

1 **New insights on the dominance of cryptophytes in**  
2 **Antarctic coastal waters: a case study in Gerlache Strait**

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26 **Running Head:** Cryptophytes in Antarctic coastal waters

27

1 **Abstract**

2 Changes in phytoplankton composition from large diatoms to small cryptophytes  
3 and their implications to the food web have been previously associated with  
4 rapid warming of surface waters in the western Antarctic Peninsula (WAP).  
5 However, ecological and physiological attributes that favor dominance of these  
6 flagellates in the region have not been fully explored. The overall aim of this  
7 work was to characterize the phytoplankton pigments and assemblages in  
8 relation to environmental conditions during three successive summer cruises  
9 (2013, 2014 and 2015) in the Gerlache Strait – a coastal area in the northern  
10 WAP. Data on phytoplankton (through HPLC/CHEMTAX pigment analysis) and  
11 associated physical (water column structure) and chemical (macronutrients)  
12 parameters were determined. Cryptophytes were conspicuously found in  
13 shallow mixed layers, under stratified conditions, as the main contributors to  
14 total phytoplankton biomass. Their greatest contributions were associated with  
15 warmer surface waters at the northwestern sector of the strait. Other  
16 phytoplankton groups (*Phaeocystis antarctica* in 2013 and small diatoms in both  
17 2014 and 2015) were also important components. Photoprotective carotenoids  
18 (mainly alloxanthin), with an important role in preventing photodamage caused  
19 by excess light, were closely linked with the dominance of cryptophytes at  
20 surface layers. The results of this study suggest that the prevalence of  
21 cryptophytes in WAP coastal waters can be, to a great extent, due to a  
22 particular ability of those small flagellates to successfully grow in highly  
23 illuminated conditions in shallow upper mixed layers and strong water column  
24 stratification.

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26 **Keywords:** Southern Ocean, Northern Antarctic Peninsula, regional warming,  
27 phytoplankton functional groups, cryptophytes, photophysiology.

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## 2 **1. Introduction**

3

4         The Southern Ocean environment is rapidly changing, although the  
5 magnitude and direction of changes vary regionally. The western Antarctic  
6 Peninsula (WAP) is amongst the world's most sensitive regions to climate  
7 change (e.g. Turner et al., 2005; Steig et al., 2009). The WAP area is distinctive  
8 among Antarctic regions due to its NE-SW geographic orientation and direct  
9 exposure to prevailing westerly atmospheric and oceanic circulation (Ducklow et  
10 al., 2013). It also responds distinctly to climate change, with observed  
11 significant sea ice decreases and rapid winter warming over the last decades  
12 (Stammerjohn et al., 2012; Ducklow et al., 2013; Saba et al., 2013). Its NE-SW  
13 coastal orientation produces a strong latitudinal climate gradient in both  
14 temperature and sea ice cover and is characterized by a shorter/longer ice  
15 season and more maritime/continental conditions in the northern/southern  
16 areas, respectively (Stammerjohn et al., 2008; Montes-Hugo et al., 2009;  
17 Ducklow et al., 2013). Additionally, climate variability in the WAP is strongly  
18 influenced by the El Niño Southern Oscillation (ENSO) and the Southern  
19 Annular Mode (SAM), two main climate patterns that have an effect on  
20 environmental variability in the Southern Ocean (Stammerjohn et al., 2008). As  
21 life histories of most polar organisms are attuned to sea ice seasonality, recent  
22 warming and consequent decline in sea ice cover have been associated with  
23 changes in key food web trophic levels in the northern WAP region, including  
24 reduction in phytoplankton biomass, shifts in phytoplankton community  
25 composition from large diatoms to small flagellated cryptophytes, and decrease

1 in the abundance of Antarctic krill (Moline et al., 2004; Ducklow et al., 2007;  
2 Montes-Hugo et al., 2009; Mendes et al., 2013).

3         Phytoplankton blooms around the WAP are typically associated with  
4 development of a shallow surface mixed layer, which promotes phytoplankton  
5 growth by increasing light availability, and by taking advantage of iron inputs  
6 from glacial melt water into the upper water column (e.g. Prézelin et al., 2000;  
7 Mendes et al., 2012; Venables et al., 2013). Although Antarctic blooms are  
8 commonly dominated by diatoms, some studies have noted the increasing  
9 importance of cryptophytes that can prevail over diatoms in the WAP region.  
10 This is particularly true in areas of glacial ice melting water discharge and/or  
11 associated with low surface salinities and highly stable water column, where  
12 those organisms stay by active swimming (Moline and Prézelin, 1996; Moline et  
13 al., 2004; Mendes et al., 2013). Shifts from diatoms to cryptophytes dominance  
14 have been previously attributed to sedimentation of large diatoms (Castro et al.,  
15 2002), advection (Moline and Prézelin, 1996), grazing (Garibotti et al., 2003),  
16 and even to preference/physiological tolerance of cryptophytes to lower salinity  
17 waters (Moline et al., 2004). A recurrent transition from diatoms to cryptophytes  
18 represents a fundamental decrease in the size spectrum of the phytoplankton  
19 community, which can impact grazing efficiencies of different zooplankton  
20 species, enhancing microbial activity in the region and, consequently, promoting  
21 changes in carbon fluxes within the water column (Rodríguez et al., 2002;  
22 Ducklow et al., 2013). In addition, these organisms are generally less efficient in  
23 absorbing and exporting carbon, as compared to diatoms (e.g. Schloss et al.,  
24 2007), and, therefore, less capable to contribute with lowering CO<sub>2</sub> partial  
25 pressure in surface layers, leading to CO<sub>2</sub> outgassing in our study region (Kerr

1 et al., this issue). As phytoplankton supports oceanic food webs and plays a key  
2 role on the resilience of the WAP marine ecosystem, changes in abundance  
3 and composition of phytoplankton assemblages may have a direct effect on the  
4 structure and functioning of the entire regional ecosystem.

