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

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ABSTRACT

This study focuses on the potential explanations for a *Phaeocystis antarctica* summer bloom occurred in stratified waters of Terra Nova Bay (TNB) - which is part of the Antarctic Special Protected Area (n.161) in the Ross Sea - trough a multi-parameter correlative approach. Many previous studies have highlighted that water column stratification typically favors diatom dominance compared to the colonial haptophyte *P. antarctica,* in the Ross Sea, and this correlation has often been used to explain the historic dominance of diatoms in TNB.

To explore the spatial and temporal progression of *P. antarctica* bloom in coastal waters, four stations were sampled three times each between December 31, 2009 and January 13, 2010.

Taxonomic and pigment composition of phytoplankton communities, macro-nutrient concentrations and various different indices, all indicated the relative dominance of *P. antarctica*. Cell abundances revealed that *P. antarctica* contributed 79% of total cell counts in the upper 25 m and 93% in the lower photic zone. Similarly, a strong correlation was observed between Chl-a and the Hex:Fuco pigment ratio, corroborating the microscopic analyses. Recent studies have shown that iron can trigger colonial *P. antarctica* blooms. Based on the Hex:Chl-c_3 proxy for iron limitation in *P. antarctica*, we hypothesize that anomalously higher iron fluxes were responsible for the unusual bloom of colonial *P. antarctica* observed in TNB.

1. Introduction

Coastal Antarctic pelagic food webs are primarily based on two main photoautotrophic communities comprising: diatoms and haptophytes (e.g. *Phaeocystis antarctica*) (DiTullio and Smith, 1996; Alderkamp et al., 2012; Smith et al., 2014; Mangoni et al., 2017). The relative dominance of diatoms and haptophytes varies on different temporal and spatial scales and thereby can have major implications on trophodynamics and CO_2 drawdown processes in the Ross Sea (Sweeney et al., 2000; Arrigo et al., 1999, 2002; Saggiomo et al., 2000; Schoemann et al., 2005; Peloquin and Smith, 2007; Rivaro et al., 2017; Mangoni et al., 2018). *P. antarctica* populations can exist as both solitary cells (3–4 μm in size) and palmelloides colonies (> 2 mm) that can differ by several orders of magnitude in 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; Elliott et al., 2009; Tang et al., 2008), so that diatom blooms may represent a critical ecological link between primary production and higher trophic levels in the Ross Sea.

Mixed layer depth (MLD) has been correlated to phytoplankton community structure, with diatoms and *Phaeocystis* populations dominating under shallower and deeper MLD conditions, respectively (DiTullio and Smith, 1996; Arrigo et al., 2000; Mathot et al., 2000; Arrigo and van Dijken, 2004; Arrigo et al., 2010; Mills et al., 2010). According to the accepted current paradigm, water column stratification favors diatom dominance under high light conditions due to their physiological superiority in photoprotection and their high tolerance to photoinhibition compared to *P. antarctica* populations (Saggiomo et al., 2002; Kropuenske et al., 2009; Mangoni et al., 2009; Arrigo et al., 2010; Mills et al., 2010). In addition, water column iron bioavailability is critical for sustaining high diatom relative growth rates in high macronutrient regions such as the Ross Sea (Martin et al., 1990). As a result,

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diatoms typically dominate in iron enriched stratified waters like 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 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 well as their ability to efficiently photosynthesize under relatively low or fluctuating light levels due to vertical mixing of the water column (Schoemann et al., 2005; Sedwick et al., 2007; Garcia et al., 2009; Alderkamp et al., 2012). Recent studies have implicated high iron conditions in triggering colony formation in *P. antarctica* (e.g, Bender et al., 2018). Previous work also showed that *P. antarctica* can dominate in stratified waters when iron and light levels are high (Feng et al., 2010). Although photophysiological processes are no doubt important for sustaining diatom blooms in 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 (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 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).

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 Asper, 2001), and 65%–85% of the austral spring production as well as 36%–45% of the annual production (Smith et al., 2006). After the seasonal decline of colonial *P. antarctica* in the central Ross Sea, phytoplankton communities are typically dominated by diverse populations of diatoms and flagellated single-celled *Phaeocystis*, which tend to dominate in summer (Garrison et al., 2003; Smith et al., 2014). In 2006, a European Long Term Ecological Research (LTER) site was initiated 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 to 1995) all document that the phytoplankton blooms during summer consist primarily of diatoms (Saggiomo et al., 1998, 2000; Innamorati et al., 2000; Nuccio 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 in 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.

2. Materials and methods

Sampling was conducted in the coastal TNB area during austral summer 2009–2010 as part of the "LTER-Marine Observatory of Antarctic Specially Protected Area – Terra Nova Bay (MOA-TNB) 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 phytoplankton biomass measurements, have been recorded since 1989 as a component of various 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 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 the marginal ice zone of Tethys Bay, (Fig. 1). The depths of the four coastal stations varied with the shallowest being FAR (100 m) and the deepest SMN (500 m). The other two stations (SLC and PTF) had a depth of approximately 200 m. The areal extent of the sampling area was ≈30 Km^2.

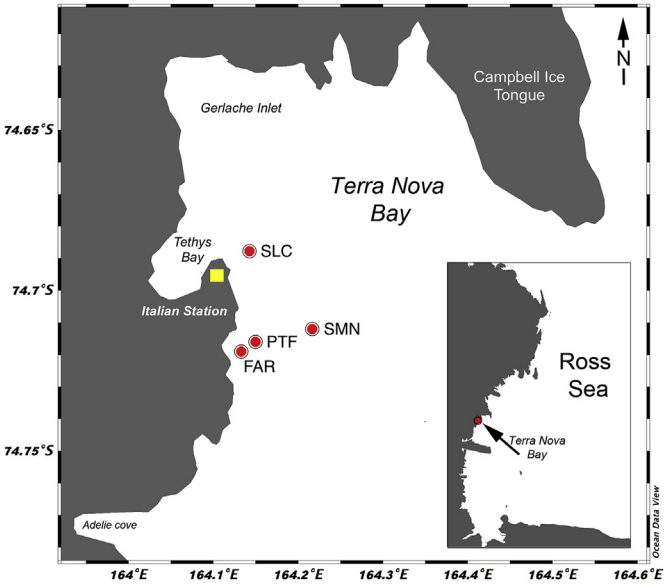


Fig. 1. Map of the sampling sites during the 2009–10 austral summer in Terra Nova Bay (Antarctica) (ASPA n°161). Faraglioni (FAR), Portofino (PTF), Santa Maria Novella (SMN) and Santa Lucia (SLC) stations were sampled three times each.

The stations FAR, PTF, SMN and SLC were sampled three times each between December 31, 2009 and January 13, 2010 with the 3 sampling time periods designated as T1, T2 and T3 (Table 1).

