 6a). Three groups were formed, two of which were diatom groups: one correlating the species *Planktoniella sol* (Psol) and *C. marginatus* (Cmar) with the WCE and the other correlating *T. nitszchioides* (Tnitz), *Fragilariopsis kerguelensis* (Fkerg), *C. pennatum* (Cpen), *Minidiscus* sp. (Minid) and *Pseudo-nitzschia* cf. *punges* with the Malvines Current. A third group related the taxa *P. minimum* (Pmi), *P. dentatum* (Pdent) and *Gymnodinium* sp. (Gym) to the Brazil Current (Figure 6a).

The environmental parameters also showed a clear separation in relation to the sampling regions (Figure 6b). Dissolved oxygen was removed from the CAP plot as it was inversely proportional to temperature. Temperature and salinity were correlated with the eddies, while nutrients (phosphate and nitrite) were correlated with the Brazil and Malvines Currents.

DISCUSSION

The present study showed the effect of eddy activity on the phytoplankton community of the BMC. The literature shows that eddies promote changes in phytoplankton composition (Chen et al. 2007). The formation of cyclonic and anticyclonic eddies is known in the BMC (Garzolli & Garraffo 1989, Garcia et al. 2004, Angel-Benavides et al. 2012, Pezzi et al. 2021), where warm eddies are formed by the branching of the southern extension of the BC, which

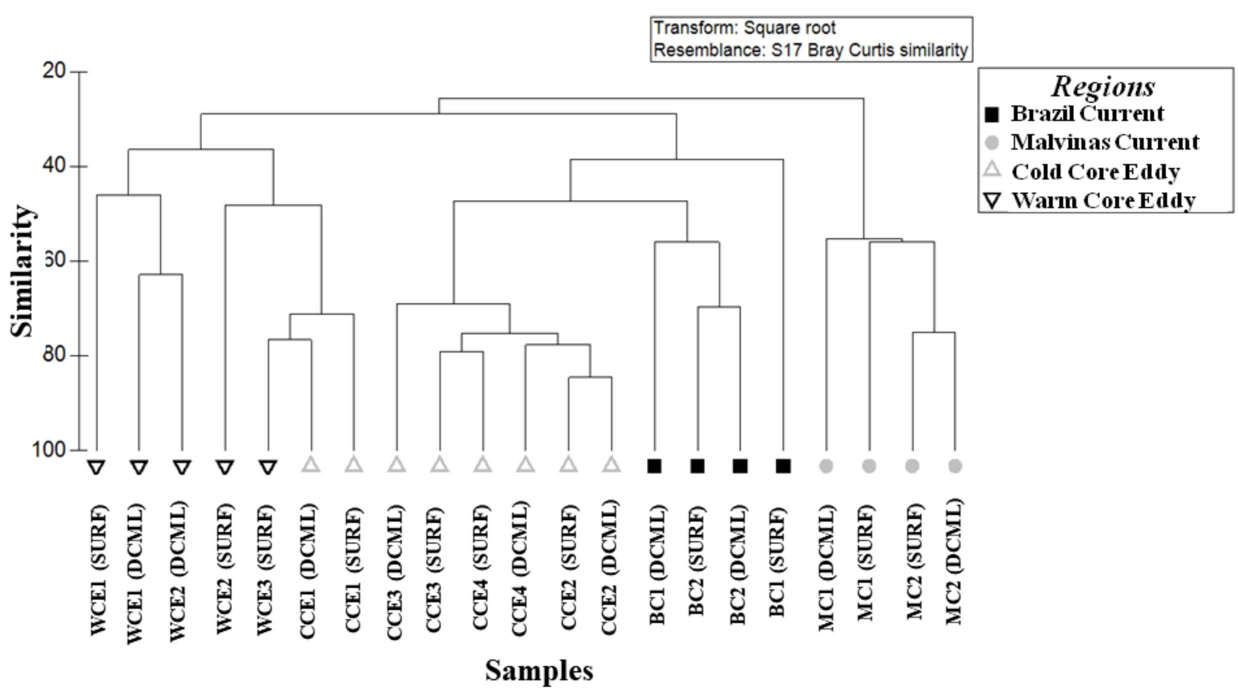

Figure 3. Cluster analysis based on phytoplankton community structure. A Bray-Curtis similarity matrix was subjected to an average linkage algorithm.

