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Phaeocystis antarctica unusual summer bloom in stratified antarctic coastal waters (Terra Nova Bay, Ross Sea)

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51 **1. Introduction**

52 Coastal Antarctic pelagic food webs are primarily based on two main photoautotrophic 53 communities comprising: diatoms and haptophytes (e.g. Phaeocystis antarctica) (DiTullio and 54 Smith, 1996; Alderkamp et al., 2012; Smith et al., 2014; Mangoni et al., 2017). The relative 55 dominance of diatoms and haptophytes varies on different temporal and spatial scales and thereby 56 can have major implications on trophodynamics and CO₂ drawdown processes in the Ross Sea 57 (Sweeney et al., 2000; Arrigo et al., 1999; Saggiomo et al., 2000; Arrigo et al., 2002; Schoemann et al., 2005; Peloquin and Smith, 2007). P. antarctica populations can exist as both solitary cells (3-4 58 59 μ m in size) and palmelloides colonies (> 2 mm) that can differ by several orders of magnitude in 60 size (Mathot et al., 2000; Schoemann et al., 2005). Grazing rates on Phaeocystis appear to be low due to the large size of colonies (Caron et al., 2000; Lonsdale et al., 2000; Elliot et al., 2009; Tang 61 et al., 2008), so that diatom blooms may represent a critical ecological link between primary 62 production and higher trophic levels in the Ross Sea. 63

64 Mixed layer depth (MLD) has been correlated to phytoplankton community structure, with diatoms and *Phaeocystis* populations dominating under shallower and deeper MLD conditions, 65 respectively (DiTullio and Smith, 1996; Arrigo et al., 2000; Mathot et al., 2000; Arrigo and van 66 67 Dijken, 2004; Arrigo et al., 2010; Mills et al., 2010). According to the accepted current paradigm, 68 water column stratification favors diatom dominance under high light conditions due to their 69 physiological superiority in photoprotection and their high tolerance to photoinhibition compared to 70 P. antarctica populations (Saggiomo et al., 2002; Kropuenske et al., 2009; Mangoni et al., 2009; 71 Arrigo et al., 2010; Mills et al., 2010). In addition, water column iron bioavailability is critical for 72 sustaining high diatom relative growth rates in high macronutrient regions such as the Ross Sea 73 (Martin et al., 1990). As a result, diatoms typically dominate in iron enriched stratified waters like 74 marginal ice zones (Smith and Nelson, 1985; Garrison et al., 2003; Mangoni et al., 2004; Wang et al., 2014), or near melting pack ice (Sedwick and DiTullio, 1997; Saggiomo et al., 2002). In 75

76 contrast, the competitive advantage of *P. antarctica* over diatoms is thought to be due to their lower iron half-saturation constants for growth, potential to luxuriously store iron within the colonies, as 77 well as their ability to efficiently photosynthesize under relatively low or fluctuating light levels due 78 to vertical mixing of the water column (Schoemann et al., 2005; Sedwick et al., 2007; Garcia et al., 79 80 2009; Alderkamp et al., 2012). Recent studies have implicated high iron conditions in triggering 81 colony formation in P. antarctica (e.g., Bender et al., 2018). Previous work also showed that P. 82 antarctica can dominate in stratified waters when iron and light levels are high (Feng et al., 2010). 83 Although photo-physiological processes are no doubt important for sustaining diatom blooms in 84 stratified surface waters of the Ross Sea, an increasing number of studies have revealed that diatom growth can also be co-limited by Vitamin B_{12} and iron, especially during the austral summer 85 86 (Bertrand et al., 2007, 2011). In contrast, P. antarctica populations are not as susceptible as diatoms to co-limitation by Vitamin B_{12} , presumably due to the consortium of Vitamin B_{12} -producing 87 88 bacteria housed within the colonial matrix (Bertrand et al., 2007; Delmont et al., 2015).

Although diatoms and *Phaeocystis* populations typically coexist throughout the Ross Sea (Garrison et al., 2005) each taxon can form nearly monospecific blooms that can leave distinct biogeochemical signatures in the water column. For example, per unit phosphorus, *Phaeocystis* populations can assimilate nearly twice the carbon and nitrogen of diatoms (Arrigo et al., 1999; Dunbar et al., 2003, Hales and Takahashi, 2004).

94 In the open Ross Sea, chlorophyll-a concentrations within blooms of *P. antarctica* can exceed 15 mg m⁻³ (Smith et al., 1996; Smith and Gordon 1997; Arrigo et al., 1999; Smith and 95 Asper, 2001), and 65%–85% of the austral spring production as well as 36%–45% of the annual 96 97 production (Smith et al., 2006). After the seasonal decline of colonial P. antarctica in the central 98 Ross Sea phytoplankton communities are typically dominated by diverse populations of diatoms 99 and flagellated single-celled *Phaeocystis*, which tend to dominate in summer (Garrison et al., 2003; 100 Smith et al., 2014). In 2006, a European Long Term Ecological Research (LTER) site was initiated 101 near the Italian station (Mario Zucchelli) in TNB (http://www.lteritalia.it/?q=macrositi/it17-

stazioni-di-ricerca-antartide). Both LTER data as well as previous Italian expeditions to TNB (from 1987-1995) all document that the phytoplankton blooms during summer consist primarily of diatoms (Saggiomo et al., 1998; Innamorati et al., 2000; Nuccio et al., 2000; Saggiomo et al., 2000). Understanding the dynamics controlling the influence of bottom-up factors on phytoplankton species composition in Antarctic coastal waters as well as the open Southern Ocean, represents an important research area given the impact of biogeochemical cycling in the Southern Ocean on climate change processes (Boyd and Doney, 2003; Boyd et al., 2008).

In order to contribute ecological information to the Italian LTER program in TNB, four stations were occupied during the austral summer of 2009-2010. We determined various hydrographic and biological parameters to assess the relationship between the water column structure, nutrient and biochemical concentrations with the phytoplankton community.

To shed light on this topic, here we document the occurrence of an anomalous *P. antarctica* bloom occurred on the coastal area of Terra Nova Bay (Ross Sea) during the austral summer 2009-2010 and provide potential explanations using a multi-parameter correlation approach.

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117 **2. Materials and methods**

Sampling was conducted in the coastal TNB area during austral summer 2009-2010 as part of the 118 119 "LTER-Marine Observatory of Antarctic Specially Protected Area – Terra Nova Bay (MOA-TNB) 120 Project", funded by the Italian National Program for Antarctic Research (PNRA 2009/A1.13). Physical-chemical features of the water column at these LTER stations, together with 121 phytoplankton biomass measurements, have been recorded since 1989 as a component of various 122 123 oceanographic expeditions funded by PNRA (Innamorati et al., 1991; Nuccio et al., 2000; Misic et al., 2006, Povero et al., 2006, 2012). The phytoplankton community was investigated at three LTER 124 125 coastal stations, identified as: (1) Portofino (PTF), (2) Santa Maria Novella (SMN), and (3) Faraglioni (FAR). An additional station, Santa Lucia (SLC), was also sampled and is located near 126 the marginal ice zone of Tethys Bay, (Fig.1). The depths of the four coastal stations varied with the 127

- 128 shallowest being FAR (100m) and the deepest SMN (500m). The other two stations (SLC and PTF)
- had a depth of approximately 200m. The areal extent of the sampling area was $\approx 30 \text{ Km}^2$.
- 130 The stations FAR, PTF, SMN and SLC were sampled three times each between December 31,
- 131 2009 and January 13, 2010 with the 3 sampling time periods designated as T1, T2 and T3 (Table 1).
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Figure 1. Map of the sampling sites during the 2009-10 austral summer in Terra Nova Bay
(Antarctica) (ASPA n°161). Faraglioni (FAR), Portofino (PTF), Santa Maria Novella (SMN) and
Santa Lucia (SLC) stations were sampled three times each.