5 In other Antarctic coastal areas, particularly in the Ross Sea, where  
6 diatom-dominated blooms are found in summer and *Phaeocystis antarctica*  
7 prevails in spring, ambient light has been hypothesized as one of the key  
8 drivers of seasonal shifts in phytoplankton community composition (Smith et al.,  
9 2010). Those observed patterns in the Ross Sea have been attributed to  
10 decreases in surface mixed layer depths along the growing season, since  
11 deeper mixed layers favor *P. antarctica* more than diatoms (Arrigo et al., 1999;  
12 Smith et al., 2006), apparently due to its photosynthetic plasticity (Kropuenske  
13 et al., 2009). However, in the WAP region, to our knowledge, no  
14 experimental/field investigations are available on the responses of marine  
15 phytoplankton assemblages under different light conditions. It should be  
16 considered that early retreat of sea ice, together with observed increase in sea  
17 surface temperature in the WAP region, may lead to development of a shallow  
18 mixing layer and strong vertical water column stratification, confining planktonic  
19 organisms near the surface and, thus, exposed to high irradiance (Moreau et  
20 al., 2010). Under such conditions, marine microorganisms can be inept for  
21 photorepair (Kaiser and Herndl, 1997) and may not recover from high irradiance  
22 exposure. We hypothesize that the gradual dominance of cryptophytes in  
23 coastal waters of the WAP is associated with their ability to grow under high  
24 irradiance exposure in strongly stratified shallow mixing surface layers, due to  
25 pigment protection capability. In this context, the main goal of the present study

1 was to characterize the phytoplankton assemblages (through pigment  
2 composition) and hydrographic parameters associated with coastal waters  
3 where cryptophytes have been shown to dominate or have a significant  
4 biomass contribution. To reach this goal, three oceanographic surveys were  
5 conducted in a coastal region of the northern WAP (Gerlache Strait) during late  
6 summer (February) of 2013, 2014 and 2015.

7

## 8 **2. Material and methods**

9

### 10 2.1. Study area and sampling

11 The coastal region of the WAP is punctuated by islands, promontories,  
12 and small peninsulas, and includes a complex network of straits, bays, and  
13 passages between islands and the continental mainland. Here, physical,  
14 chemical and biological sampling were undertaken during three consecutive  
15 oceanographic cruises carried out within the coastal and sheltered waters of the  
16 Gerlache Strait (Fig. 1), during late summers of 2013 (12–15 February), 2014  
17 (8–11 February) and 2015 (8–10 February). The Gerlache Strait, a relatively  
18 confined region, separates the Antarctic Peninsula from Brabant and Anvers  
19 Islands (Fig. 1). The main surface circulation pattern within the strait is driven by  
20 the Gerlache Strait Current, which flows northeastward along the strait (Zhou et  
21 al., 2002). This current carries the Gerlache waters into the Bransfield Strait,  
22 where its main flow joins the Bransfield Strait Current along the northeastern  
23 margin of the Bransfield Strait (Zhou et al., 2002, 2006).

24 Hydrographic data (temperature and salinity) and water samples were  
25 collected using a combined Sea-Bird CTD/Carrousel 911+system® equipped

1 with 24 five-liter Niskin bottles. Surface water samples were taken in all CTD  
2 (conductivity–temperature–depth) stations for dissolved nutrient and  
3 phytoplankton pigments analyses (Fig. 1). At some stations, chosen according  
4 with the fluorescence profiles (WetLabs® profiling fluorometer), seawater  
5 samples were taken from several depths (between the surface and 100 m) to  
6 better characterize the vertical distribution of phytoplankton communities.  
7 However, due to the absence of deep chlorophyll maximum (DCM) layers,  
8 seawater samples at these selected stations were generally collected at regular  
9 depths: 5, 15, 25, 50, 75 and 100 m.

10

## 11 2.2. Water column stability/stratification parameters

12 The potential density ( $\rho$ ,  $\text{kg m}^{-3}$ ) was calculated based on temperature,  
13 salinity and pressure data in order to evaluate the physical structure of water  
14 column. The upper mixed layer depth (UMLD) was determined based on  
15 density profiles, according to the criteria established by de Boyer Montégut et  
16 al. (2004), i.e., the depth at which potential density deviate from its 10 m depth  
17 value by a threshold of  $\Delta\rho = 0.03 \text{ kg m}^{-3}$ . The water column stability ( $E$ ;  
18 hereafter referred to as stability) was estimated using vertical density variations,  
19 as function of the buoyancy or the Brunt-Väisälä frequency ( $N^2$ ), which is  
20 determined by:

$$21 \quad N^2 = - \frac{g}{\rho} \frac{\partial \rho}{\partial z} (\text{rad}^2 \text{s}^{-2})$$