retains the physicochemical properties of this current (Garzolli & Garraffo 1989, Pezzi et al. 2021). In the present study, the BC and the WCE regions shared species. Furthermore, these regions offered conditions that promoted the occurrence of tropical species, e.g., *P. sol* and *Corythodinium tesselatum* (Balech 1988, Sournia 1978), both present in the WCE, indicating the tropical origin of this eddy.

Phytoplankton organisms are usually trapped by anticyclonic eddies, which at the southern hemisphere corresponds to the WCE. Pezzi et al. (2021), who studied the same area, observed that these eddies preventing access to nutrients from external sources and thus reducing phytoplankton biomass and productivity (Thompson et al. 2007). In this study, we observed a reduction in total cell density to 928 x 10^5 cel.L $^{-1}$, mainly in the phylum Bacillariophyta, on the surface of the WCE. In warmer waters, the occurrence of individual cells and colonies of diatoms is reduced due to greater stratification and lower nutrient supply (Kenitz et al. 2020). These effects were associated with the WCE that promoted the decrease in density of individual cells (*Minidiscus* sp., *N. longissima*) and colonies (*Pseudo-nitzschia* cf. pungens, *T. nitzschioides, F. kerguelensis* and *T. labelula*) of diatoms.

According to Cotti-Rausch et al. (2016), biomass can be increased at the edges of anticyclonic eddies when interacting with

Table III. List of Deep Chlorophyll Maximum Layer (DCML) indicator species, Brazil Current (BC), Malvinas Current (MC) and Cold Regions (Malvinas Current and Cold Core Eddy) with percentage (%) and significance value of indVal (p).

Species	%	P Value	Indicator
Dictyocha fibula	79	0.045	DCML
Protoperidinium sp.	77	0.050	DCML
Nitzschia sp.	96	0.010	Brazil Current
Asteromphalus sarcophagus	86	0.015	Brazil Current
Membraneis cf. *challengeri*	100	0.005	Malvines Current
Pseudo-nitzschia sp.	99	0.005	Malvines Current
Chaetoceros dichaeta	98	0.005	Malvines Current
Tripos lineatus	95	0.005	Malvines Current
Nitzschia longissima	93	0.020	Malvines Current
Corethron pennatum	93	0.005	Malvines Current
Navicula sp.	86	0.005	Malvines Current
Thalassionema frauenfeldii	86	0.005	Malvines Current
Chaetoceros peruvianus	84	0.005	Malvines Current
Leptocylindrus minimus	81	0.015	Malvines Current
Phalacroma rotundatum	66	0.035	Malvines Current
Planktoniella sol	77	0.03	Warm Core Eddy
Fragilariopsis kerguelensis	93	0.015	Cold Regions
Gonyaulax scrippsae	91	0.010	Cold Regions
Porosira glacialis	91	0.005	Cold Regions

the edges of cyclonic eddies. In our sampling design, an interaction was observed between the surface of WCE3 station and the edge of the cyclonic eddy (CCE2), causing an increase in total density compared to the surface of the central sttions (WCE1 and WCE2). This increase in biomass is possibly linked to the change in environmental conditions, that is, the lower temperatures and salinity and higher dissolved oxygen in WCE3.

Several studies indicate that cold eddies enhance the productivity and concentrations of phytoplankton organisms in the oceans, influencing the marine trophic web (Bibby et al. 2008, Belkin et al. 2022). In the CCE studied here, the total cell density was high, close to that of the BMC (sum of the total densities of the BC and MC). The temperate colony-forming diatoms *T. nitzschioides*, *F. kerguelensis* and *T. gravida* were stimulated as result of the cold character of the feature. Diatoms generally form colonies with increased nutrient and grazing (Kenitz et al. 2020). In the study by Chen et al. (2007), the abundance of diatoms, especially of the colonial forms of *Chaetoceros*, *Thalassionema*, *Nitzschia* and *Bacteriastrum*, was elevated by the CCE.