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Vertical profiles of temperature and salinity were acquired using an Idronaut 304 CTD. Water samples were collected by 5-L Niskin bottles in order to determine various physical and biological parameters including: inorganic nutrient concentrations, total chlorophyll *a* biomass (Chl-a), HPLC accessory pigment concentrations, phytoplankton cell concentrations via microscopy, elemental and

biochemical analyses of particulate organic matter. Meteorological data (air temperature, velocity of
wind) and solar irradiance were reported from 25 December to the end of the research activities.
Wind speed, air temperature and daily average of photosynthetically active radiation (PAR) date
were obtained from 'Meteo Climatological Observatory at the Italian Station (Mario Zucchelli
Station, MZS) of PNRA (http://www.climantartide.it).

149 2.1.Pigment Analyses

Four liters of seawater were drawn from the Niskin bottles and, after careful mixing, sub 150 151 samples were aliquoted for the analysis of total and fractionated Chl-a concentrations, and for the analysis of accessory pigments to determine the phytoplankton community. For the analysis of total 152 Chl-a, 500 ml of sea water were filtered from each depth through Whatman GF/F filters (25-mm 153 154 diameter). Size-fractionated Chl-a sea water samples were filtered through polycarbonate Nuclepore polycarbonate membranes (2 µm pore size), and a Nitex mesh (20 µm). The filtrate from each was 155 then collected on Whatman GF/F filters thereby resulting in a <2µm and a <20µm fraction, 156 respectively (see Mangoni et al. (2004) and Jeffrey et al. (2005) for additional details). The analyses 157 of size-fractionated Chl-a and phaeopigments (Phaeo) were carried out according to Holm-Hansen 158 159 et al. (1965) using a Spex Fluoromax spectrofluorometer. The instrument was calibrated and 160 checked daily with a Chl-a standard solution (Anacystis nidulans, Sigma). In order to determine 161 accessory pigments using high performance liquid chromatography (HPLC) two liters of seawater 162 were filtered onto Whatman GF/F filters (47 mm diameter) and stored at -80° C until onshore pigment analysis was performed. HPLC pigment separations were made on an Agilent 1100 HPLC 163 according to the method outlined in Vidussi el al. (1996) as modified by Brunet and Mangoni 164 (2010). The system was equipped with an HP 1050 photodiode array detector and a HP 1046A 165 166 fluorescence detector for the determination of chlorophyll degradation products. Calibration of the instruments was carried out using 20 different pigment standards provided by the International 167 Agency for ¹⁴C Determination, VKI Water Quality Institute, Copenhagen, Denmark. Three major 168 169 marker pigments were used to identify the contribution of the major phytoplankton taxa:

fucoxanthin (Fuco) as predominantly diagnostic for diatoms and 19'-hexanoyloxyfucoxanthin
(Hex) and Chlorophyll-c₃ (Chl-c₃) for *Phaeocystis antarctica* (DiTullio et al., 2003; DiTullio et al.,
2007; van Leeuwe et al., 2014). In addition, we used phaeophorbide *a* (PhaeoB *a*) as a grazing
marker as reported by Barlow et al. (1993).

174 2.2.Cell Counts

For microscopic analysis of phytoplankton cell densities, 500 ml water samples were collected and
preserved with formaldehyde (4% final concentration). Cell counts were performed with an inverted
light microscope (Zeiss Axiophot) according to the Utermöhl method (Utermöhl, 1958).

178 2.3.Nutrient Analyses and Silicate to Nitrate Ratios

Water samples for the determination of inorganic nutrient [NO₂⁻, NO₃⁻, NH₄⁺, PO₄³⁻, Si(OH)₄] 179 180 concentrations were filtered and collected in 20 ml vials and immediately stored at -20°C until analysis. The analyses were performed using a FlowSys Systea autoanalyzer, following the 181 182 procedures described by Hansen and Grassoff (1983). The ambient Si/N ratio was used as proxy to identity the possible effect of phytoplankton community composition on the water column 183 184 chemistry in TNB. In fact silicate and nitrate concentrations in the deep waters of the Ross Sea are 185 approximately 76 μ M and 32 μ M, respectively, yielding a silicate to nitrate (Si/N) ratio of ~ 2.5 186 (Gordon et al., 2000). Changes in the ambient Si/N ratio can reflect both physiological changes in diatom nutrient uptake (e.g. iron limitation) as well as changes due to phytoplankton species 187 188 composition. For example, under high iron and macronutrient replete conditions, the Si/N 189 assimilation ratio in diatoms is ~ 1 (Brzezinski, 1985). Under low iron conditions, diatom Si/N 190 uptake ratios are elevated to values > 2 (Hutchins and Bruland, 1998; Takeda, 1998).

191 2.4. Elemental and biochemical analyses of particulate organic matter

192 Aliquots of 500-2000 ml of seawater were filtered depending upon the particular biochemical

193 parameter. Water samples were filtered onto combusted Whatman GF/F filters for analyses of

- 194 particulate organic carbon (POC), particulate organic nitrogen (PON), particulate carbohydrates
- 195 (CHO) and particulate proteins (PRT). POC/PON analyses were carried out after exposing filters to

196	HCl fumes for 24h to remove the inorganic carbon fraction (Hedges and Stern, 1984).										
197	Cycloexanone 2,4-dinitrophenyl hydrazone was used as the calibration standard. Analyses were										
198	performed on an elemental analyser (Model 1100 CHN; Carlo Erba). CHO analyses were carried										
199	out following the phenol-sulphuric acid colorimetric method (Dubois et al., 1956). Absorbances										
200	were measured at 490 nm. Solutions of D(+)glucose were used as the calibration standard. The PRT										
201	assay was based on the reaction between protein amino acids and the copper sulphate-Folin										
202	Ciocalteu reagent (Hartree, 1972). Protein absorbance was measured at 650 nm using bovine serum										
203	albumin as the calibration standard. Both CHO and PRT analyses were performed using a Jasco										
204	V530 spectrophotometer.										
205	2.5.Statistical analysis										
206	Relationships between depth, Hex:Chl-c ₃ ratio, Hex:Fuco ratio, PO ₄ , Si(OH) ₄ , NO ₃ , Chl-a,										
207	temperature and salinity were investigated through Spearman correlation matrix. To investigate the										
208	relationships among environmental variables and biological features, a multivariate approach based										
209	on principal component analysis (PCA) was carried out using the XLSTAT 2017 software.										
210											
211	3. Results										
212	3.1.Environmental Parameters and Hydrography										

Atmospheric air temperatures were generally warmer (from -1° C to $+1^{\circ}$ C) during the week before the first sampling time point (T1) between December 31 and January 03 compared to the second sampling time period (T2) during the presence of a wind event (Jan 04 to Jan 08) when air temperatures decreased to approximately -2.5° C (Fig 2).

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Figure 2. Meteorological data from December 25, 2009 to January 13, 2010 in Terra Nova Bay
 (Antarctica). Wind speed (m sec⁻¹), air temperature (°C) and daily average of photosynthetically
 active radiation (PAR) (E m-² d⁻¹) were measured.