22 where  $g$  is gravity and  $\rho$  is the potential density of seawater. Stability was  
23 further estimated from:

1 
$$E = \frac{N^2}{g} (10^{-6} \text{ rad}^2 \text{ m}^{-1})$$

2 Average stability values (between 0 and 100 m depth) were used in the  
3 statistical analyses.

4

### 5 2.3. Nutrient analysis

6 Surface water samples were filtered through cellulose acetate membrane  
7 filters to determine dissolved inorganic nutrients (DIN: nitrate, nitrite and  
8 ammonium; phosphate and silicic acid). Nutrients were analyzed onboard using  
9 a FEMTO<sup>®</sup> spectrophotometer, following the analytical recommendations in  
10 Aminot and Chaussepied (1983). Orthophosphate was measured by reaction  
11 with ammonium molybdate, with absorption readings at 885 nm. Silicic acid  
12 measurements, in the form of reactive Si, were corrected for sea salt  
13 interference.

14

### 15 2.4. HPLC–CHEMTAX analysis

16 For phytoplankton pigment analysis, seawater samples (0.5–2.5 L) were  
17 filtered under low vacuum through GF/F filters and filters were immediately  
18 frozen in liquid nitrogen for later HPLC pigment analysis. In the laboratory, the  
19 filters were placed in a screw-cap centrifuge tube with 3 mL of 95% cold-  
20 buffered methanol (2% ammonium acetate) containing 0.05 mg L<sup>-1</sup> trans-β-apo-  
21 8'-carotenal (Fluka) as internal standard. Samples were sonicated for 5 min in  
22 an ice-water bath, placed at –20°C for 1h, and then centrifuged at 1100 g for 5  
23 min at 3°C. The supernatants were filtered through Fluoropore PTFE membrane  
24 filters (0.2 μm pore size) to separate the extract from remains of filter and cell



1 debris. Immediately prior to injection, 1000  $\mu$ L of sample was mixed with 400  $\mu$ L  
2 of Milli-Q water in 2.0 mL amber glass sample vials, which then were placed in  
3 the HPLC cooling rack (4°C). Methodological procedures for HPLC analysis  
4 (using a monomeric C8 column with a pyridine-containing mobile phase) are  
5 fully described in Zapata et al. (2000). The limit of detection and limit of  
6 quantification of this method were calculated and discussed in Mendes et al.  
7 (2007). Pigments were identified from both absorbance spectra and retention  
8 times from the signals in the photodiode array detector (SPD-M20A; 190 to 800  
9 nm; 1 nm wavelength accuracy) or fluorescence detector (RF-10AXL; Ex. 430  
10 nm/Em.670 nm). Peaks were integrated using LC-Solution software, but all  
11 peak integrations were manually checked and corrected, when necessary. The  
12 HPLC system was previously calibrated with pigment standards from DHI  
13 (Institute for Water and Environment, Denmark). For correction of both losses  
14 and volume changes, the concentrations of pigments were normalized to the  
15 internal standard.

16 The CHEMTAX v1.95 matrix factorization software routine (Mackey et al.  
17 1996) was used to determine phytoplankton community composition from HPLC  
18 pigment concentrations. The CHEMTAX estimates the relative contribution of  
19 microalgal groups to the overall biomass concentration, calculated from the  
20 class-specific accessory pigments and total chlorophyll *a* (Chl *a*). Although  
21 concentration of Chl *a* is not an absolute measure of algal biomass, such as  
22 carbon, it can be used as a biomass “indicator” or “index” (Huot et al. 2007).  
23 Therefore, in this work, we use the term Chl *a* referring to either total biomass or  
24 relative biomass attributed to the corresponding taxonomic groups, as has been  
25 widely applied with the CHEMTAX approach. This software package has been

1 extensively and successfully used in Southern Ocean studies (e.g. Wright et al.,  
2 2010; Kozłowski et al., 2011; Mendes et al., 2015) to determine the distribution  
3 of phytoplankton functional groups. The basis for calculations and procedures is  
4 fully described in Mendes et al. (2012). Based on identified diagnostic pigments,  
5 six algal groups were loaded on CHEMTAX: diatoms, dinoflagellates-1  
6 (peridinin-containing dinoflagellates), "*Phaeocystis antarctica*", cryptophytes,  
7 green flagellates (chlorophyll *b* containing) and "chemotaxonomic group" (a  
8 group including peridinin-lacking autotrophic dinoflagellates and other algal  
9 groups such as Parmales and chrysophytes). Data from each cruise were run  
10 separately in order to take into account potential variations in optimization of  
11 CHEMTAX procedures. Pigment-based estimates were verified by microscope  
12 (the dominant phytoplankton taxa for each sampling year are listed in Table S1;  
13 see Supplementary Material).