Dinoflagellates, in turn, were predominant in terms of cell density and relative abundance; *Azadinium* sp., *G. scrippsae*, *O. laticeps*, *O. graciles*, and *P. minimum* were favored by the cold conditions of the CCE, reaching higher densities in relation to the BMC. The autotrophic dinoflagellate *O. laticeps* was first recorded in the South Atlantic at maximum concentrations of 400 cel.L $^{-1}$, in the coastal regions south of Argentina, by Fabro & Almadoz (2021). In our study, cell density was high, ranging from 215 x 10^5 cel.L $^{-1}$ (BMC) to 308 x 10^5 cel.L $^{-1}$ (CCE off the continental shelf), indicating that the nutrient input in the CCE favored the development of autotrophic species such as *O. laticeps* and *G. scrippsae* (Naik et al. 2011). Thus, the increase in autotrophic prey (diatoms and dinoflagellates) ultimately benefits heterotrophic and mixotrophic species such as *Azadinium* sp., *P. minimum*, and *O. graciles* (Hanson et al. 2007, Duhamel et al. 2019, Naik et al. 2011).

The higher density of dinoflagellates in the CCE confirms that this type of feature supports a greater abundance of organisms, which due to their high nutritional value, benefit the zooplankton and consequently the entire

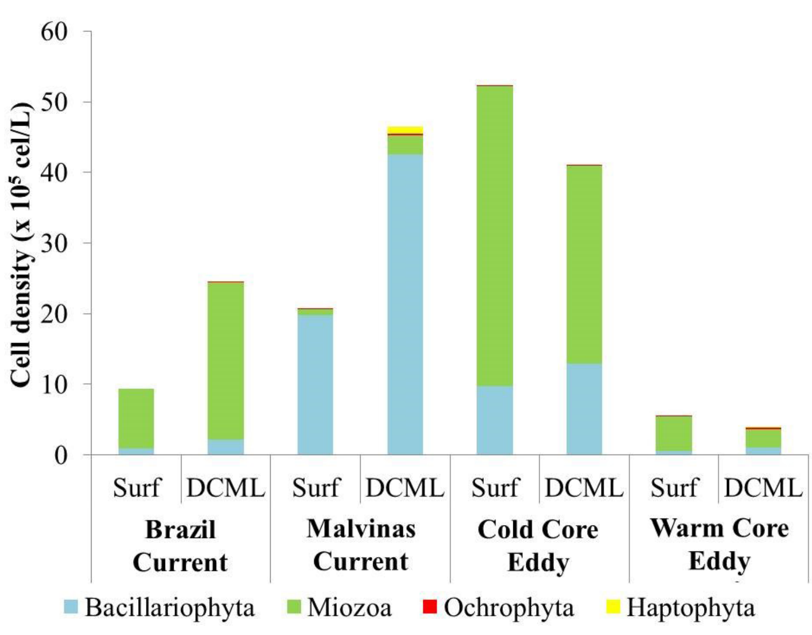

Figure 4. Cell density (x 10^5 cel.L^{-1}) per each phylum on the surface (Surf) and Deep Chlorophyll Maximum Layer (DCML) of the Brazil Current, Malvinas Current, Cold-Core and Warm-Core Eddies.

marine trophic web (Waite et al. 2019, Belkin et al. 2022). According to Coria-Monter et al. (2014), the greater abundance of dinoflagellates in cold eddies can be explained by the migration of these organisms to nutrient-rich regions or by the herbivory that reduces diatom populations.

Dinoflagellates were also more representative in the BC. There was a particularly higher cell density, frequency and relative abundance of *Karlodinium* sp. (17,377 x 10^5cel.L^{-1}) and *P. dentatum* (7,065 x 10^5 cel.L^{-1}). According to Guo et al. (2016), *P. dentatum* blooms greater than x 10^6 cel.L^{-1} were observed during the spring in the Changjiang estuary and were related to elevated temperatures (18-22 °C). This species is able to store phosphate and dominate the phytoplankton community during low concentrations of this nutrient (Li et al. 2011).