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).

2.1. Pigment analyses

Four liters of seawater were drawn from the Niskin bottles and, after careful mixing, sub 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 Chl-a, 500 ml of sea water were filtered from each depth through Whatman GF/F filters (25-mm diameter). Size-fractionated

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

Station name	Lat. S	Long. W	Bottom depth (m)	Date	Sampling periods	SST (°C)	SSS	σ_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
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

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 then collected on Whatman GF/F filters thereby resulting in a < 2 μm and a < 20 μm fraction, respectively (see Mangoni et al. (2004) and Jeffrey et al. (2005) for additional details). The analyses of size-fractionated Chl-a and phaeopigments (Phaeo) were carried out according to Holm-Hansen et al. (1965) using a Spex Fluoromax spectrofluorometer. The instrument was calibrated and checked daily with a Chl-a standard solution (*Anacystis nidulans*, Sigma). In order to determine accessory pigments using high performance liquid chromatography (HPLC), 2 L of seawater 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 according to the method outlined in Vidussi el al. (1996) as modified by Brunet and Mangoni (2010). The system was equipped with an HP 1050 photodiode array detector and a HP 1046 A 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 Agency for ^{14}C Determination, VKI Water Quality Institute, Copenhagen, Denmark. Three major 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-c_3 (Chl-c_3) for *Phaeocystis antarctica* (DiTullio et al., 2003, 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).

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).

2.3. Nutrient analyses and silicate to nitrate ratios

Water samples for the determination of inorganic nutrient [NO_2^-, NO_3^-, NH_4^+, PO_4^{3-}, $Si(OH)_4$] 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 procedures described by Hansen and Grasshoff (1983). The ambient Si/N ratio was used as proxy to identity the possible effect of phytoplankton community composition on the water column chemistry in TNB. In fact silicate and nitrate concentrations in the deep waters of the Ross Sea are approximately 76 μM and 32 μM, respectively, yielding a silicate to nitrate (Si/N) ratio of ~2.5 (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 composition. For example, under high iron and macronutrient replete conditions, the Si/N assimilation ratio in diatoms is ~1 (Brzezinski, 1985). Under low iron conditions, diatom Si/N uptake ratios are elevated to values > 2 (Hutchins and Bruland, 1998; Takeda, 1998).

2.4. Elemental and biochemical analyses of particulate organic matter

Aliquots of 500–2000 ml of seawater were filtered depending upon the particular biochemical parameter. Water samples were filtered onto combusted Whatman GF/F filters for analyses of particulate organic carbon (POC), particulate organic nitrogen (PON), particulate carbohydrates (CHO) and particulate proteins (PRT). POC/PON analyses were carried out after exposing filters to HCl fumes for 24 h to remove the inorganic carbon fraction (Hedges and Stern, 1984). Cycloexanone 2,4-dinitrophenyl hydrazone was used as the calibration standard. Analyses were performed on an elemental analyser (Model 1100 CHN; Carlo Erba). CHO analyses were carried out following the phenol-sulphuric acid colorimetric method (Dubois et al., 1956). Absorbances were measured at 490 nm. Solutions of D(+)glucose were used as the calibration standard. The PRT assay was based on the reaction between protein amino acids and the copper sulphate-Folin Ciocalteu reagent (Hartree, 1972). Protein absorbance was measured at 650 nm using bovine serum albumin as the calibration standard. Both CHO and PRT analyses were performed using a Jasco V530 spectrophotometer.

2.5. Statistical analysis

Relationships between depth, Hex:Chl-c_3 ratio, Hex:Fuco ratio, PO_4, $Si(OH)_4$, NO_3, Chl-a, temperature and salinity were investigated through Spearman correlation matrix. To investigate the relationships among environmental variables and biological features, a multivariate approach based on principal component analysis (PCA) was carried out using the XLSTAT 2017 software.