14 As phytoplankton may alter their pigment composition based on  
15 environmental conditions (Higgins et al., 2011), photo-pigment indices were  
16 derived to assess the changing contribution of chlorophylls and carotenoids to  
17 the total pigment (TP) pool. The carotenoids were separated into photosynthetic  
18 carotenoids (PSC) and photoprotective carotenoids (PPC). In this study, the  
19 PSC included 19'-butanoyloxyfucoxanthin, 19'-hexanoyloxyfucoxanthin,  
20 fucoxanthin and peridinin, while the PPC were composed by alloxanthin,  
21 diadinoxanthin, diatoxanthin,  $\beta,\beta$ -carotene and  $\beta,\epsilon$ -carotene. Accordingly, three  
22 photo-pigment indices were derived and used here following Barlow et al.  
23 (2007):  $\text{Chl}a_{\text{TP}}$  (chlorophyll *a* to total pigments),  $\text{PSC}_{\text{TP}}$  (photosynthetic  
24 carotenoids to total pigments) and  $\text{PPC}_{\text{TP}}$  (photoprotective carotenoids to total

1 pigments). These indices were used to investigate phytoplankton pigment  
2 adaptations in response to environment light regimes.

3

#### 4 2.5. Statistical analysis

5 Relationships between biomass of phytoplankton groups and  
6 environmental variables at surface (first CTD sampling depth, 5-10 m; except  
7 for determining water column structure, where data from the upper 100 m were  
8 used) were explored by Canonical Correspondence Analysis (CCA; Ter Braak  
9 and Prentice, 1988) using CANOCO for Windows 4.5 software. This analysis  
10 was performed in order to identify the main patterns of the phytoplankton  
11 community structure, with respect to environmental variables. Biotic variables  
12 were represented by the CHEMTAX-derived taxonomical groups' biomass (mg  
13 m<sup>-3</sup> of Chl a). Environmental variables included water column stability (Stability),  
14 upper mixed layer depth (UMLD), sea surface temperature (T), sea surface  
15 salinity (Salinity), dissolved inorganic nitrogen (DIN), phosphate and silicic acid.  
16 All variables were log-transformed before analysis to reduce the influence of  
17 different scales in the data sets. Monte-Carlo tests were run based on 499  
18 permutations under a reduced model (p<0.05) in order to evaluate the  
19 significance of the CCA.

20

### 21 **3. Results**

22

#### 23 3.1. Environmental setting

1           The mean sea surface temperature showed slight differences among  
2 years, although generally higher and maximum values were registered in 2013  
3 ( $1.32 \pm 0.45$  °C) and lowest in 2015 ( $1.12 \pm 0.42$  °C; Table 1). Mean sea surface  
4 salinity (Fig. 2) was very similar in both 2014 and 2015, but markedly lower than  
5 in 2013, when the highest surface salinity values were observed ( $33.93 \pm 0.15$ ;  
6 Table 1). This can also be observed in the 0-150 m T/S diagram from the three  
7 studied years (Fig. S2 in Supplementary Material), where no typical water  
8 masses could be identified in the upper 150 m.

9           The high salinity values observed in 2013 led to a significant decrease in  
10 water column stability, accompanied by higher values of UMLD, i.e., deeper  
11 mixed layer (see Table 1). Relatively shallow mixed layers, with average depths  
12 less than 25 m, were recorded during the three summers. Spatial  
13 oceanographic features in Gerlache Strait were similar among years, with a  
14 conspicuous region at the northwestern sector of the strait characterized by an  
15 upper layer of warmer water (see surface distribution values in Fig. 3). At St. 4,  
16 in the channel between Brabant and Anvers Island (see Fig. 1), there was also  
17 a relatively warm surface layer. A marked hydrographic front at the northeastern  
18 end of the Gerlache Strait was also depicted (Sts. 15, 16 and 17), influenced by  
19 cooler and more saline waters from the Bransfield Strait.

20           Surface nutrient concentrations showed high interannual variation (Table  
21 1). DIN ranged from 13.56 to 40.15  $\mu\text{M}$ , with the lowest mean values recorded  
22 in 2014 ( $19.62 \pm 3.26$   $\mu\text{M}$ ) and highest in 2015 ( $30.45 \pm 7.51$   $\mu\text{M}$ ). Silicic acid  
23 varied from 26.54 to 96.31  $\mu\text{M}$ , with maximum mean values observed in 2015  
24 ( $75.09 \pm 10.67$   $\mu\text{M}$ ). Phosphate varied between 0.31 and 2.14  $\mu\text{M}$ , with  
25 minimum mean values observed in 2014 ( $0.64 \pm 0.23$   $\mu\text{M}$ ).

1

## 2 3.2. Phytoplankton biomass and community composition

3           During the study period, surface Chl *a* concentration values, used here  
4 as phytoplankton biomass index, ranged between 0.24 and 2.29 mg m<sup>-3</sup> (see  
5 Table 1; and Fig. S1 in Supplementary Material). The higher mean surface Chl  
6 *a* concentrations were recorded in 2014 (1.54 ± 0.39 mg m<sup>-3</sup>) (Table 1),  
7 although the highest value was observed in 2013 (2.29 mg m<sup>-3</sup> at St. 12). The  
8 main phytoplankton groups in the region were cryptophytes, diatoms and *P.*  
9 *antarctica*, contributing to, on average, more than 70% of the total Chl *a*.  
10 Although those three phytoplankton groups together comprised most of the  
11 biomass in the region, cryptophytes were the dominant group at the surface  
12 (Fig. 4) and the greatest contributions (>75% in 2013; >65% in 2014; >50% in  
13 2015) were observed in association with warmer surface waters at the  
14 northwestern sector of the Gerlache Strait (Fig. 3). In addition, cryptophytes  
15 were conspicuously found in the upper layer (0–25 m), above the pycnocline, as  
16 the main contributors to total phytoplankton biomass (Fig. 5). Apparently, the  
17 distribution of cryptophytes biomass in the Gerlache Strait was mostly  
18 associated with the sea surface temperature (Fig. 6), rather than salinity (Fig.  
19 S3 in Supplementary Material). *P. antarctica* appeared as the second most  
20 representative taxonomic group in 2013 (Fig. 4a), being replaced by diatoms in  
21 2014 (Fig. 4b) and 2015 (Fig. 4c); both groups surpassing the cryptophytes  
22 below 25 m depth, where their contributions were always below 20% of the total  
23 Chl *a*. Green flagellates, dinoflagellates and the “chemotaxonomic group”  
24 showed much lower biomass and were combined and hereafter presented as