A predominance of *Karlodinium* sp. was recorded in waters with low phosphate values

Table IV. Total density (x 10^5 cel/L^{-1}) of organisms present in the BMC (Brazil Current and Malvines Current) and in the Warm Core Eddy (WCE) and Cold Core Eddy (CCE) and frequency of occurrence (F.O.: VF - Very Frequent, F - Frequent, I - Infrequent, and S - Sporadic). Values highlighted in red and bold represent density reduction and increase, respectively, compared to BMC.

Species	F.O	BMC	Warm Core Eddy	Cold Core Eddy
Azadinium sp.	VF	26	**77**	**13246**
Chaetoceros dichaeta	I	876	0	**58**
Corethron pennatum	F	404	**10**	**106**
Dictyocha fibula	F	173	**250**	**58**
Nitzschia sp.	I	646	**39**	**29**
Fragilariopsis kerguelensis	VF	4370	**327**	**5381**
Gonyaulax scrippsae	F	106	0	**501**
Oxytoxum laticeps	F	202	0	**308**
Leptocylindrus minimus	I	164	**29**	0
Minidiscus sp.	VF	31324	**4938**	**14170**
Nitzschia longissima	VF	1607	**39**	**327**
Phaeocystis antarctica	I	1001	**10**	0
Porosira glacialis	F	1405	0	**308**
Prorocentrum dentatum	VF	7065	**116**	**29**
Pseudo-nitzschia cf. *punges*	I	21765	**116**	**29**
Pseudo-nitzschia cf. *delicatissima*	F	424	0	**202**
Thalassionema nitzschioides	VF	231	**5**	**347**
Thalassiosira gravida	F	500	**173**	**1174**
Tripos lineatus	F	221	**29**	0
Octactis speculum	I	212	**19**	**29**
Oxytoxum graciles	VF	2242	**53**	**10704**
Prorocentrum minimum	F	2387	**164**	**8962**
Karlodinium sp.	VF	18203	**1366**	**3311**

in Southern Brazil (Islabão et al. 2017). According to Zhou et al. (2015), the phagotrophic activity of *Karlodinium veneficum* (D. Ballantine) J. Larsen controls the biomass of *P. dentatum* and alters the predominance of both organisms. Phagotrophic activity can also be deduced from the greater abundance of *Karlodinium* sp. in the DCML of the WCE in relation to the DCML of the CCE, as highlighted by Belkin et al. (2022). These authors suggest that changes in phagotrophy take place as a consequence of phosphorus limitation. In the present study, low concentrations of phosphate were found in the WCE. In contrast, in the CCE, *Karlodinium* sp. was more abundant on the surface, where phosphate levels were elevated, suggesting autotrophic activity and thus confirming the mixotrophy of the species (Lin et al. 2017).

In the South Atlantic, *A. sarchophagos* has been associated with warmer, saltier waters of coastal regions (Gonçalves-Araujo et al. 2012, Ferronato et al. 2021). Our data confirm the tropical character of *A. sarchophagos* (Tomas 1997), which is an indicator of the BC within the BMC. Another diatom found mainly in tropical and subtropical waters is *P. sol* (Silva-Cunha & Eskinazi-Leça 1990, Silva-Cunha et al. 2019). Its oceanic life form and preference for subtropical WCE conditions make it an indicator species of these conditions. In contrast, the temperate species *C. dichaeta*, *C. peruvianus*, *P. rotundatum*, *T. frauenfeldii*, and *T. lineatus* and the polar species *C. pennatum* and *M.* cf. *challengeri* (Cupp 1943, Tomas 1997, Balech 1988) along with *L. minimus*, *Navicula* sp., *N. longissima*, and *Pseudo-nitzschia* sp. were indicators of the MC. Thus, the physicochemical characteristics of the studied regions reflected changes in the composition of the phytoplankton and in the distribution of these species characterized by different environmental tolerances.

The phylum Bacillariophyta prevailed (in terms of cell density and relative abundance) in the MC, co-occurring with *Phaeocystis* cf.

