

A review of past and present summer primary production processes in the Ross Sea in relation to changing ecosystems

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Received 1 July 2018 / Accepted 09 September 2018

Abstract: We analyse primary production processes during austral summer 1996 and 2001 in different environmental conditions such as ice-free waters and extensive ice-covered areas. Spatio-temporal distribution of phytoplankton biomass and functional groups along with photosynthetic parameters are presented. Production vs irradiance (PvsE) experiments were performed using ¹⁴C incubations at several stations and three or four different depths to define the eco-physiology of phytoplankton communities.

The results of the oceanographic campaign conducted in ice-free waters of the Ross Sea (summer 1996) emphasize that these ecosystems are characterized by high nutrient low chlorophyll (HNLC) conditions due to limiting factors (eg. Fe). Conversely, the results of the oceanographic cruise in extensively packice-covered areas (summer 2001) indicate that the average phytoplankton biomass (estimated from Chl_a) was about three times the values recorded in ice-free conditions, but the primary production was relatively lower. In fact, *in situ* primary production and PvsE experiments over few days show that high primary production values occurred in most of the area, but only within the first five meters of the water column and the melting pack ice. Notwithstanding some high values of phytoplankton biomass during the 2001 campaign, water column stability, similar irradiance levels along the water column, photosynthetic capacity was suppressed in deeper layers, indicating a low carrying capacity of the pelagic ecosystem due to iron limitation, as shown by low values of the photo-chemical efficiency of photosystem II (PSII), variable fluorescence and maximal fluorescence ratio (Fv/Fm). In contrast with a very high variability in phytoplankton biomass at several temporal and spatial scales, photosynthetic parameters (P_{max}^B , α , E_k) varied within narrow ranges.

Relevant changes in phytoplankton abundance and species composition are reported in this study although the environmental factors that drive these changes in primary production processes and prevalence of principal functional groups of phytoplankton communities compared to the past (1996 and 2001) are still unknown. The effect of these changes on the carrying capacity of Ross Sea ecosystems, carbon export and the potentially new asset of the food web will need to be determined.

Key words: Phytoplankton functional groups, photosynthetic parameters, global change, Southern Ocean.

1. Introduction

The Ross Sea is a globally important site of sea ice production in two permanent polynias (Tamura et al., 2008; Ohshima et al., 2016) and bottom water formation (Jacobs, 2004; Budillon et al., 2011). Rates of primary production

can be very high, often exceeding 2 gCm⁻² d⁻¹ (Smith & Gordon, 1997; Saggiomo et al., 1998; Arrigo et al., 1999, 2000), which makes the Ross Sea the most productive sector of the Southern Ocean on an annual basis (Arrigo et al., 1998). In this region, large phytoplankton blooms can trigger significant biological sequestration of atmospheric

CO₂ via the formation and export of particulate organic carbon to the deep waters where the Antarctic bottom water (AABW) moves northwards (Arrigo et al., 2008).

In spring, impressive phytoplankton blooms are observed at landfast-ice and platelet-ice (Guglielmo et al., 2004; Saggiomo M et al., 2017) and at ice melting in offshore areas (Carrada et al., 2000; Saggiomo et al., 2000). Large numbers of organisms at different trophic levels (krill, birds, seals, whales) convey along the ice margins (Saino & Guglielmo, 2000). The production of meltwater was related to the generation of a stratified surface layer and to the release of micronutrients and epontic algae into the water which can increase primary production within marginal ice zones (MIZ) (Smith & Nelson, 1985, Arrigo et al., 1998; Mangoni et al., 2004; Geibert et al., 2010; Taylor et al., 2013). During the austral summer, a sharp drop in primary production is observed after pack ice dispersal due to two major processes: the deepening of the upper mixed layer and iron limitation (Sedwick et al., 2011; Alderkamp et al., 2012; Smith & Jones, 2014). These processes may also explain why offshore ecosystems during austral summer showed high nutrient low chlorophyll (HNLC) conditions in ice-free areas (Saggiomo et al., 1998, 2002; Pelouquin & Smith, 2007; Wang & Moore, 2011).

Phytoplankton species composition and physiology are likely to influence carbon (C) export to depth (DiTullio et al., 2000). Blooms of diatoms (such as *Fragilariopsis cylindrus*) have historically dominated production in open waters of the western Ross Sea during summer, whereas blooms of haptophytes (*Phaeocystis antarctica*) have been found to dominate the larger Ross Sea polynya during spring and early summer (DiTullio & Smith, 1996; Arrigo et al., 1999). These two taxa coexist throughout the Ross Sea (Smith et al., 2014), although each taxon can form nearly monospecific blooms that leave distinctive biogeochemical imprints (DiTullio et al., 2000; Smith et al., 2010; Mangoni et al., 2017).