1 “others” (Fig. 4), except for the statistical analyzes (CCA), where the individual  
2 groups were used separately.

3

### 4 3.3. Photo-pigment indices

5       There was a parallel variability in photo-pigment indices with changes in  
6 community structure at stations along the Gerlache Strait (Fig. 7). The  $Chl_{aTP}$   
7 index varied between 0.4 and 0.6, with highest values found in the surface  
8 layers and associated with a community dominated by cryptophytes. Similarly to  
9  $Chl_{aTP}$ , the  $PPC_{TP}$  at the surface increased, following the higher proportion of  
10 cryptophytes (Fig. 7a). In contrast, increases in surface  $PSC_{TP}$  were mainly  
11 associated with higher proportions of both diatoms (Fig. 7b) and *P. antarctica*  
12 (Fig. 7c), declining to  $\sim 0.1$  in samples with dominance of cryptophytes. The  
13 photo-pigment indices in deeper layers (Figs. 7d-f) were generally constant, and  
14 no particular trend was associated with any phytoplankton group. It is also  
15 noteworthy that the  $PSC_{TP}$  was generally greater in deep than surface layers,  
16 while  $PPC_{TP}$  was higher at the surface, especially in regions with a clear  
17 dominance of cryptophytes ( $> 60\%$  of total Chl *a*), where  $PPC_{TP}$  exceed  $PSC_{TP}$   
18 (Fig. 7a).

19

### 20 3.4. Phytoplankton response to environmental drivers

21       Relationships between phytoplankton and environmental variables  
22 showed that the seven selected variables significantly contributed ( $p < 0.01$ ) to  
23 explain the spatial distribution of phytoplankton groups, based on a Monte Carlo  
24 test on F-ratio. The multivariate analysis showed a strong association between

1 phytoplankton groups and seawater physical and chemical properties (Fig. 8).  
2 The CCA explained 90.6% of the variance associated with the phytoplankton-  
3 environment relationship. The first canonical axis alone explained 65.2% of the  
4 variance. Cryptophytes were found to be strongly associated with high values of  
5 temperature, stability and Chl *a*, and negatively associated with nutrient  
6 concentrations, UMLD and salinity. *P. antarctica* had an opposite trend with  
7 respect to these environmental variables, being strongly associated with high  
8 magnitudes of salinity, UMLD, DIN and phosphate concentrations, and  
9 negatively associated with temperature, Chl *a* and stability. The diatoms and  
10 other minor groups were associated with low values of both temperature and  
11 Chl *a*, high silicic acid concentrations, and intermediate values of other  
12 variables such as stability, salinity and UMLD.

13 In order to visually illustrate the effects of environmental drivers on  
14 cryptophytes abundance in the region, spatial variations (along sampling  
15 stations) in both cryptophytes biomass ( $\text{mg m}^{-3}$  Chl *a*) and physical parameters  
16 (temperature, UMLD and stability) are shown in Fig. 9 for the 2013 sampling  
17 year. At both ends of the strait, deeper UMLD were associated with lower  
18 temperature and stability values, where biomass levels were also low. In  
19 contrast, between stations G09 and G13, significantly higher cryptophytes  
20 biomass levels were coupled with warm and stable waters, and shallow UMLD  
21 (10-20m).

22

#### 23 **4. Discussion**

24

1           A recent long-term study (Moreau et al., 2015), based on satellite-derived  
2 data, evaluated the impact of climate change on primary production (PP) in the  
3 WAP area covered in this work. It was concluded that climate changes had an  
4 overall positive impact on PP, mainly due to decrease in sea ice spatial and  
5 temporal extent, which, in turn, increases the length of the phytoplankton  
6 production season and, therefore, enhances annual PP rates. Scarcity of *in-situ*  
7 data, however, leaves open questions regarding the effects of climate change  
8 on composition/structure of phytoplankton communities.