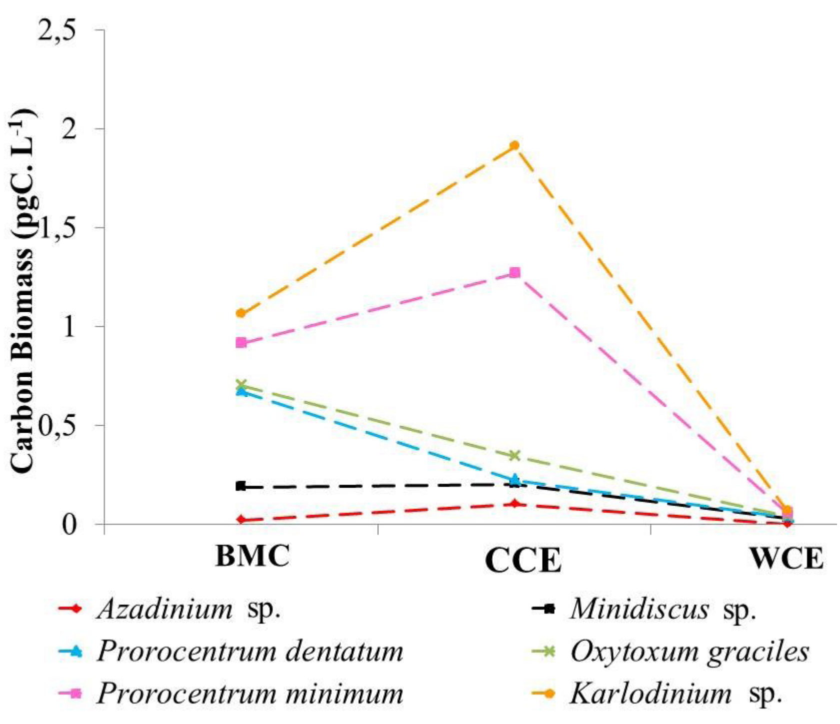

Figure 5. **Carbon Biomass (x 10^6 pgC.L^{-1}) of the Dominant, Abundant, Very frenquent and Frequent species at the Brazil-Malvinas Confluence (BMC), Cold-Core Eddy (CCE), and Warm-Core Eddy (WCE).**

globosa in the DCML. Some studies show that diatoms and *Phaeocystis* sp. are representative in the neritic regions of BMC bathed by cold and nutrient-rich waters, where *Phaeocystis* sp. is benefited by the same conditions as those found at greater depths such as in the DCML (Gonçalvez-Araujo et al. 2012, Garcia et al. 2008).

An interesting finding in our study was that data from the DCML of the analyzed regions revealed that the WCE promoted a reduction in phytoplankton densities. The DCML is influenced in contrasting ways by the different types of eddies (Cornec et al. 2021). The effects of upwelling (cold) eddies are restricted to the DCML, caused by the increase in nutrient concentrations (Bibby et al. 2008, Dai et al. 2020). Warm-core eddies, however, increase the concentration of pigments (chlorophyll) in cells without raising the biomass of the community through photoacclimation processes (Cornec et al. 2021). This was indicated by the low density in the WCE in our study.

Organisms smaller than 20 µm were the most representative in frequency and abundance. They included, for example, *Azadinium* sp., *Minidiscus* sp., *P. dentatum, P. minimum*, and *Karlodinium* sp. In Argentine waters and the MC, *Azadinium* sp. (> x 10^6 cel /L^1) blooms are frequent and compete with *Thalassiosira* cells (Akselman & Negri 2012). Several studies show that this size class is predominant in oligotrophic regions and exhibits a low sedimentation rate, with carbon being remineralized in the euphotic zone (Marañón 2015). However, the BMC is considered an important sink for atmospheric CO_2, potentiated by the influence of the MC (Garcia et al. 2004), which presented larger cells of *Karlodinium* sp., *Prorocentrum dentatum*, and *O. graciles*. CO_2 concentrations vary under the influence of eddies (Pezzi et al. 2021).