Following the wind event, air temperatures gradually increased during the T3 sampling period (Jan 09 to Jan 13) to above zero. Relatively low wind velocities (< 5.14 m sec⁻¹) were recorded for the week leading up to the T1 sampling time point with sustained winds of 10 m sec⁻¹ with gusts of 20-30 m sec⁻¹ occurring during the three day T2 sampling period between Jan 05 and Jan 08 (Fig 2). The wind event during the T2 sampling period decreased the upper water column stratification as evidenced by vertical profiles of density (Fig 3). The MLD at all stations was < 10m (using a</p>

conservative $\Delta \sigma_t = 0.125$ criterion). For example, the MLD at Station FAR was calculated to be 4m,
10m, and 3m during the T1, T2 and T3 sampling periods. Daily integrated irradiance levels were
generally higher during the T1 and T3 sampling periods and were lower during the low pressure
disturbance occurring within the T2 sampling period (Fig 2).
3.2.Water Column Stratification and Stability
The average water column stability index (E) observed in the upper 40 m of the water column at the
4 sampling stations during T1 was relatively high ($E = 2,024 \times 10^{-8} \text{ m}^{-1}$) compared to average values
observed during the vertical mixing event that occurred during T2 (e.g. $1,157 \times 10^{-8} \text{ m}^{-1}$) and the
subsequent re-stratification period occurring during T3 (18,69 x10 ⁻⁸ m ⁻¹ : Table 1). The breakdown
in vertical stratification of the water column during T2 is also evident from the σ_t vertical profiles
especially at the FAR station, where the lowest (537 $\times 10^{-8}$ m ⁻¹) value of water column stability was
observed (Table 1 and Fig 3). But even at this station the MLD only increased to 10m during the T2
period.
CERTIN



Figure 3. σ_t profiles at four stations during the 2009-2010 austral season in Terra Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the sampling periods are indicated as T1, T2 and T3.

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258 3.3. Nutrient Concentrations and N/P, Si/N ratios

259 Macro-nutrient concentrations in the photic zone were generally non-limiting with integral average

260 nitrate concentrations > 10 μ M in the upper 25m throughout the 3 sampling periods (Table 2).

261 During the course of the sampling period the nitrate to phosphate (N/P) in-situ ratio was

approximately 15.7 for all depths and stations sampled (Fig 4).



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Figure 4. Correlation between N/P ratio and $\Delta N/\Delta P$ ratio.

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The Si/N ratios recorded in TNB were approximately 2.5 at depth and ranged from 3 to 15 in most of the samples collected in the upper 25m at all 4 stations (Figure 5). The largest temporal deviation from the hypothetical 1:1 Si/N line was observed in the upper 10m during the T1 sampling period

269 before the wind event (i.e. during T2).



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Figure 5. Variation of the ambient silicate/nitrate ratio vs silicate concentration during the 2009-2010 austral season in Terra Nova Bay (Antarctica). Si/N ratios were determined in the upper water column (< 25 m depth, open symbols) and below 25m (solid symbols). The hypothetical Si/N drawdown ratio by diatoms under iron replete (solid line) and iron deplete (dashed line) conditions are also shown and assume a Si/N assimilation ratio by diatoms of 1 and 2.5, respectively.</p>

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278 3.4. Phytoplankton biomass, POC and PON concentrations

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279 Phytoplankton biomass was estimated using spectrofluorometric Chl-a concentrations (Fig 6)
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- and particulate organic carbon (POC) and nitrogen (PON) (Table 2).
- 281 In general, the Chl-a vertical profiles at specific sampling time points were similar at all stations
- 282 (Fig 6). Chl-a concentrations were maximal in near surface waters (ca.10m) at all stations and
- ranged from ~ 6 to 8 mg Chl-a m^{-3} during the T1 sampling period (Fig 6). During the T2 sampling
- 284 period, enhanced vertical mixing resulted in lower Chl-a concentrations in the upper layer (< 25m)
- relative to deeper waters (e.g. 50-120m; Fig 6).





Figure 6. Chl-a profiles at four stations during the 2009-2010 austral season in Terra Nova Bay
(Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the
sampling periods are indicated as T1, T2 and T3.

292 For example, the integral average Chl-a concentration in the upper layer (< 25m) during T1, T2 and T3 represented 71%, 54% and 36%, respectively, of the total water column integral average 293 at all 4 stations (Tables 2, 4). Total integrated Chl-a values (averaged for all 4 stations) in the layer 294 0-80m revealed the same temporal trend with the highest Chl-a values measured during T1 (275±57 295 mg m⁻²) and decreasing values at T2 (258 ± 20 mg m⁻²) and T3 (176 ± 29 mg m⁻²) (Table 4). 296 297 Generally, the micro size-class (> 20μ m) dominated the entire area reaching a maximum of 84% at station SLC 2 (below 25 m) and a minimum of 29% at station SMN 3 (upper 25 m). In the upper 298 299 25 meters of water column the percentage of micro decreased from T1 to T3, while below 25 m we observed a relative increase at SMN and FAR with values exceeding 70%. Lower Phaeo/Chl-a 300 ratios and phaephorbide concentrations were measured in the water column throughout the three 301

302 sampling periods (Table 2).

Vertical profiles of POC and PON were similar to total Chl-a profiles (Figs S1 and S2). For 303 instance, the highest POC levels were also measured in surface waters (< 10m) at all stations during 304 305 the T1 sampling period. Similar to the Chl-a trend, the integrated water column (to 80m) average POC value (for all 4 stations) was highest at T1 ($39.1 + 13.6 \text{ gC m}^{-2}$) and lowest at T3 ($30.1 \pm 4.0 \text{ gC}$) 306 m^{-2} : Table 4). PON integrated values followed the same trend as POC with the highest values 307 measured at T1 (6.2 \pm 1.4 gN m⁻²) and the lowest at T3 (4.7 \pm 0.6 gN m⁻²). The integrated POC:Chl-a 308 ratio at T1 and T2 time were 180 and 200 respectively, with a maximun of 288 at T3 when we 309 310 found a strong differences between the upper (0-25 m) and deeper layer (410 and 166). The 311 integrated protein:carbohydrate (PRT:CHO) ratio ranged from 1.5 (T1) to 1.8 (T3) with slightly higher values in the upper layer of the water column during T1 and T2. 312 Phytoplankton composition was assessed using microscopic cell counts and HPLC pigment 313

314 composition (Table 3, Fig 7).

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Figure 7. Hex:Fuco ratio profiles at four stations during the 2009-2010 austral season in Terra
 Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and
 the sampling periods were indicated as T1, T2 and T3.

As is typical of the Ross Sea polynya, the TNB phytoplankton assemblages was dominated by 325 diatoms and the colonial haptophyte, *Phaeocystis antarctica*. In terms of cell abundances, the P. 326 327 antarctica population dominated the community assemblage throughout the sampling periods at all stations (Table 3). In fact, colonial *P. antarctica* cells comprised an average of 79±14% of the total 328 329 phytoplankton cell abundance in the upper 10m and approximately $93\pm5\%$ in deeper waters (50-80m; Table 3). Relative diatom populations (i.e. % total) were more prevalent in the upper 10m of 330 the water column compared to 50-80m. In addition, enhanced vertical mixing from the wind event 331 332 during the early T2 sampling period caused an increase of 4-10 fold (at SLC) in the % diatom 333 abundance in the upper 10m during the T3 time period relative to T2 (Table 3). The diatom community composition at all stations and times was dominated by four species that represented 334 335 approximately 88±5% of the total diatom cell abundance with *Fragilariopsis cylindrus* dominating 336 the diatom biomass.