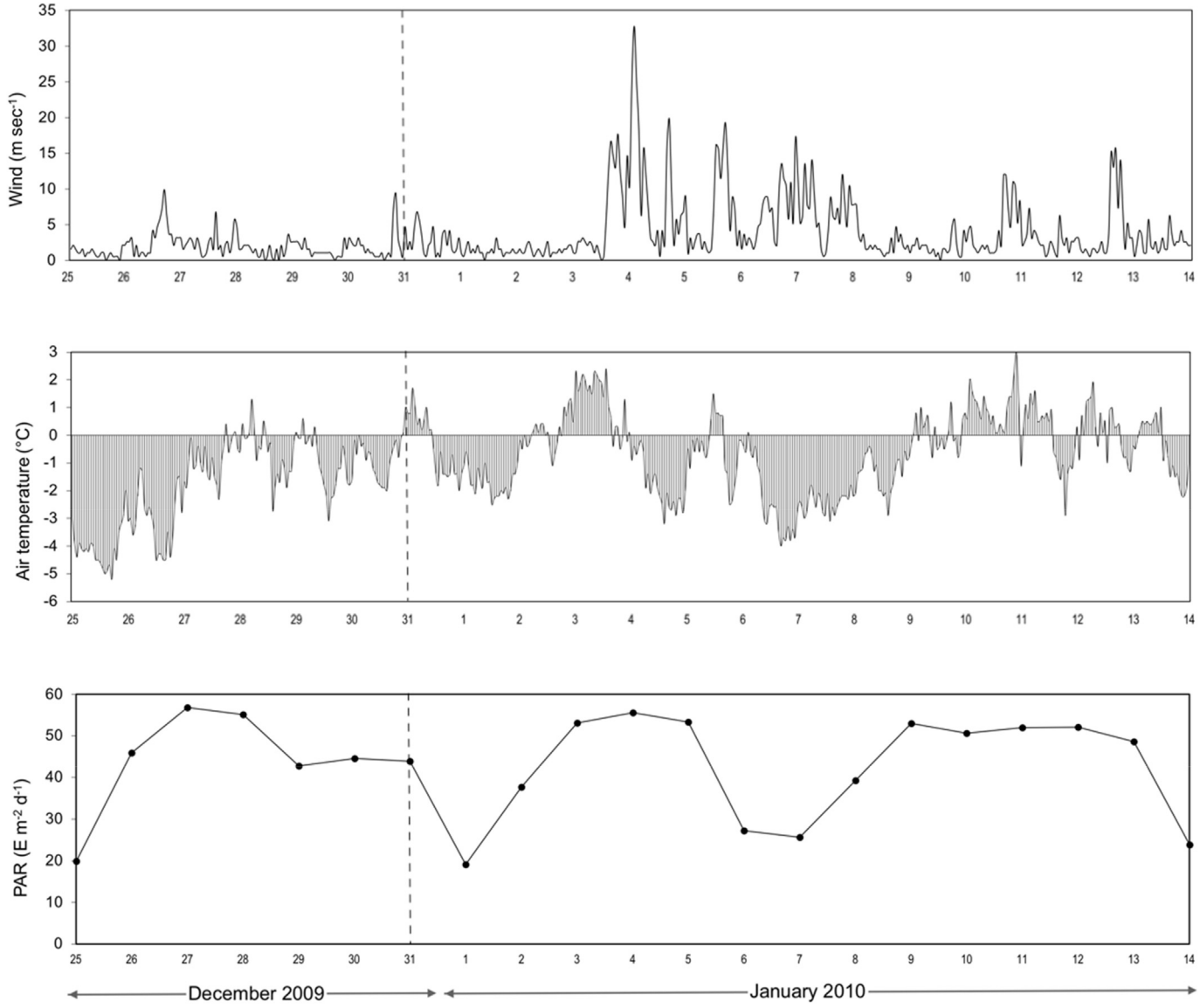


Fig. 2. Meteorological data from December 25, 2009 to January 13, 2010 in Terra Nova Bay (Antarctica). Wind speed (m sec^{-1}), air temperature (°C) and daily average of photosynthetically active radiation (PAR) (E m^{-2} d^{-1}) were measured.

3. Results

3.1. Environmental parameters and hydrography

Atmospheric air temperatures were generally warmer (from -1 °C to +1 °C) during the week before the first sampling time point (T1) between December 31 and January 3 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).

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 ($< 5.14\,m\,s^{-1}$) were recorded for the week leading up to the T1 sampling time point with sustained winds of $10\,m\,s^{-1}$ with gusts of 20–30 $m\,s^{-1}$ 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 < 10 m (using a conservative $\Delta\sigma_t = 0.125$ criterion). For example, the MLD at Station FAR was calculated to be 4 m, 10 m, and 3 m 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 ($E = 2024 \times 10^{-8}\,m^{-1}$) compared to average values observed during the vertical mixing event that occurred during T2 (e.g. $1157 \times 10^{-8}\,m^{-1}$) and the subsequent re-stratification period occurring during T3 ($18{,}69 \times 10^{-8}\,m^{-1}$: 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 10 m during the T2 period.

3.3. Nutrient concentrations and N/P, Si/N ratios

Macro-nutrient concentrations in the photic zone were generally non-limiting with integral average nitrate concentrations > 10 μM in

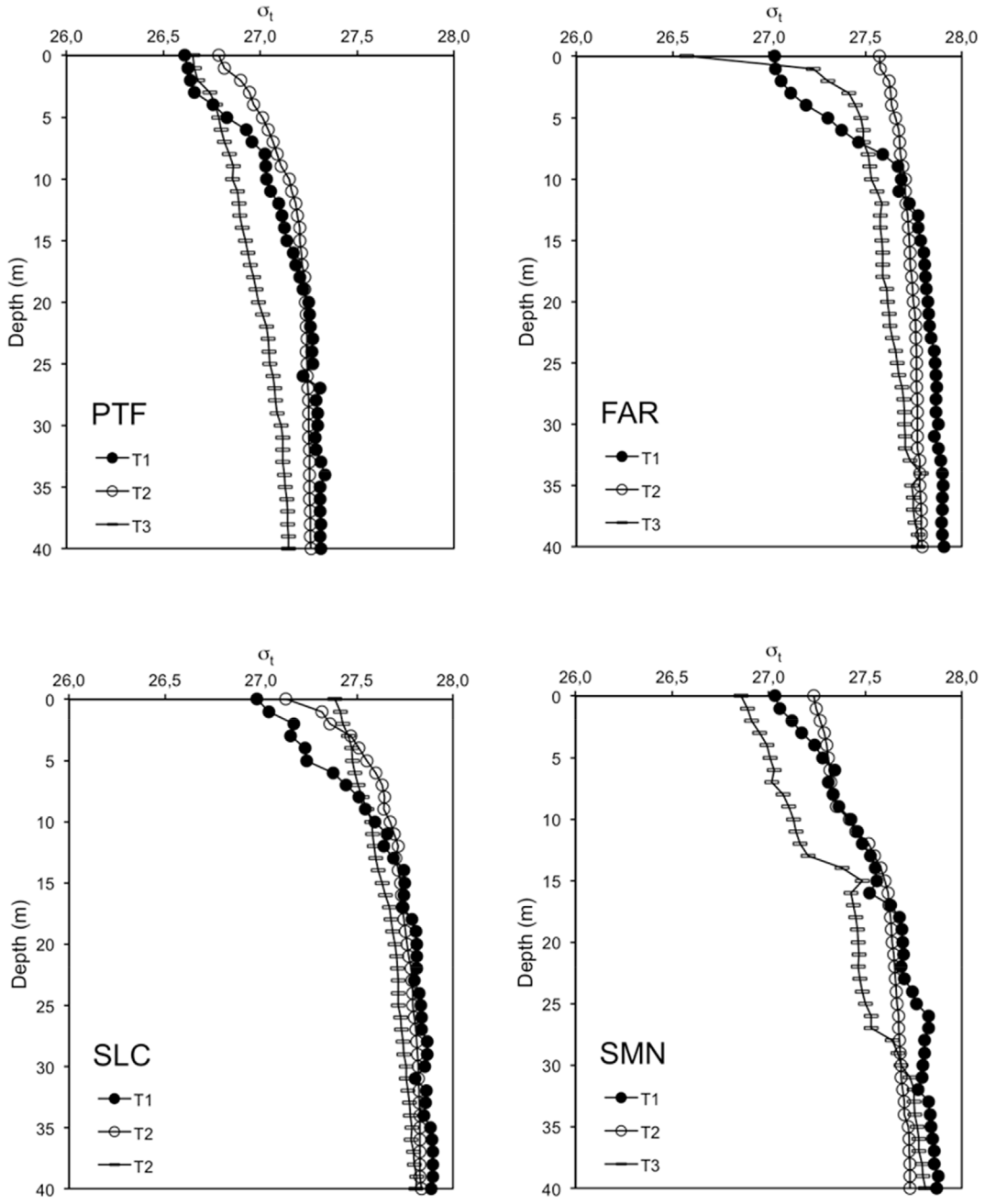


Fig. 3. σ_t profiles at four stations during the 2009–2010 austral season in Terra Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the sampling periods are indicated as T1, T2 and T3.

the upper 25 m throughout the 3 sampling periods (Table 2). 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).

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 25 m at all 4 stations (Fig. 5). The largest temporal deviation from the hypothetical 1:1 Si/N line was observed in the upper 10 m during the T1 sampling period before the wind event (i.e. during T2).

3.4. Phytoplankton biomass, POC and PON concentrations

Phytoplankton biomass was estimated using spectrofluorometric Chl-a concentrations (Fig. 6) and particulate organic carbon (POC) and nitrogen (PON) (Table 2).