9           Stratification is a primary condition for seasonal development of algal  
10 blooms (Margalef et al., 1979), mainly after a turbulent condition, as it creates a  
11 stable surface layer that allows for the maintenance of phytoplankton in a  
12 favorable light regime. On the other hand, physical gradients in coastal waters  
13 under contrasting stratification conditions are important environmental factors  
14 controlling the size structure and species composition of Antarctic  
15 phytoplankton (e.g. Rodríguez et al., 2002; Mendes et al., 2012). It has been  
16 suggested that the critical depth, or the depth at which water-column net growth  
17 equals respiration, ranges from 50 to 80 m in the Southern Ocean during the  
18 growth season (Nelson and Smith, 1991; Boyd et al., 1995). In the present  
19 work, shallower mixed layers (< 25 m; Table 1) than those critical-depth  
20 estimates were found throughout the Gerlache Strait and cryptophytes emerged  
21 as the most important phytoplankton group in the three years period (Fig. 4),  
22 and were mainly confined within the relatively warm waters in the surface layers  
23 (Fig. 3). Particularly, the highest cryptophytes biomass was associated with  
24 strong water column stratification, indicated by a strong stability (see CCA  
25 results in Fig. 8) at the northwestern sector of the Strait, characterized by a



1 warmer upper layer. A generally negative association with salinity (see Fig. 8),  
2 was probably due to an influence of this variable on water column stratification,  
3 as suggested by the close relation between salinity and density profiles (see  
4 Fig. S4 in the Supplementary Material), although a direct negative relationship  
5 of cryptophytes with salinity was not possible to demonstrate for the three  
6 studied years (Fig. S3 in the Supplementary Material). Opposite association  
7 with nutrient levels (Fig. 8), on the other hand, is an indication of consumption  
8 within the relatively dense cryptophyte patch. However, the generally high  
9 concentrations of N, P and Si in the surface layer (see Table 1) do not suggest  
10 a limitation by those macronutrients. Although cryptophytes were the major  
11 group contributing to total phytoplankton biomass (Chl *a*) in the region, during  
12 the studied years, *P. antarctica* occurred associated with more saline, nutrient-  
13 rich waters, in 2013, while diatoms were moderately correlated with both water  
14 column stability and high silicic acid concentrations that prevailed particularly in  
15 2015. Those different patterns between groups (*P. antarctica* vs. diatoms) may  
16 be related to different stages in phytoplankton development and succession in  
17 the 3-year period.

18 Part of the upper ocean warming in the region is thought to be due to  
19 atmospheric conditions, with heat transfer facilitated by greater amounts of ice-  
20 free waters from spring to autumn (Ducklow et al., 2013). The WAP has been  
21 pointed out amongst the regions with the highest rates of regional warming  
22 anywhere (+7°C in air temperature since 1950; Turner et al., 2013). In addition,  
23 a significant source of heat input to the WAP region is due to intrusions of warm  
24 mid-depth Upper Circumpolar Deep Water from the Antarctic Circumpolar  
25 Current along the glacially scoured canyons in the inner shelf regions

1 (Martinson and McKee, 2012). Based on data presented here, including results  
2 in Moreau et al. (2015), we believe that the Gerlache Strait region is being  
3 affected by several environmental factors (e.g. early retreat of sea ice and  
4 increase in sea surface temperature) that may lead to widespread upper water  
5 column stratification. This certainly favors opportunistic small-sized and motile  
6 species, such as cryptophytes (this study and Mendes et al., 2013). In order to  
7 summarize the conditions leading to cryptophytes domination in the Gerlache  
8 Strait, a conceptual graph is shown for the region, evidencing the main  
9 processes observed in the present work (Fig. 10).

10 Under shallow mixed layers and stratified conditions, marine organisms  
11 are confined to surface waters that are highly exposed to irradiance, as  
12 observed in early spring of 2006 in the WAP (Moreau et al., 2010). Due  
13 primarily to a greater exposure to direct incoming irradiance, including a  
14 particularly high exposure of the WAP region to the atmospheric ozone hole,  
15 photoinhibition by both PAR and UVB radiation have apparently increased  
16 during the austral spring, affecting photosynthesis (Moreau et al., 2015).  
17 Although a connection of cryptophytes with stratified conditions along the WAP  
18 has been previously discussed (e.g. Moline and Prézelin, 1996; Moline et al.,  
19 2004; Mendes et al., 2013), an association of this group with high light exposure  
20 has not been explicitly addressed, partly due to difficulty in quantifying their  
21 photosynthetic responses in the environment. Here, we hypothesize that  
22 cryptophytes would bear photophysiological plasticity to tolerate high  
23 irradiances in the upper layers of the Antarctic coastal waters and thrive under  
24 such conditions. In order to optimize aquatic photosynthesis, light capture has  
25 to be carefully balanced with the photoprotective capacity to avoid over-