337 The diagnostic photosynthetic pigments fucoxanthin (Fuco) and 19'hexanoyloxyfucoxanthin (Hex) that reflective of diatoms and *P. antarctica* dominance were reported (Fig 7). The highest 338 339 Hex:Fuco ratios (ca. 3 to 4) were generally found in the upper 10m during the T1 period with lower ratios (i.e. <1) observed during T3 (Fig 7). Moreover, the Hex:Chl-c₃ ratio can be used as diagnostic 340 341 of *P. antarctica* populations because these pigment markers are not typically present in diatoms of the Ross Sea (DiTullio et al., 2003). In addition, pigment ratios such as Hex:Fuco and Hex:Chl-c₃, 342 343 can be influenced by environmental variables such as iron concentrations (DiTullio et al., 2007; van Leeuwe and Stefals, 2007). During T1 sampling, the Hex:Chl-c₃ ratios (4-6) were 2-3 fold higher in 344 the upper 10m compared to ratios (~2) measured in the lower photic zone (Fig 8). Similarly, 345 Hex:Chl-c₃ ratios were higher in the upper 25m compared to the lower zone except for the T3 346 347 sampling at the SMN station where low values were also observed near the surface (Fig 8). In the 348 upper 25m, the Hex:Chl-c₃ ratios decreased during the T2 sampling period at 3 of the 4 stations.



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Figure 8. Hex:Chl- c_3 profiles at four stations during the 2009-2010 austral season in Terra Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the sampling periods are indicated as T1, T2 and T3.

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359 **3.6.** *Principale Component Analysis*

A multivariate approach based on principal component analysis (PCA) was carried out to
investigate the relationships among environmental variables (e.g. temperature, salinity, nutrients)
and biological features including phytoplankton biomass and pigments ratio (e.g. Chl-a, Hex:Fuco,
Hex:Chl-c₃). The first two principal components (F1 and F2) explained 79.7 % of the total variance,
with F1 and F2 accounting for 46% and 34.7% respectively (Fig 9).

The F1 component mainly explained the environmental variability, while F2 the biological one. 365 366 The Si(OH)₄ and NO₃⁻ concentrations were positively correlated with salinity and depth along the negative F1 axis, while the Hex:Chl-c₃ ratio was directly correlated with temperature along the 367 368 positive F1 axis. In the Ross Sea, high Hex: Fuco ratios are typically indicative of a community 369 composition that is dominated by the presence of *P. antarctica*. Hex:Fuco ratios were significantly 370 correlated with total phytoplankton biomass (Chl-a) as revealed by the Spearman correlation index and the correlation was also shown along the positive F2 axis of the PCA analysis (Table 5, Fig 9). 371 372 The observations in the first quadrant of the PCA were represented by shallow water samples (i.e. 5-10 m) collected between December 31, 2009 and January 6, 2010. The second quadrant was 373 characterized by the presence of samples collected between January 08 to 11 in the first 25 m of the 374 375 water column, in which temperature and the Hex:Chl-c₃ ratio were strongly correlated (Fig 9). 376 Other observations between the third and fourth quadrants show high correlations of high nutrient concentrations and high salinity associated with increasing depth (Fig 9). An inverse correlation 377 378 was observed between the higher salinity and nutrient concentrations in deeper waters and the 379 higher temperature and Hex:Chl-c₃ ratios in surface waters (Table 5, Fig 9).



Biplot (axes F1 and F2: 82,72 %)

Active variables
 Active observations

Observation	Obs1	Obs2	Obs3	Obs4	Obs5	Obs6	Obs7	Obs8	Obs9	Obs10
Station	DTE 1	DTE 1	DTE 1	DTE 1	DTE 1	DTE 1	DTE 1	EAR 1	EAR 1	EAP 1
Station			E II I				F II I	L'AN L	TAK I	
Depth (m)	0	5	10	25	50	80	120	0	5	10
Observation	Obs11	Obs12	Obs13	Obs14	Obs15	Obs16	Obs17	Obs18	Obs19	Obs20
Station	FAR 1	FAR 1	FAR 1	SMN 1	SMN 1	SMN 1	SMN 1	SMN 1	SMN 1	SMN 1
Depth (m)	25	50	80	0	5	10	25	50	80	120
Observation	Obs21	Obs22	Obs23	Obs24	Obs25	Obs26	Obs27	Obs28	Obs29	Obs30
Station	PTF 2	PTF 2	PTF 2	PTF 2	PTF 2	PTF 2	PTF 2	SLC 2	SLC 2	SLC 2
Depth (m)	0	5	10	25	50	80	120	0	5	10
Observation	Obs31	Obs32	Obs33	Obs34	Obs35	Obs36	Obs37	Obs38	Obs39	Obs40
Station	SLC 2	SLC 2	SLC 2	SLC 2	FAR 2	FAR 2	FAR 2	FAR 2	FAR 2	FAR 2
Depth (m)	25	50	80	120	0	5	10	25	50	80
Observation	Obs41	Obs42	Obs43	Obs44	Obs45	Obs46	Obs47	Obs48	Obs49	Obs50
Station	SMN 2	SMN 2	SMN 2	SMN 2	SMN 2	SMN 2	SMN 2	PTF 3	PTF 3	PTF 3
Depth (m)	0	5	10	25	50	80	120	0	5	10
Observation	Obs51	Obs52	Obs53	Obs54	Obs55	Obs56	Obs57	Obs58	Obs59	Obs60
Station	PTF 3	PTF 3	PTF 3	PTF 3	FAR 3	FAR 3	FAR 3	FAR 3	FAR 3	FAR 3
Depth (m)	25	50	80	120	0	5	10	25	50	80
Observation	Obs60	Obs61	Obs62	Obs63	Obs64	Obs65	Obs66	Obs67		
Station	FAR 3	SLC 3	SLC 3	SLC 3	SLC 3	SLC 3	SLC 3	SLC 3		
Depth (m)	80	0	5	10	25	50	80	120		

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Figure 9. Results of principal component analysis (PCA). The multivariate approach was applied to
 environmental (temperature, salinity, nutrients) and biological variables (Chl-a, Hex:Fuco, Hex:Chl C₃). The table reported the correspondence from observations with station and sample depth.

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388 **4. Discussion**

389 During the austral summer 2009-2010, an intense phytoplankton bloom was observed in the surface

390 stratified waters of coastal TNB region. Several lines of evidence, ranging from microscopic cell

counts, chemotaxonomic pigment ratios, macronutrient ratio indices (e.g. Si/NO₃), revealed the
 dominance of *Phaeocystis antarctica* populations in the upper (< 25m) water column.