In general, the Chl-a vertical profiles at specific sampling time points were similar at all stations (Fig. 6). Chl-a concentrations were maximal in near surface waters (ca. 10 m) 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 period, enhanced vertical mixing resulted in lower Chl-a concentrations in the upper layer (< 25 m) relative to deeper waters (e.g. 50–120 m; Fig. 6).

For example, the integral average Chl-a concentration in the upper layer (< 25 m) during T1, T2 and T3 represented 71%, 54% and 36%, respectively, of the total water column integral average at all 4 stations (Tables 2 and 4). Total integrated Chl-a values (averaged for all 4 stations) in the layer 0–80 m revealed the same temporal trend with the highest Chl-a values measured during T1 (275 ± 57 mg m^{-2}) and decreasing values at T2 (258 ± 20 mg m^{-2}) and T3 (176 ± 29 mg m^{-2}) (Table 4). Generally, the micro size-class (> 20 μm) dominated the

Table 2
Nutrient, total Chl-a, size fraction Chl-a [micro- (> 20 μm), nano-(20-2 μm), pico-(< 2 μm)], 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 25 m of the water column (A) and below 25 m (B) during the sampling periods (T1, T2 and T3).

A

Station name	Sampling periods	NH_4^+ (μM)	$NO_3^- + NO_2^-$ (μM)	PO_4^{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})
PTF	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
SLC	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
FAR	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
SMC	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

B

Station name	Sampling periods	NH_4^+ (μM)	$NO_3^- + NO_2^-$ (μM)	PO_4^{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})
PTF	T1	0.73	27.30	2.06	72.61	2.14	79.7	8.9	11.2	0.50	26	209	109	129
	T2	0.14	24.57	2.19	67.34	2.46	83.0	8.1	8.7	0.46	64	390	158	311
	T3	0.90	24.78	2.07	72.65	2.22	66.9	20.3	12.7	0.48	56	403	252	357
SLC	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
FAR	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
SMC	T1	0.21	29.35	2.28	72.43	1.14	61.5	24.1	14.3	0.62	20	146	39	110
	T2	0.31	23.08	2.03	65.17	2.67	75.3	17.3	7.2	0.49	44	347	195	332
	T3	0.96	25.60	2.10	71.46	2.22	75.1	11.1	13.7	0.56	44	310	341	179

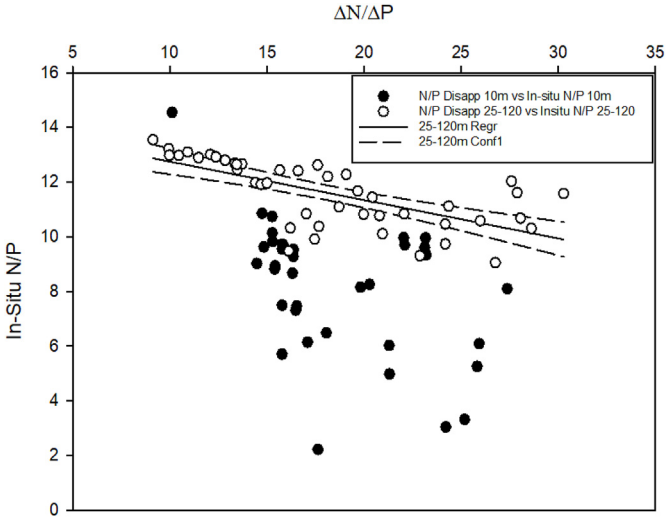


Fig. 4. Correlation between N/P ratio and ΔN/ΔP ratio.

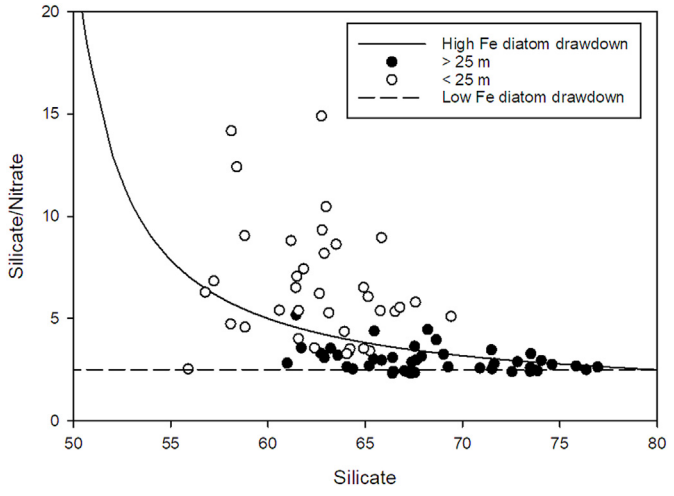


Fig. 5. Variation of the ambient silicate/nitrate ratio *vs* silicate concentration during the 2009–2010 austral season in Terra Nova Bay (Antarctica). Si/N ratios were determined in the upper water column (< 25 m depth, open symbols) and below 25 m (solid symbols). The hypothetical Si/N drawdown ratio 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.