1 excitation of the photosystems. Several protective mechanisms can be  
2 activated when light absorption exceeds its utilization in photosynthesis. One of  
3 these is non-photochemical quenching (NPQ), a feedback mechanism by which  
4 excessive light irradiation is dissipated as heat (Horton et al., 2005). This fast  
5 response to high light stress consists of two major components: energy  
6 quenching (qE), activated within seconds to minutes, and inhibitory quenching  
7 (qI) which is slower and relaxes within 1–2 h in the dark (Niyogi, 1999). The  
8 mechanisms of NPQ operation vary among different phototrophs; for instance,  
9 in green algae, qE activation requires the conversion of violaxanthin to  
10 zeaxanthin by the enzyme violaxanthin de-epoxidase (VDE) in the so-called  
11 xanthophyll cycle. On the other hand, the main xanthophyll cycle in most  
12 chromalveolates (with chlorophyll *c*-containing plastids, e.g. diatoms) involves  
13 the conversion of diadinoxanthin to diatoxanthin (Lohr et al., 2001; Goss et al.,  
14 2010). However, NPQ in cryptophytes significantly differ from other  
15 chromalveolates, in the following ways: i) they lack a light induced xanthophyll  
16 cycle; ii) their NPQ is similar to the qE of higher plants, which is flexible and  
17 presents a fast recovery; and iii) they show a direct antennae protonation in  
18 NPQ mechanism, similarly to higher plants (discussed in detail by Kaňa et al.,  
19 2012). In addition, unlike other chromalveolate microalgae, they use both  
20 chlorophyll *a/c* proteins and phycobiliproteins (acquired from a red algae  
21 symbiotic ancestral), as light harvesting pigment complex. In addition to NPQ,  
22 some cryptophytes have also been shown to display state transitions, which are  
23 also an important mechanism for balancing the excitation energy between  
24 photosystems, either under light limitation or as a protection against  
25 photoinhibition, therefore optimizing photosynthetic capacity (Cheregi et al.,

1 2015). Those characteristics confer to cryptophytes a unique effective and  
2 flexible mode of photoprotection mechanism, which could explain their biomass  
3 level within the Gerlache Strait and other similar coastal sites around the WAP.

4       Regarding effects of irradiance on accessory pigment ratios associated  
5 with the chlorophyll a/c antennae, the role of alloxanthin in cryptophytes has  
6 been recognized as a photoprotective pigment. For instance, increases in  
7 alloxanthin:Chl a ratio have been observed in cultures of cryptophytes  
8 acclimated to high light (e.g. Funk et al., 2011). Additionally, in 2014, high  
9 irradiance exposure resulted in increasing ratios of alloxanthin to Chl a, during a  
10 trial incubation experiment with natural populations dominated by cryptophytes  
11 in the region (data not shown). This also suggests a photoprotective function.  
12 Thus, although cryptophytes do not possess a xanthophyll cycle, they are able  
13 to induce synthesis of the protective carotenoid alloxanthin under light stress,  
14 presumably enhancing NPQ capacity. In agreement with this argument, in this  
15 study we found alloxanthin to be the major carotenoid that contributed to the  
16 increase in PPC proportions at surface (see Fig. S5 in Supplementary Material),  
17 in close association with the dominance of cryptophytes. Further, both  $Chl_{TP}$   
18 and  $PPC_{TP}$  indices increased concomitantly with an increase in the proportion of  
19 cryptophytes (Fig. 7a). Although those indices may have been somewhat  
20 under/over-estimated by not including phycobiliprotein concentrations, there is  
21 biochemical evidence that NPQ in cryptophytes occur mainly in the chlorophyll  
22 a/c antennae and not mediated by phycobiliproteins (MacIntyre et al., 2002).  
23 Therefore, results with pigment indices indicate an optimization of light-  
24 harvesting capability, since Chl a increase is normally associated with increase  
25 in the number of photosystems (MacIntyre et al., 2002), while providing

1 photoprotection against both excitation pressure on the photosynthetic  
2 apparatus and light induced reactive oxygen species damages (Kirk, 2011)  
3 through increases in PPC. All those adaptive strategies probably contribute in  
4 allowing cryptophytes to grow and dominate over other phytoplankton groups at  
5 stratified surface layers in the WAP coastal waters. Other organisms have also  
6 shown photophysiological advantages under high light exposure, due to a high  
7 concentration of photoprotective pigments, such as the diatom *Fragilariopsis*  
8 *cylindrus*, which dominates in highly stratified conditions in the Ross Sea (Arrigo  
9 et al., 2010), suggesting that light is a major factor in shaping phytoplankton  
10 communities in the region. In fact, in the present work, cryptophytes abundance  
11 showed a notable association with *Fragilariopsis* concentration (see Fig. S6 in  
12 Supplementary Material), suggesting an adaptation of those organisms to the  
13 prevailing light conditions in the region. However, further information on  
14 cryptophytes photoacclimation is needed to clarify whether special features in  
15 light utilization capabilities, as suggested here, are responsible for the observed  
16 dominance of cryptophytes in Antarctic coastal waters. Moreover,  
17 ecophysiological studies (both *in situ* and *in vivo*) on cryptophytes are still  
18 scarce, and photosynthetic characterization of these organisms are available  
19 only for a very few studied species.

20 In short, this study shows that the recurrent growth and dominance of  
21 cryptophytes, previously documented in the WAP region (e.g. Moline et al.,  
22 2004; Mendes et al., 2013; Gonçalves-Araujo et al., 2015), can be attributed to  
23 their abilities to grow and thrive under stratified conditions, where they have to  
24 withstand extreme light levels normally found in confined stratified upper layers.  
25 Such conditions are becoming more frequent and intense in coastal waters of

1 the WAP and will probably have significant implications to the regional food web  
2 and biodiversity patterns.

3

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23

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1 **Figure captions**

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3 **Figure 1:** Location of hydrographic stations sampled during 2013, 2014 and  
4 2015 summer cruises. The black box in the inset shows the Gerlache Strait  
5 close to the northern Antarctic Peninsula (AP). Other abbreviations are as  
6 follows: Drake Passage (DP), South Shetland Islands (SSI), Bransfield Strait  
7 (BS), Weddell Sea Shelf (WSS), Brabant Island (BI) and Anvers Island (AI). The  
8 bathymetry is represented by the color scale bar at the right.