393 Typically, diatom populations have been observed to dominate in stratified Antarctic coastal waters, in marginal sea ice zones, and near melting pack ice under presumably relatively high iron 394 395 and macronutrient concentrations (Smith and Nelson, 1985; Sedwick and DiTullio, 1997; Saggiomo et al., 2002). Since the mid-1980's, diatoms have dominated algal blooms in stratified water 396 397 columns of the western Ross Sea and especially within TNB (Innamorati et al., 1991; DiTullio and 398 Smith, 1996; Nuccio et al., 2000; Arrigo et al., 2000). Several studies have suggested that the 399 photo-physiological superiority of diatoms relative to P. antarctica in stratified waters was due to 400 their ability in photoprotection processes as well as their high tolerance to photoinhibition via heat dissipation (e.g. xanthophyll cycle) (Ryan-Keogh et al., 2017; Kropuenske et al., 2009; Mills et al., 401 2010; Arrigo et al., 2010; Alderkamp et al., 2012). In contrast, the ability of P. antarctica to 402 403 dominate over diatoms in well-mixed water columns is related to their dynamic range in the 404 photophysiological parameters α and β (the initial slope and inhibitory portion of the productivity vs irradiance curve), respectively (Mills et al., 2010). In addition, a lower iron half-saturation constant 405 406 for growth relative to diatoms has been reported (Garcia et al., 2009).

407 Measurement of cell abundances via microscopy (Utermöhl method) in this study revealed that *P*. 408 *antarctica* constituted an average of 79% (14,187,997 cells L^{-1}) of the total cell counts in the upper 409 10m of the water column and 93% (14,497,473 cells L^{-1}) in the lower zone (50-80m) during the 3 410 sampling periods (Table 3). Visual observations of the colonial *P. antarctica* bloom in surface 411 waters were also noted by the clogging of plankton and fish nets (Figs S3 and S4).

- 412 The N/P disappearance ratio was non-Redfieldian and led to higher N/P ratios (23.5±7.5) in the
- 413 upper 10m compared to those measured (15.6) in the lower photic zone (i.e. > 25m), presumably
- 414 reflective of the dominance of *P. antarctica* populations in the upper 10 m (Fig 4; Arrigo et al.,
- 415 1999; Dunbar et al., 2003).

Integrated Chl-a values ranged from 275 ± 20 mg Chl-a m⁻² during T1 to 176 ± 29 mg Chl-a 416 417 m^{-2} at T3 (Table 4). The decrease of Chl-a concentrations, integrated over the water column (0-80) m), from T1 to T3, was not probably due to zooplankton grazing on the colonial *P. antarctica* as 418 419 relatively constant levels of Phaeo:Chl-a ratio and pheophorbide concentrations were measured 420 throughout the three sampling periods (Table 2). Accordingly, previous studies have also indicated 421 that colonial blooms of *P. antarctica* are not effectively grazed in the Ross Sea (Caron et al., 2000; 422 Lonsdale et al., 2000). For example, Euphausia superba, the primary prey for a multitude of 423 predators in Antarctic waters, can graze small colonies of *P. antarctica* but not larger colonies or 424 single cells (Haberman et al., 2003). As observed for Chl-a, POC and PON concentrations integrated over the water column increased over time (Table 4). Altogether these results suggest 425 426 that factors other than only grazing, including hydrographic processes such as particle advection or 427 export (DiTullio et al., 2000) were most likely responsible for the observed biomass decrease over 428 time.

To better understand the phytoplankton dynamics, we investigated two proxies associated 429 430 with iron limited growth in the western Ross Sea: Si/NO₃ and Hex:Chl-c₃ ratios. The Hex:Chl-c₃ 431 ratio can be a useful diagnostic proxy to determine the iron physiological status of *P. antarctica* in 432 the Ross Sea (DiTullio et al., 2003). Laboratory studies on P. antarctica have shown that Hex:Chlc₃ ratios were inversely correlated with iron physiological status, such that under conditions of 433 434 severe iron limitation the Hex:Chl-c₃ ratios (5-6) were approximately two-fold higher relative to the Hex:Chl-c₃ ratios (2-3) observed under iron replete growth conditions (DiTullio et al., 2007; van 435 436 Leeuwe and Stefels, 2007). Hex:Chl-c₃ ratios were significantly correlated with depth as determined by the Spearman correlation index (Table 5). For example, high Hex:Chl-c₃ ratios (e.g. 4 to 6) were 437 observed in the upper 10m of the water column, where colonial P. antarctica populations 438 439 dominated the community structure under relatively high stratification conditions as observed during T1 (c.f. Figs 3 and 8). Lower Hex:Chl-c₃ ratios (e.g. 2-3) were observed in the deeper layer 440 441 of the water column (i.e. > 25m) suggesting that iron concentrations were relatively higher

442 compared to the upper 25m. A previous study measured a shallow ferricline depth (~ 50m) in TNB (Station NX10; Sedwick et al., 2011) during summer 2005-2006. Hence, the wind event that 443 444 occurred during T2 resulted in a deepening of the MLD relative to T1 (Table 1) and was associated with lower Hex: Chl-c₃ ratios, especially in the upper 25m as vertical mixing presumably re-supplied 445 446 iron back into the upper 25m (Figs 3 and 8). Furthermore, the high Si/NO₃ ratios observed in the upper 25m (Fig 5) can not simply reflect the uptake of silicate due to diatoms growing under Fe-447 448 sufficient conditions, explaining the dominance of *P. antarctica* in the upper 10m. We have 449 assumed that nitrate is the major provider of nitrogen to the phytoplankton community, and that 450 relatively low denitrification rates occur in TNB as previously determined in the Ross Sea polynya 451 (Gordon et al., 2000), caused enhanced vertical mixing rates and an increase in MLD that 452 presumably replenished nutrient concentrations in the upper zone (Fig 5).

453 The colonial *P. antarctica* blooms can develop under both iron-deplete and iron replete 454 growth conditions in the Ross Sea (Feng et al., 2010; Sedwick et al., 2011; Bender et al., 2018). The presence of low turbulence and presumably elevated nutrients at the beginning of the sampling 455 456 period could have favored palmelloid stage of *Phaeocystis* as suggested by Smayda and Reynolds 457 (2001). The ability of the colonial matrix of *P. antarctica* to sequester iron could be an important 458 advantage in competing with diatoms during episodic iron delivery events (Schoemann et al., 2005). Various mechanisms have been suggested to identify the mechanisms of iron re-supply during 459 460 summer in Antarctic coastal systems that can play a pivotal role in the development and maintenance of phytoplankton blooms (Sedwick et al., 2011). These processes, for TNB, include 461 462 sea ice melt, glacial melt and lateral advection from the Victoria Land coast, from the Antarctic coastal current, sediment iron re-suspension, upwelling of circumpolar deep water onto the shelf, 463 and mesoscale eddies (Sedwick et al., 1997; Sedwick et al., 2011; McGillicuddy et al., 2015; 464 465 Marsay et al., 2017; Kohut et al., 2017; Rivaro et al., 2019).

466 Based on the lower Hex:Chl-c₃ ratio during the T2 sampling period, we hypothesized that 467 wind-induced vertical mixing resupplied iron to surface waters and was instrumental in re-fueling

the *P. antarctica* bloom and favoring it at the expenses of diatoms. Relatively lower Hex:Chl- c_3 ratios were observed in the lower water column and suggest that iron levels were relatively high compared to those in the upper 10m (Fig 8). The higher Hex:Chl- c_3 ratios in the upper water column during T1 may simply reflect the consumption of iron by the high biomass of *P. antarctica* colonies. The ability of *P. antarctica* cells to continue growing even as the bloom depletes the iron available in surface waters can be another mechanism favoring their dominance over diatoms due to their lower iron half-saturation constant for growth relative to diatoms (Garcia et al., 2009).