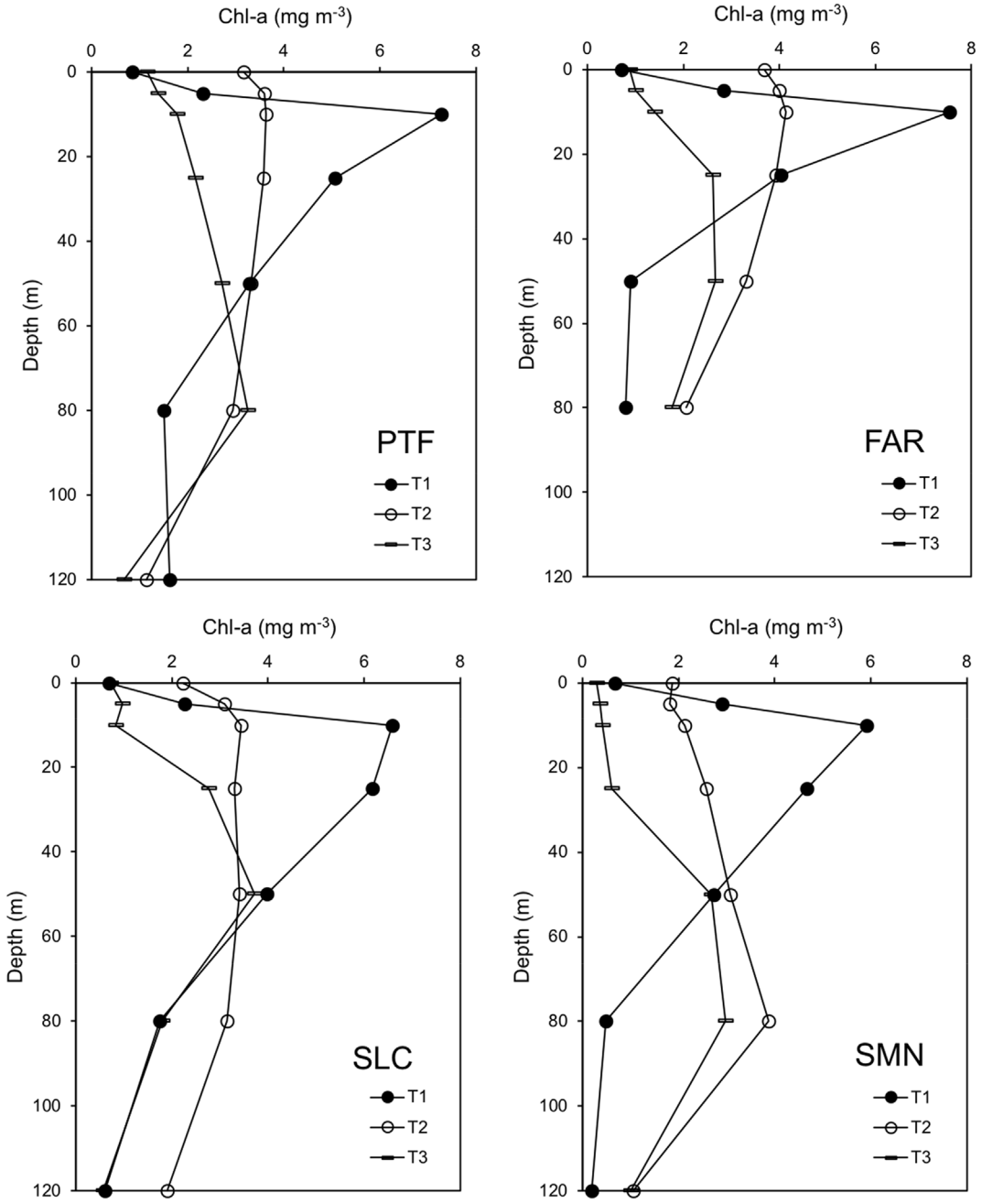


Fig. 6. Chl-a profiles at four stations during the 2009–2010 austral season in Terra Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the sampling periods are indicated as T1, T2 and T3.

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 25 m 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 ratios and phaephorbide concentrations were measured in the water column throughout the three sampling periods (Table 2).

Vertical profiles of POC and PON were similar to total Chl-a profiles (Figs. S1 and S2). For instance, the highest POC levels were also measured in surface waters (< 10 m) at all stations during the T1 sampling period. Similar to the Chl-a trend, the integrated water column (to 80 m) average POC value (for all 4 stations) was highest at T1 (39.1 ± 13.6 gC m^{-2}) and lowest at T3 (30.1 ± 4.0 gC m^{-2}; Table 4). PON integrated values followed the same trend as POC with the highest values measured at T1 (6.2 ± 1.4 gN m^{-2}) and the lowest at T3 (4.7 ± 0.6 gN m^{-2}). The integrated POC:Chl-a ratio at T1 and T2 time were 180 and 200 respectively, with a maximun of 288 at T3 when we found a strong differences between the upper (0–25 m) and deeper layer (410 and 166). The 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.

Phytoplankton composition was assessed using microscopic cell counts and HPLC pigment composition (Table 3, Fig. 7).

As is typical of the Ross Sea polynya, the TNB phytoplankton assemblages was dominated by diatoms and the colonial haptophyte, *Phaeocystis antarctica.* In terms of cell abundances, the *P. 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 phytoplankton cell abundance in the upper 10 m and approximately 93 ± 5% in deeper

Table 3
Percentage contribution of diatoms, *Phaeocystis antarctica* and other flagellates to phytoplankton community at four stations during the 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	Station depth (m)	Diatoms	*P. antartica*	Other flagellates	Station name	Sampling periods	Depth (m)	Diatoms	*P. antartica*	Other flagellates
PTF	T1	0	41.5	57.1	1.4	**FAR**	T1	0	6.7	92.2	1.1
	T2	0	5.2	93.3	1.5		T2	0	6.9	92.8	0.3
	T3	0	48.0	48.4	3.6		T3	0	20.5	78.4	1.1
	T1	10	12.5	85.6	1.9		T1	10	2.1	97.6	0.3
	T2	10	6.2	92.1	1.7		T2	10	5.8	94.1	0.1
	T3	10	14.3	73.7	12.0		T3	10	19.9	74.7	5.4
	T1	50	5.2	91.9	3.0		T1	50	8.5	91.5	0.0
	T2	50	4.8	93.7	1.5		T2	50	-	-	-
	T3	50	18.1	80.3	1.6		T3	50	0.6	99.4	0.0
	T1	80	10.4	89.0	0.6		T1	80	0.0	100	0.0
	T2	80	5.3	92.8	1.8		T2	80	4.0	95.8	0.2
	T3	80	2.3	97.5	0.2		T3	80	13.0	87.0	0.0
Station name	Sampling periods	Station depth (m)	Diatoms	*P. antartica*	Other flagellates	Station name	Sampling periods	Depth (m)	Diatoms	*P. antartica*	Other flagellates
SLC	T1	0	20.0	80.0	0.0	**SMC**	T1	0	17.0	78.4	4.6
	T2	0	6.5	81.0	12.5		T2	0	28.9	67.9	3.2
	T3	0	27.0	70.9	2.1		T3	0	34.0	64.2	1.8
	T1	10	1.0	98.3	0.8		T1	10	10.2	88.8	1.0
	T2	10	2.9	95.1	2.0		T2	10	32.8	64.6	2.6
	T3	10	22.3	74.2	3.4		T3	10	40.0	57.9	2.1
	T1	50	1.0	99.0	0.0		T1	50	6.5	92.5	1.0
	T2	50	7.2	91.3	1.5		T2	50	10.5	89.3	0.3
	T3	50	1.6	98.0	0.4		T3	50	3.5	95.2	1.3
	T1	80	2.4	97.3	0.3		T1	80	3.5	95.7	0.8
	T2	80	2.9	87.0	0.1		T2	80	8.3	91.0	0.7
	T3	80	4.1	95.9	0.0		T3	80	6.8	93.1	0.1

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).

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

waters (50–80 m; Table 3). Relative diatom populations (i.e. % total) were more prevalent in the upper 10 m of the water column compared to 50–80 m. In addition, enhanced vertical mixing from the wind event during the early T2 sampling period caused an increase of 4–10 fold (at SLC) in the % diatom abundance in the upper 10 m 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 approximately 88 ± 5% of the total diatom cell abundance with *Fragilariopsis cylindrus* dominating the diatom biomass.