9

10 **Figure 2:** Sea surface salinity values at individual sampling stations for the  
11 three sampling years in the Gerlache Strait during early February.

12

13 **Figure 3:** Surface distribution of both relative percentage contribution of  
14 cryptophytes to total chlorophyll *a* (contour lines) and potential temperature (°C;  
15 color scale) for **(a)** 2013, **(b)** 2014 and **(c)** 2015.

16

17 **Figure 4:** Average and standard deviation of depth distribution of phytoplankton  
18 groups' biomass (as Chl *a* concentration) calculated through the CHEMTAX  
19 software at the Gerlache Strait in late summer of **(a)** 2013, **(b)** 2014 and **(c)**  
20 2015. Note the different scales in chlorophyll *a* concentration.

21

22 **Figure 5:** Relationship between values of cryptophytes' biomass (as Chl *a*  
23 concentration) and total chlorophyll *a* at the surface in the Gerlache Strait during  
24 the three sampling years.

25

26 **Figure 6:** Relationship between cryptophytes' biomass (as Chl *a* concentration)  
27 and sea surface temperature (°C) for the Gerlache Strait during the three  
28 sampling years.

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30 **Figure 7:** Relationships between selected photo-pigment indices and  
31 proportions of major phytoplankton groups for surface **(a-c)** and deep **(d-f)**  
32 samples.  $Cha_{TP}$  = total chlorophyll *a* / total pigments;  $PSC_{TP}$  = photosynthetic

1 carotenoids / total pigments;  $PPC_{TP}$  = photoprotective carotenoids / total  
2 pigments. See text for more details.

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4 **Figure 8:** Canonical Correspondence Analysis ordination diagram of absolute  
5 contributions of different phytoplankton groups at sea surface. The first two  
6 ordination axes represent 54.6% of the total phytoplankton group's variance and  
7 90.6% of phytoplankton groups-environment relationships. Arrows indicate  
8 environmental variables [water column stability (Stability), upper mixed layer  
9 depth (UMLD), and sea surface temperature (T), salinity (Salinity) and dissolved  
10 inorganic nitrogen (DIN), phosphate (PO<sub>4</sub>) and silicic acid (SiO<sub>2</sub>)]. Blue crosses  
11 refer to absolute contributions of phytoplankton groups. Chemo. group =  
12 "chemotaxonomic group" and *P. antarctica* = "*Phaeocystis antarctica*". Stations  
13 are separated according to sampling year (blue circles = 2013; green triangles =  
14 2014; yellow squares = 2015). St. 10 (2013), 14 (2015) and 16 (2013) are  
15 labeled because they represent distinct environmental and biological conditions,  
16 and their vertical profiles are shown in Fig. S4 (see Supplementary Material).

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18 **Figure 9:** Absolute contributions ( $\text{mg m}^{-3}$  Chl *a*) of cryptophytes to total  
19 chlorophyll *a* estimated by CHEMTAX at individual sampling stations, using  
20 HPLC pigment data in 2013, and respective sea surface temperature, upper  
21 mixed layer depth and stability values.

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23 **Figure 10:** Schematic representation of conditions found in this work along the  
24 Gerlache Strait, where dominance of cryptophytes was observed in the  
25 summers of 2013, 2014 and 2015.

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1 **Table 1:** Average, standard deviation (in parentheses), minimum and maximum  
 2 (in square brackets) values of environmental properties at surface (except  
 3 UMLD and Stability) in the three sampling years (2013, 2014 and 2015).

<b>Environmental properties</b>	<b>2013 (n=16)</b>	<b>2014 (n=16)</b>	<b>2015 (n=15)</b>
Temperature (°C)	1.32 (0.45) [0.86; 2.14]	1.21 (0.32) [0.68; 1.78]	1.12 (0.42) [0.33; 1.81]
Salinity	33.93 (0.15) [33.59; 34.21]	33.62 (0.18) [33.30; 34.02]	33.69 (0.24) [33.33; 34.20]
UMLD (m)	24.3 (12.8) [10; 48]	18.6 (8.5) [10; 39]	16.1 (5.4) [10; 27]
Stability ( $10^{-6}$ rad <sup>2</sup> m <sup>-1</sup> )	4.29 (1.52) [2.19; 7.92]	6.77 (1.49) [3.58; 9.00]	6.32 (2.01) [1.89; 8.83]
DIN ( $\mu$ M)	28.07 (1.32) [25.82; 30.98]	19.62 (3.26) [13.56; 25.08]	30.45 (7.51) [20.41; 40.15]
Phosphate ( $\mu$ M)	1.59 (0.27) [1.17; 2.14]	0.64 (0.23) [0.31; 1.08]	1.65 (0.32) [1.10; 2.13]
Silicic acid ( $\mu$ M)	40.38 (1.74) [37.95; 44.25]	30.49 (1.76) [26.54; 32.60]	75.09 (10.67) [59.37; 96.31]
Chlorophyll <i>a</i> (mg m <sup>-3</sup> )	1.22 (0.38) [0.66; 2.29]	1.54 (0.39) [0.95; 2.12]	1.01 (0.42) [0.24; 1.87]

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