475 In addition to iron limitation, evidence for the co-limitation of iron and Vitamin B_{12} on phytoplankton growth has been observed in the Ross Sea (Bertrand et al., 2007; Bertrand et al., 476 2011). Since only certain bacterial species in polar waters have the ability to synthesize Vitamin 477 478 B₁₂, the possibility exists that a mutualistic symbiosis can develop between certain bacterial groups 479 that produce Vitamin B₁₂ (e.g., SAR 92, Oceanospirillaceaea spp. and Cryomorphaceae spp.) and 480 colonial P. antarctica cells as was recently shown in the Amundsen Sea (Bertrand et al., 2015; Delmont et al., 2015). The addition of iron alone has been shown to stimulate the growth of P. 481 482 antarctica cells while the addition of both iron and Vitamin B₁₂ stimulated diatoms in the Ross Sea (Bertrand et al., 2007). Hence, it is conceivable that the diatom community in TNB were co-limited 483 484 by iron and Vitamin B_{12} (e.g. Bertrand et al., 2007). Although our data do not allow us to fully demonstrate the mechanisms underlying the anomalous *P. antarctica* bloom, we hypothesize that 485 486 changes in the supply of Vitamin B_{12} in TNB, perhaps due to a shift in the bacterial community composition could explain this result. This change in Vitamin B₁₂ availability would preferentially 487 488 favor the growth of *P. antarctica* colonies over diatoms by allowing *P. antarctica* cells to sequester both iron and B₁₂ inside the colonies and away from diatoms, thereby conferring *P. antarctica* with 489 490 a competitive edge. Further studies measuring iron and Vitamin B₁₂ concentrations in TNB are 491 needed to test this hypothesis.

492 Even after several decades of study, spatial and temporal uncoupling of diatom and
493 *Phaeocystis* blooms obscures our understanding of bloom dynamics in the Ross Sea (DiTullio and

494 Smith, 1996; Smith et al., 2000). Our data do not allow us to identify the mechanism underlying the 495 anomalous *P. antarctica* bloom. Understanding the dynamics controlling the influence of bottom-up 496 factors such as iron and Vitamin B_{12} on phytoplankton species composition in Antarctic coastal 497 waters, as well as the open Southern Ocean, continues to represent an important research area, given 498 the impact of biogeochemical cycling in the Southern Ocean on climate change processes (Boyd 499 and Doney, 2002).

500 The austral summer blooms in the western Ross Sea are responsible for carbon export to deeper 501 waters (Arrigo et al., 2008) and changes in the phytoplankton community structure can have a 502 strong impact on the carbon flux and biogeochemical properties of the water column. The colonial 503 haptophyte Phaeocystis antarctica bloom that developed in TNB under a stably stratified water 504 column with a shallow MLD during summer 2009-2010, does not conform to our current understanding regarding climatological bloom dynamics in TNB. Changes in the delivery of iron 505 506 and/or Vitamin B₁₂ are the most likely factors impacting the change in the phytoplankton 507 community composition in TNB.

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Station name	Lat. S	Long. W	Bottom depth (m)	Date	Sampling periods	SST (°C)	SSS	Sigma-t (kg m ⁻³)	Water Column Stability (E) (10 ⁻⁸ m ⁻¹)	Wind speed (m sec ⁻¹)	Air Temp (°C)	Light (E m ⁻² d ⁻¹)
PTF	74°42.1	164°09	200	31-Dec	T1	0.87	33.90	26.61	1711	4	-0,81	44
				05-Jan	T2	-0.08	34.05	26.79	1157	12	-0,46	53
				09-Jan	T3	0.30	33.91	26.65	1203	4	0,08	53
SLC			200	01-Jan	T1	0.26	33.62	26.98	2210	2	-1.70	19
	74°41.16	164°07.94		06-Jan	T2	-0.38	33.77	27.13	1718	13	-2.34	27
				11-Jan	T3	0.00	34,11	27.39	1026	5	-0.06	52
)				
FAR			100	02-Jan	T1	0.38	33.69	27.03	2140	3	0.12	38
	74°42.7	164°13		06-Jan	T2	0.03	34.34	27.57	537	13	-2.34	27
				10-Jan	T3	0.91	33.16	26.57	2923	8	0.95	51
							K i					
SMC	74°43	164°13	500	03-Jan	T1	0.78	33.72	27.03	2035	12	1.24	53
				08-Jan	T2	0.03	33.92	27.23	1214	4	-1.37	39
				13-Jan	T3	1.05	33.53	26.86	2323	5	-0.51	49

4

5 Table 1. Hydrographic measurements made during the 2009-10 austral season in Terra Nova Bay (Antarctica). Station sampling sites and (time 6 period of sampling) are denoted for each of the variables. Sea surface temperature (SST) and sea surface salinity (SSS) were used to calculate sea 7 surface density (Sigma-t). Water column stability (E) in the upper 40m was calculated according to the method of Knauss and Garfield, 2017. The 8 daily average values of surface wind speed, atmospheric temperature and irradiance were tabulated.