According to Pezzi et al. (2021), the WCE in the BMC is a source of CO_2 to the atmosphere and, accordingly promoted the lowest carbon biomass of organisms in the present study. Cold

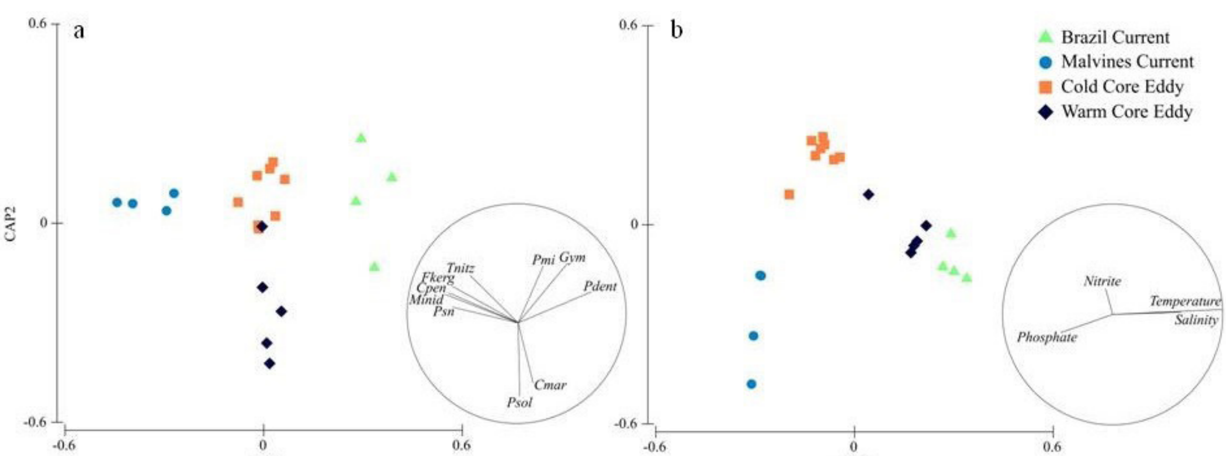

Figure 6. a - The CAP plots on phytoplankton community among the species *Planktoniella sol* (Psol), *C. marginatus* (Cmar), *T. nitszchioides* (Tnitz), *Fragilariopsis kerguelensis* (Fkerg), *C. pennatum* (Cpen), *Minidiscus* sp. (Minid), *Pseudo-nitzschia* cf. *punges*, *P. minimum* (Pmi), *P. dentatum* (Pdent) and *Gymnodinium* sp. (Gym) and b - the environmental factors: Salinity, Temperature, Phosphate and Nitrite. Note: Cold-Core Eddy (CCE), Warm Core Eddy (WCE), Brazil Current (BC), and Malvinas Current (MC).

regions enhance the oceans' uptake of CO_2. Under these conditions, the CCE promoted the highest carbon biomass values of dinoflagellates, except of *P. dentatum* (influenced by phosphate concentrations) and of the diatom *Minidiscus* sp. Thus, our hypothesis of increasing carbon biomass was confirmed for the CCE.

The above data suggest the greatest contribution of organisms smaller than 20 µm, characteristic of warm and oligotrophic environments (Hillebrand et al. 2022), to the carbon biomass, indicating a low trophic efficiency of the biological carbon pump because small cells tend to retain a higher concentration of carbon and are easily predated, while larger cells tend to be denser and less palatable (Marañón 2015). In addition, the shorter life cycles, faster reproductive rates or earlier developmental stages of the species can also be reflected in cell size (Finkel et al. 2010).

The present study showed the effect of eddies on the phytoplankton community in the BMC. The Cold-Core Eddy activity promoted a higher diversity of phytoplankton and cell density of dinoflagellates, as well as changes in the carbon biomass of the most representative species. Diatoms were more representative in cell density in the Malvinas Current. Nineteen species were indicators of the Deep Chlorophyll Maximum Layer, Brazil Current and the Malvinas Current, Warm-Core Eddy, and cold regions (Brazil Current and Cold-Core Eddy). Organisms < 20 µm were more abundant and dominant in the regions (Brazil Current, Malvinas Current, Warm-Core Eddy and Warm-Core Eddy), suggesting their greater contribution to carbon biomass.

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