The diagnostic photosynthetic pigments fucoxanthin (Fuco) and 19'hexanoyloxyfucoxanthin (Hex) that reflective of diatoms and *P. antarctica* dominance were reported (Fig. 7). The highest Hex:Fuco ratios (ca. 3 to 4) were generally found in the upper 10 m during the T1 period with lower ratios (i.e. < 1) observed during T3 (Fig. 7). Moreover, the Hex:Chl-c_3 ratio can be used as diagnostic 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-c_3, can be influenced by environmental variables such as iron concentrations (DiTullio et al., 2007; van Leeuwe and Stefels, 2007). During T1 sampling, the Hex:Chl-c_3 ratios (4–6) were 2–3 fold higher in the upper 10 m compared to ratios (~2) measured in the lower photic zone (Fig. 8). Similarly, Hex:Chl-c_3 ratios were higher in the upper 25 m compared to the lower zone, except for the T3 sampling at the SMN station where low values were also observed near the surface (Fig. 8). In the upper 25 m, the Hex:Chl-c_3 ratios decreased during the T2 sampling period at 3 of the 4 stations.

3.5. 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-c_3). 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. The $Si(OH)_4$ and NO_3^- concentrations

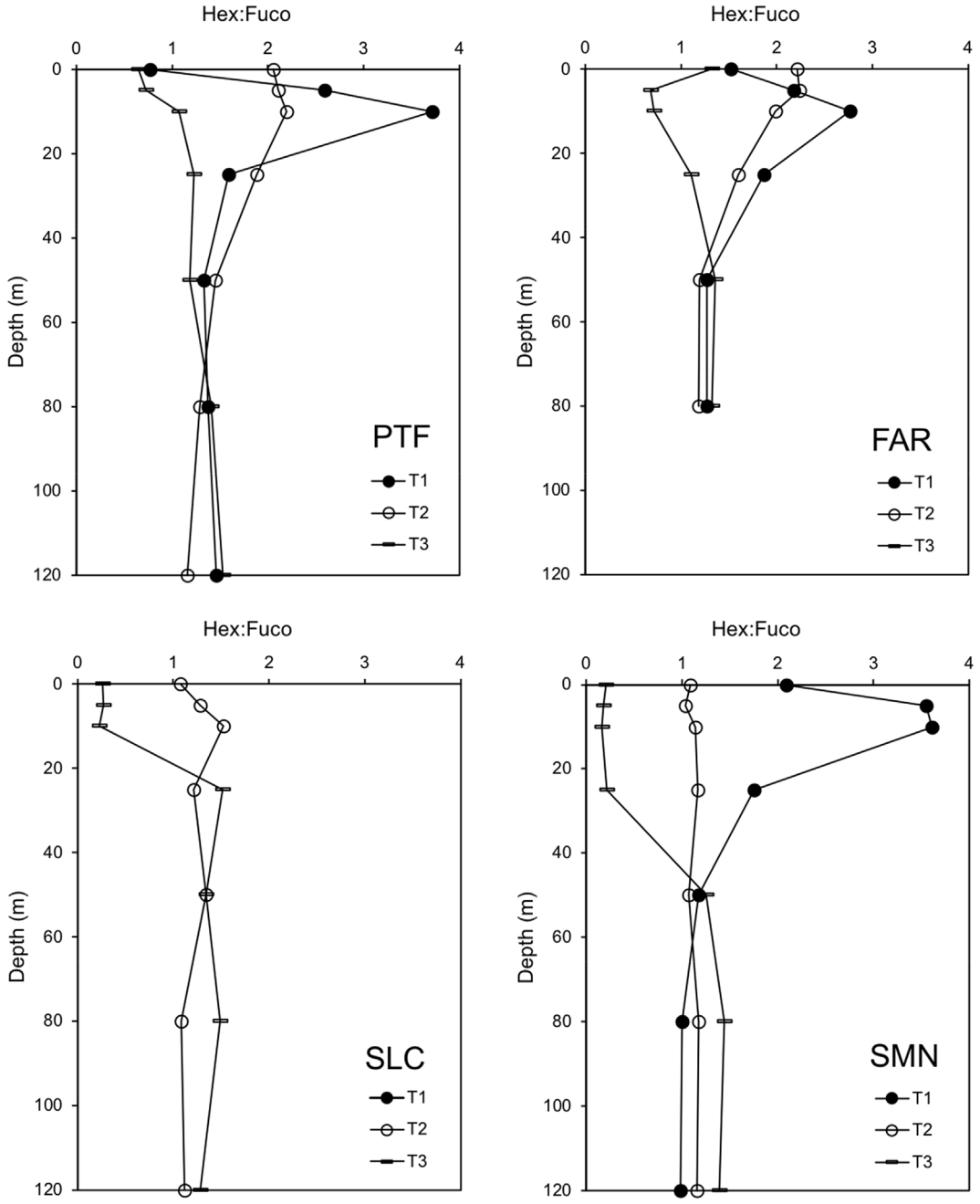


Fig. 7. Hex:Fuco ratio profiles at four stations during the 2009–2010 austral season in Terra Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the sampling periods were indicated as T1, T2 and T3.

were positively correlated with salinity and depth along the negative F1 axis, while the Hex:Chl-c_3 ratio was directly correlated with temperature along the positive F1 axis. In the Ross Sea, high Hex:Fuco ratios are typically indicative of a community composition that is dominated by the presence of *P. antarctica*. Hex:Fuco ratios were significantly 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).

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 characterized by the presence of samples collected between January 08 to 11 in the first 25 m of the water column, in which temperature and the Hex:Chl-c_3 ratio were strongly correlated (Fig. 9). 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 was observed between the higher salinity and nutrient concentrations in deeper waters and the higher temperature and Hex:Chl-c_3 ratios in surface waters (Table 5, Fig. 9).

4. Discussion

During the austral summer 2009–2010, an intense phytoplankton bloom was observed in the surface stratified waters of coastal TNB region. Several lines of evidence, ranging from microscopic cell counts, chemotaxonomic pigment ratios, macronutrient ratio indices (e.g. Si/NO_3), revealed the dominance of *Phaeocystis antarctica* populations in the upper (< 25 m) water column.