9

Sampling periods	$\mathbf{NH_4}^+$ ($\mu \mathbf{M}$)	NO ₃ ⁻ + NO ₂ ⁻ (μM)	PO4 ³⁻ (µM)	Si(OH) ₄ (µM)	Chl-a (mg m ⁻³)	Micro- (%)	Nano- (%)	Pico- (%)	Pheo/ Chl-a	PON (mg m ⁻³)	POC (mg m ⁻³)	CHO (mg m ⁻³)	PRT (mg m ⁻³)
T1	0.91	10.71	1.06	65.14	3.88	68.7	14.4	16.8	0.45	133	780	352	636
T2	0.34	18.95	1.98	64.09	3.49	86.7	3.1	10.0	0.44	81	587	287	437
T3	0.45	12.47	1.25	62.68	1.64	43.6	31.1	25.1	0.42	65	173	173	367
•		•		•		•							
T1	1.32	9.88	1.59	60.16	3.93	69.8	20.9	9.1	0.49	131	912	562	703
T2	0.77	13.93	1.32	65.69	3.02	71.6	13.0	15.3	0.50	100	632	321	526
T3	0.88	13.07	1.32	66.83	1.33	39.1	33.1	27.7	0.52	51	316	130	299
		•		•									
T1	0.43	11.32	1.61	60.90	3.78	70.0	22.3	7.6	0.47	129	604	281	516
T2	0.33	18.57	1.91	63.99	3.93	81.8	7.8	10.2	0.43	79	473	253	465
T3	0.50	11.74	1.28	66.01	1.47	46.4	26.9	26.1	0.44	57	341	151	314
				•									
T1	0.39	10.48	1.24	64.29	3,54	75.5	16.1	8.3	0.40	90	572	380	550
T2	0.08	16.23	1.61	58.62	2.10	60.9	22.8	16.1	0.41	73	569	282	447
T3	0.25	9.86	1.06	60.28	0.42	28.3	38.9	32.6	0.72	37	328	231	116
							$\overline{}$	A	<u> </u>				
a	 +	No	DO 3-	(IVOID)						DOM	DOG	CTTO .	DDT
Sampling	NH_4	$NO_3 +$	PO_4	S1(OH) ₄	Chl-a	Micro-	Nano-	Pico-	Pheo/	PON	POC	CHO	PRI
periods	(μΜ)	NO_2^{-1}	(μΜ)	(μΜ)	$(mg m^{\sim})$	(%)	(%)	(%)	Chl-a	$(mg m^{-5})$	$(\mathbf{mg} \mathbf{m}^{\circ})$	$(mg m^{\sim})$	$(mg m^{-5})$
T1	0.73	27.30	2.06	72.61	2.14	79.7	8.9	11.2	0.50	26	209	109	129
Т2	0.14	24.57	2.19	67.34	2.46	83.0	8.1	8.7	0.46	64	390	158	311
Т3	0.90	24.78	2.07	72.65	2.22	66.9	20.3	12.7	0.48	56	403	252	357
T1	0.31	26.87	2.26	66.40	2.11	76.5	15.3	8.1	0.51	39	303	159	213
T2	0.47	22.52	1.83	62.74	2.81	84.1	9.6	6.2	0.49	64	444	257	371
T3	1.08	27.11	2.26	74.28	2.03	69.9	9.4	20.6	0.61	39	257	143	204
						•			•	•			
T1	0.19	28.56	2.23	67.26	0.85	72.8	19.0	8.1	0.50	23	141	88	88
T2	0.56	24.07	2.07	67.35	2.68	82.1	6.8	10.9	0.52	40	296	134	268
T3	0.66	28.21	2.43	75.78	2.21	80.5	10.9	8.5	0.51	43	319	119	221
T1	0.21	29.35	2.28	72.43	1.14	61.5	24.1	14.3	0.62	20	146	39	110
T1 T2	0.21 0.31	29.35 23.08	2.28 2.03	72.43 65.17	1.14 2.67	61.5 75.3	24.1 17.3	14.3 7.2	0.62 0.49	20 44	146 347	39 195	110 332
	periods T1 T2 T3 Sampling periods T1 T2 T3 T1 T2 T3 T1 T2 T3 T1 T2 T3	periods (μM) T1 0.91 T2 0.34 T3 0.45 T1 1.32 T2 0.77 T3 0.88 T1 0.43 T2 0.33 T3 0.50 T1 0.39 T2 0.08 T3 0.25 Sampling periods NH ₄ + (μM) T1 T1 0.73 T2 0.14 T3 0.90 T1 0.31 T2 0.47 T3 1.08 T1 0.19 T2 0.56	periods (μ M) NO ₂ - (μ M) T1 0.91 10.71 T2 0.34 18.95 T3 0.45 12.47 T1 1.32 9.88 T2 0.77 13.93 T3 0.88 13.07 T1 0.43 11.32 T2 0.33 18.57 T3 0.50 11.74 T1 0.39 10.48 T2 0.08 16.23 T3 0.25 9.86 Sampling periods NH ₄ ⁺ NO ₃ ⁻ + M(μ M) 11 0.73 27.30 T2 0.14 24.57 73 T3 0.90 24.78 10.90 T1 0.31 26.87 11.132 T2 0.47 22.52 13 T3 0.90 24.78 11 T1 0.19 28.56 12 T2 0.56 24.07 11 <td>periods (μM) NO₂⁻ (μM) (μM) T1 0.91 10.71 1.06 T2 0.34 18.95 1.98 T3 0.45 12.47 1.25 T1 1.32 9.88 1.59 T2 0.77 13.93 1.32 T3 0.88 13.07 1.32 T1 0.43 11.32 1.61 T2 0.33 18.57 1.91 T3 0.50 11.74 1.28 T1 0.39 10.48 1.24 T2 0.08 16.23 1.61 T3 0.25 9.86 1.06 Sampling periods NH₄⁺ NO₃⁺ + PO₄³⁻ (μM) μ μ μ T1 0.73 27.30 2.06 T2 0.14 24.57 2.19 T3 0.90 24.78 2.07 T1 0.31</td> <td>periods (μM) NO₂⁻ (μM) (μM) (μM) (μM) T1 0.91 10.71 1.06 65.14 T2 0.34 18.95 1.98 64.09 T3 0.45 12.47 1.25 62.68 T1 1.32 9.88 1.59 60.16 T2 0.77 13.93 1.32 65.69 T3 0.88 13.07 1.32 66.83 T1 0.43 11.32 1.61 60.90 T2 0.33 18.57 1.91 63.99 T3 0.50 11.74 1.28 66.01 T1 0.39 10.48 1.24 64.29 T2 0.08 16.23 1.61 58.62 T3 0.25 9.86 1.06 60.28 Sampling NH₄⁺ NO₃⁺ + PO₄³ Si(OH)₄ (μM) T1 0.73 27.30 2.06 72.65 <t< td=""><td>periods (μM) NO₂: (μM) (μM) (μM) (μM) ($mg m^{-3}$) T1 0.91 10.71 1.06 65.14 3.88 T2 0.34 18.95 1.98 64.09 3.49 T3 0.45 12.47 1.25 62.68 1.64 T1 1.32 9.88 1.59 60.16 3.93 T2 0.77 13.93 1.32 65.69 3.02 T3 0.88 13.07 1.32 66.83 1.33 T1 0.43 11.32 1.61 60.90 3.78 T2 0.33 18.57 1.91 63.99 3.93 T3 0.50 11.74 1.28 66.01 1.47 T1 0.39 10.48 1.24 64.29 3.54 T2 0.08 16.23 1.61 58.62 2.10 T3 0.25 9.86 1.06 60.28 0.42 T1</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td></t<></td>	periods (μ M) NO ₂ ⁻ (μ M) (μ M) T1 0.91 10.71 1.06 T2 0.34 18.95 1.98 T3 0.45 12.47 1.25 T1 1.32 9.88 1.59 T2 0.77 13.93 1.32 T3 0.88 13.07 1.32 T1 0.43 11.32 1.61 T2 0.33 18.57 1.91 T3 0.50 11.74 1.28 T1 0.39 10.48 1.24 T2 0.08 16.23 1.61 T3 0.25 9.86 1.06 Sampling periods NH ₄ ⁺ NO ₃ ⁺ + PO ₄ ³⁻ (μ M) μ μ μ T1 0.73 27.30 2.06 T2 0.14 24.57 2.19 T3 0.90 24.78 2.07 T1 0.31	periods (μ M) NO ₂ ⁻ (μ M) (μ M) (μ M) (μ M) T1 0.91 10.71 1.06 65.14 T2 0.34 18.95 1.98 64.09 T3 0.45 12.47 1.25 62.68 T1 1.32 9.88 1.59 60.16 T2 0.77 13.93 1.32 65.69 T3 0.88 13.07 1.32 66.83 T1 0.43 11.32 1.61 60.90 T2 0.33 18.57 1.91 63.99 T3 0.50 11.74 1.28 66.01 T1 0.39 10.48 1.24 64.29 T2 0.08 16.23 1.61 58.62 T3 0.25 9.86 1.06 60.28 Sampling NH ₄ ⁺ NO ₃ ⁺ + PO ₄ ³ Si(OH) ₄ (μ M) T1 0.73 27.30 2.06 72.65 <t< td=""><td>periods (μM) NO₂: (μM) (μM) (μM) (μM) ($mg m^{-3}$) T1 0.91 10.71 1.06 65.14 3.88 T2 0.34 18.95 1.98 64.09 3.49 T3 0.45 12.47 1.25 62.68 1.64 T1 1.32 9.88 1.59 60.16 3.93 T2 0.77 13.93 1.32 65.69 3.02 T3 0.88 13.07 1.32 66.83 1.33 T1 0.43 11.32 1.61 60.90 3.78 T2 0.33 18.57 1.91 63.99 3.93 T3 0.50 11.74 1.28 66.01 1.47 T1 0.39 10.48 1.24 64.29 3.54 T2 0.08 16.23 1.61 58.62 2.10 T3 0.25 9.86 1.06 60.28 0.42 T1</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td><td>$\begin{array}{ c c c c c c c c c c c c c c c c c c c$</td></t<>	periods (μ M) NO ₂ : (μ M) (μ M) (μ M) (μ M) ($mg m^{-3}$) T1 0.91 10.71 1.06 65.14 3.88 T2 0.34 18.95 1.98 64.09 3.49 T3 0.45 12.47 1.25 62.68 1.64 T1 1.32 9.88 1.59 60.16 3.93 T2 0.77 13.93 1.32 65.69 3.02 T3 0.88 13.07 1.32 66.83 1.33 T1 0.43 11.32 1.61 60.90 3.78 T2 0.33 18.57 1.91 63.99 3.93 T3 0.50 11.74 1.28 66.01 1.47 T1 0.39 10.48 1.24 64.29 3.54 T2 0.08 16.23 1.61 58.62 2.10 T3 0.25 9.86 1.06 60.28 0.42 T1	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$\begin{array}{ c c c c c c c c c c c c c c c c c c c$