Typically, diatom populations have been observed to dominate in stratified Antarctic coastal waters, in marginal sea ice zones, and near

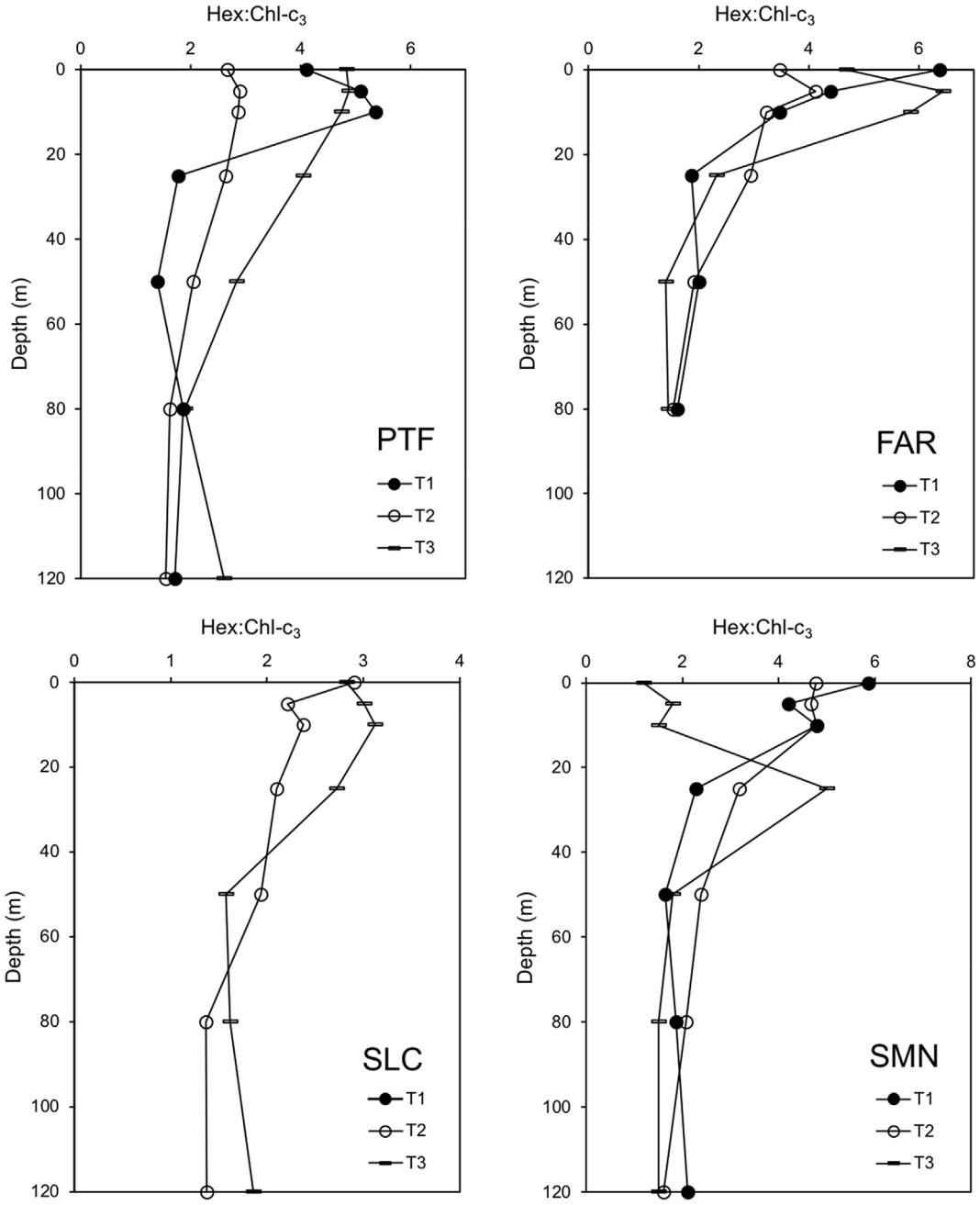
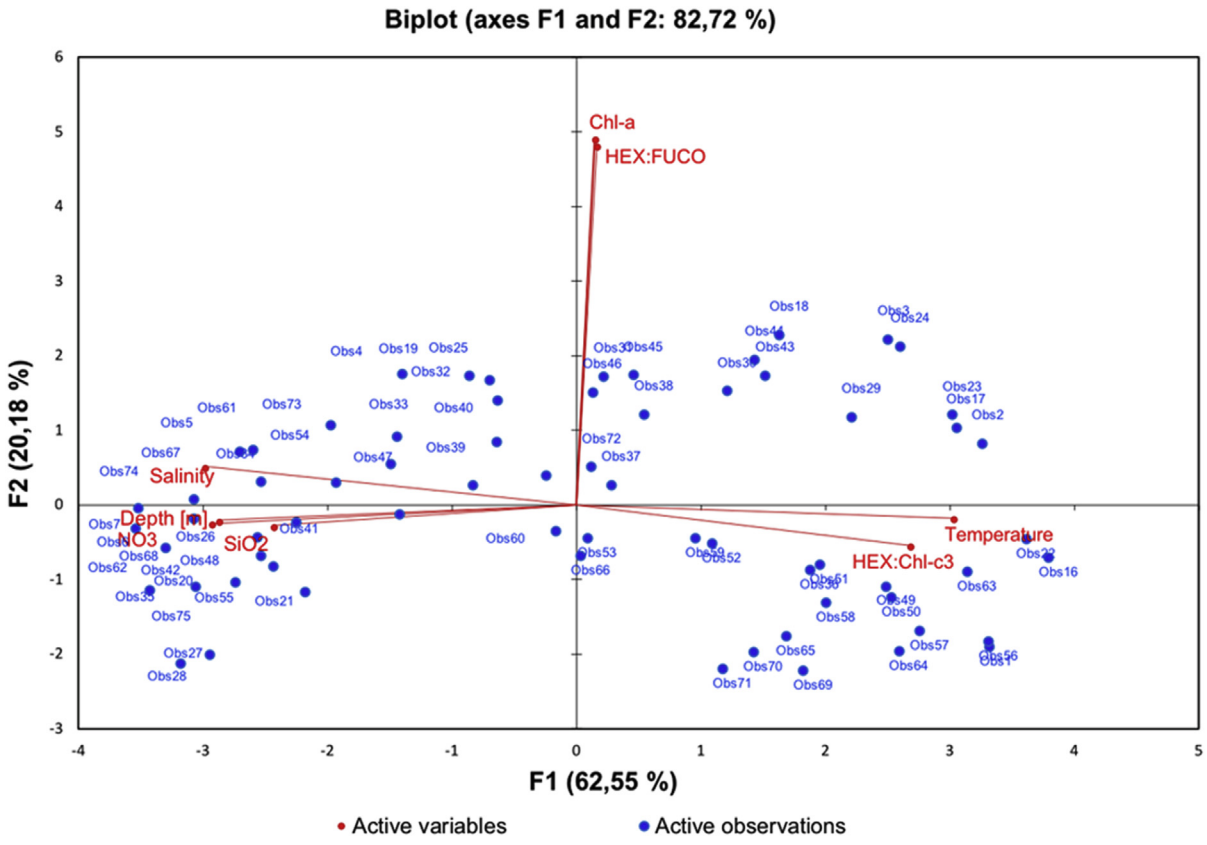


Fig. 8. Hex:Chl-c_3 profiles at four stations during the 2009–2010 austral season in Terra Nova Bay (Antarctica). The stations PTF, FAR, SLC and SMN were sampled three times each and the sampling periods are indicated as T1, T2 and T3.

melting pack ice under presumably relatively high iron 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 columns of the western Ross Sea and especially within TNB (Innamorati et al., 1991; DiTullio and Smith, 1996; Nuccio et al., 2000; Arrigo et al., 2000). Several studies have suggested that the photo-physiological superiority of diatoms relative to *P. antarctica* in stratified waters was due to 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., 2010; Arrigo et al., 2010; Alderkamp et al., 2012). In contrast, the ability of *P. antarctica* to dominate over diatoms in well-mixed water columns is related to their dynamic range in the 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 for growth relative to diatoms has been reported (Garcia et al., 2009).

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

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



Observation	Obs1	Obs2	Obs3	Obs4	Obs5	Obs6	Obs7	Obs8	Obs9	Obs10
Station	PTF 1	PTF 1	PTF 1	PTF 1	PTF 1	PTF 1	PTF 1	FAR 1	FAR 1	FAR 1
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		

Fig. 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-c_3). The table reported the correspondence from observations with station and sample depth.

Integrated Chl-a values ranged from 275 ± 20 mg Chl-a m^{-2} during T1 to 176 ± 29 mg Chl-a 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 relatively constant levels of Phaeo:Chl-a ratio and pheophorbide concentrations were measured throughout the three sampling periods (Table 2). Accordingly, previous studies have also indicated that colonial blooms of *P. antarctica* are not effectively grazed in the Ross Sea (Caron et al., 2000; Lonsdale et al., 2000). For example, *Euphausia superba,* the primary prey for a multitude of predators in Antarctic waters, can graze small colonies of *P. antarctica* but not larger colonies or 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 that factors other than only grazing, including hydrographic processes such as particle advection or export (DiTullio et al., 2003) were most likely responsible for the observed biomass decrease over time.

To better understand the phytoplankton dynamics, we investigated

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

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**

two proxies associated with iron limited growth in the western Ross Sea: Si/NO_3 and Hex:Chl-c_3 ratios. The Hex:Chl-c_3 ratio can be a useful diagnostic proxy to determine the iron physiological status of *P. antarctica* in the Ross Sea (DiTullio et al., 2003). Laboratory studies on *P. antarctica* have shown that Hex:Chl-c_3 ratios were inversely correlated with iron physiological status, such that under conditions of severe iron limitation the Hex:Chl-c_3 ratios (5–6) were approximately two-fold higher relative to the Hex:Chl-c_3 ratios (2–3) observed under iron replete growth conditions (DiTullio et al., 2007; van Leeuwe and Stefels, 2007). Hex:Chl-c_3 ratios were significantly correlated with depth as determined by the Spearman correlation index (Table 5). For example, high Hex:Chl-c_3 ratios (e.g. 4 to 6) were observed in the upper 10 m of the water column, where colonial *P. antarctica* populations dominated the community structure under relatively high stratification conditions as observed during T1 (c.f. Figs. 3 and 8). Lower Hex:Chl-c_3 ratios (e.g. 2–3) were observed in the deeper layer of the water column (i.e. > 25 m) suggesting that iron concentrations were relatively higher compared to the upper 25 m. A previous study measured a shallow ferricline depth (~50 m) in TNB (Station NX10; Sedwick et al., 2011) during summer 2005–2006. Hence, the wind event that occurred during T2 resulted in a deepening of the MLD relative to T1 (Table 1) and was associated with lower Hex:Chl-c_3 ratios, especially in the upper 25 m as vertical mixing presumably re-supplied iron back into the upper 25 m (Figs. 3 and 8). Furthermore, the high Si/NO_3 ratios observed in the upper 25 m (Fig. 5) can not simply reflect the uptake of silicate due to diatoms growing under Fe-sufficient conditions, explaining the dominance of *P. antarctica* in the upper 10 m. We have assumed that nitrate is the major provider of nitrogen to the phytoplankton community, and that relatively low denitrification rates occur in TNB as previously determined in the Ross Sea polynya (Gordon et al., 2000), caused enhanced vertical mixing rates and an increase in MLD that presumably replenished nutrient concentrations in the upper zone (Fig. 5).

The colonial *P. antarctica* blooms can develop under both iron-deplete and iron replete 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 period could have favored palmelloid stage of *Phaeocystis* as suggested by Smayda and Reynolds (2001). The ability of the colonial matrix of *P. antarctica* to sequester iron could be an important 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 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 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, and mesoscale eddies (Sedwick and DiTullio, 1997; Sedwick et al., 2011; McGillicuddy et al., 2015; Marsay et al., 2017; Kohut et al., 2017; Rivaro et al., 2019).

Based on the lower Hex:Chl-c_3 ratio during the T2 sampling period, we hypothesized that 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 10 m (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).

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, 2011). Since only certain bacterial species in polar waters have the ability to synthesize Vitamin B_{12}, the possibility exists that a mutualistic symbiosis can develop between certain bacterial groups that produce Vitamin B_{12} (e.g., SAR 92, *Oceanospirillaceaea* spp. and *Cryomorphaceae* spp.) and 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. antarctica* cells while the addition of both iron and Vitamin B_{12} stimulated diatoms in the Ross Sea (Bertrand et al., 2007). Hence, it is conceivable that the diatom community in TNB were co-limited 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 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 B_{12} availability would preferentially favor the growth of *P. antarctica* colonies over diatoms by allowing *P. antarctica* cells to sequester both iron and B_{12} inside the colonies and away from diatoms, thereby conferring *P. antarctica* with a competitive edge. Further studies measuring iron and Vitamin B_{12} concentrations in TNB are needed to test this hypothesis.

Even after several decades of study, spatial and temporal uncoupling of diatom and *Phaeocystis* blooms obscures our understanding of bloom dynamics in the Ross Sea (DiTullio and Smith, 1996; Smith et al., 2000). Our data do not allow us to identify the mechanism underlying the anomalous *P. antarctica* bloom. Understanding the dynamics controlling the influence of bottom-up factors such as iron and Vitamin B_{12} on phytoplankton species composition in Antarctic coastal waters, as well as the open Southern Ocean, continues to represent an important research area, given the impact of biogeochemical cycling in the Southern Ocean on climate change processes (Boyd and Doney, 2003).

The austral summer blooms in the western Ross Sea are responsible for carbon export to deeper waters (Arrigo et al., 2000) and changes in the phytoplankton community structure can have a strong impact on the carbon flux and biogeochemical properties of the water column. The colonial haptophyte *Phaeocystis antarctica* bloom that developed in TNB under a stably stratified water 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 and/or Vitamin B_{12} are the most likely factors impacting the change in the phytoplankton community composition in TNB.

Acknowledgments

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Appendix A. Supplementary data

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