Table 2. Nutrient, total Chl-a, size fraction Chl-a [micro- (>20μm), nano-(20-2μm), pico-(<2μm)], PON, POC, CHO, PRT concentrations and
 Phaeo/Chl-a ratios at four stations during the 2009-10 austral season in Terra Nova Bay (Antarctica). Means were integrated along the upper 25m of
 the water column (A) and below 25m (B) during the sampling periods (T1, T2 and T3).

Station name	Sampling periods	Station depth	Diatoms	P. antartica	Other flagellates	
PTF	T1	0	41.5	57.1	1.4	-
111	T2	0	5.2	93.3	1.5	
	T3	0	48.0	48.4	3.6	
	T1	10	12.5	85.6	1.9	
	T2	10	6.2	92.1	1.7	
	T3	10	14.3	73.7	12.0	
	T1	50	5.2	91.9	3.0	
	T2	50	4.8	93.7	1.5	
	T3	50	18.1	80.3	1.6	
	T1	80	10.4	89.0	0.6	
	T2	80	5.3	92.8	1.8	
	T3	80	2.3	97.5	0.2	

Station name	Sampling periods	Depth (m)	Diatoms	P. antartica	Other flagellates
FAR	T1	0	6.7	92.2	1.1
	T2	0	6.9	92.8	0.3
	T3	0	20.5	78.4	1.1
	T1	10	2.1	97.6	0.3
	T2	10	5.8	94.1	0.1
	T3	10	19.9	74.7	5.4
	IT	50	8.5	91.5	0.0
	T2	50	-	-	-
	T3	50	0.6	99.4	0.0
	5				
	T1	80	0.0	100	0.0
	T2	80	4.0	95.8	0.2
	T3	80	13.0	87.0	0.0

Other flagellates

> 4.6 3.2 1.8 1.0 2.6 2.1 1.0 0.3 1.3 0.8 0.7 0.1

18 19

Station name	Sampling periods	Station depth (m)	Diatoms	P. antartica	Other flagellates	K	Station name	Sampling periods	Depth (m)	Diatoms	P. antartica
SLC	T1	0	20.0	80.0	0.0		SMC	T1	0	17.0	78.4
	T2	0	6.5	81.0	12.5			T2	0	28.9	67.9
	T3	0	27.0	70.9	2.1			T3	0	34.0	64.2
	T1	10	1.0	98.3	0.8			T1	10	10.2	88.8
	T2	10	2.9	95.1	2.0			T2	10	32.8	64.6
	T3	10	22.3	74.2	3.4			T3	10	40.0	57.9
	T1	50	1.0	99.0	0.0			T1	50	6.5	92.5
	T2	50	7.2	91.3	1.5			T2	50	10.5	89.3
	T3	50	1.6	98.0	0.4			T3	50	3.5	95.2
	T1	80	2.4	97.3	0.3			T1	80	3.5	95.7
	T2	80	2.9	87.0	0.1			T2	80	8.3	91.0
	T3	80	4.1	95.9	0.0			T3	80	6.8	93.1

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21 Table 3. Percentage contribution of diatoms, *Phaeocystis antarctica* and other flagellates to phytoplankton community at four stations during the

22 2009-10 austral season in Terra Nova Bay (Antarctica). Cell counts were made at 0, 10, 50 and 80 m during the sampling periods (T1, T2 and T3).

Station name	Sampling periods	Chl-a (mg m ⁻²)	PON (mg m ⁻²)	POC (mg m ⁻²)	CHO (mg m ⁻²)	PRT (mg m ⁻²)			
PTF	T1	301	5510	36834	20863	29322			
	T2	269	6678	42682	20926	32427			
	T3	194	5488	35279	21433	30596			
SLC	T1	338	8267	58801	35160	45450			
	T2	262	6989	45898	26403	38611			
	T3	200	4460	27206	14772	24080			
FAR	T1	208	5878	28779	15537	22246			
	T2	271	4820	30451	15449	28590			
	T3	173	4183	26723	11234	21968			
SMC	T1	251	5172	31908	16186	27794			
	T2	229	5188	39914	19615	32942			
	T3	137	4080	31023	28781	14949			

Table 4. Chl-a, PON, POC, CHO and PRT concentrations at four stations during the 2009-10 austral season in Terra Nova Bay (Antarctica). Values are the means integrated throughout the water column (0-80 m) for the sampling periods (T1, T2 and T3).

Variables	Depth [m]	Hex:Chl-c ₃	Hex:Fuco	PO ₄	Si(OH) ₄	NO ₃	Chl-a	Temperature	Salinity
Depth [m]	1	-0.728	-0.121	0.800	0.667	0.851	-0.080	-0.906	0.854
Hex:Chl-c ₃	-0.728	1	0.102	-0.723	-0.616	-0.782	-0.141	0.810	-0.797
Hex:Fuco	-0.121	0.102	1	0.054	-0.067	-0.091	0.571	0.036	0.011
PO ₄	0.800	-0.723	0.054	1	0.605	0.930	0.026	-0.894	0.867
Si(OH) ₄	0.667	-0.616	-0.067	0.605	1	0.655	-0.126	-0.701	0.683
NO ₃	0.851	-0.782	-0.091	0.930	0.655	1	-0.062	-0.945	0.903
Chl-a	-0.080	-0.141	0.571	0.026	-0.126	-0.062	1	0.013	0.081
Temperature	-0.906	0.810	0.036	-0.894	-0.701	-0.945	0.013	1	-0.946
Salinity	0.854	-0.797	0.011	0.867	0.683	0.903	0.081	-0.946	1

Table 5. Spearman correlation matrix showing the relationship among physical, chemical and biological variables. Values in bold are significant p<0,05.

Highlights

- During the austral summer 2009-2010, an intense phytoplankton bloom was observed in the surface stratified waters of coastal Terra Nova Bay region.
- Several lines of evidence, ranging from microscopic cell counts, chemotaxonomic pigment ratios, macronutrient ratio indices, revealed the dominance of *Phaeocystis antarctica* populations in the upper water column.
- Visual observations of the colonial *P. antarctica* bloom in surface waters were also noted by the clogging of plankton and fish nets.
- By using a multi-parameter correlation approach we hypothesize that anomalously higher iron fluxes were responsible for the unusual bloom of colonial *P. antarctica* observed in Terra Nova Bay.

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