In the latest 10 years, relevant changes in the abundance and species composition of phytoplankton in offshore waters of the Ross Sea have been recorded during austral summer in prolonged ice cover conditions (Mangoni et al., 2004; Smith et al., 2006) as well as in ice-free waters (Kohut et al., 2017; Mangoni et al. 2017) Such phenomenon could have a major impact on both C export and trophic structure of the Ross Sea ecosystem.

The aim of this study is to assess the seasonal limiting factors and the carrying capacity of the Ross Sea in different environmental ecosystems for ice-free waters during austral summer 1996 and in anomalous ice-covered systems during austral summer 2001. The effect of the anomalous ice coverage in 2001 on phytoplankton assemblages is reported in Mangoni et al. (2004). In this study, data about primary production processes which have never been published before are analysed. We compare the 2001

data about ice-covered areas with those collected in ice-free waters in 1996 (Saggiomo et al., 2002) and discuss the implications of prolonged ice coverage on the primary production processes. Different environmental conditions during austral summer in 1996 and 2001 are discussed in light of the recent changes in phytoplankton abundance and species composition in the Ross Sea ecosystems.

2. Materials and methods

Study areas. During the oceanographic cruise in 1996, 38 hydrological stations were sampled in different ecological contexts (Fig. 1) (Saggiomo et al., 2002). Primary production was measured at 28 stations and PvsE experiments were performed at 18 stations at 3 or 4 depths. The cruise in 2001 was conducted on the R.V. Italice from 11 January to 19 February within the frame of the XVI Italian Antarctic Research Expedition. The sampling plan included 30 stations (Fig. 2), PvsE measurements were performed in order to obtain photosynthetic parameters to study the eco-physiology of phytoplankton communities. Three stations located in the southwestern part of the Ross Sea were replicated over time.

Phytoplankton biomass. In both years, for determination of total phytoplankton biomass, 500ml of seawater were filtered onto 25 mm Whatman GF/F filters. Spectrofluorometric analyses of Chlorophyll-a (Chla) and phaeopigments (Phaeo) were made using a Spex Fluoromax

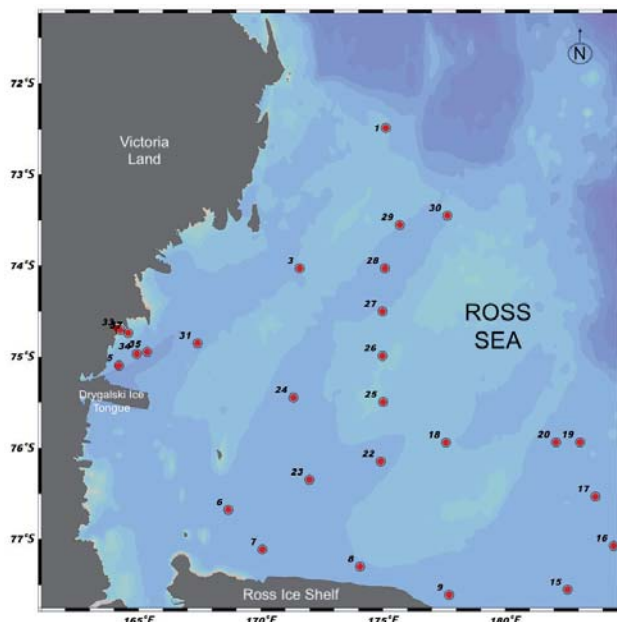


Figure 1. Sampling stations in the ice-free waters of the Ross Sea (Antarctica) during summer 1996.

spectrofluorometer (Holm-Hansen et al., 1965). The instrument was checked daily with a solution of Chl a from *Anacystis nidulans* (Sigma).

Phytoplankton functional groups. In 2001, HPLC analyses were performed at 4–7 depths at 41 hydrological stations (Fig. 2). Five litres of water were filtered onto 47mm Whatman GF/F filters. HPLC analyses were performed using a Hewlett-Packard HPLC (mod. 1100) according to protocol by Mantoura & Llewellyn (1983) and modified by Brunet & Mangoni (2010). For more details see Mangoni et al. (2004). The concentrations of pigments were used to estimate the contribution of the main functional groups to the total Chl a using a matrix factorisation software (CHEMTAX) (Mackey et al., 1996; Wright et al., 2010).

Primary production. Primary production measurements were performed at *in situ* simulated conditions. Samples collected at the optical depths were incubated in light and dark polycarbonate (Nalgene) 450-ml bottles with 1 ml (740 KBq) of NaH 14 CO $_3$ for 4-6 hours in running surface sea water. The different light intensities were obtained using electroformed nickel screens (Veco Int. Co., USA). After incubation, samples were filtered on Whatman GF/F filters. Filters after acidification were processed as reported in the next paragraph.

Photosynthetic parameters. PvsE measurements were performed at 3 or 4 depths in 30 stations during 2001 and in 18 stations during 1966 in order to obtain photosynthetic parameters of phytoplankton community (Babin et

al., 1994). At each depth, which was selected according to both irradiance and hydrographic structure, sub-samples of water (50 ml) were collected in 12 culture flasks and inoculated with 740 KBq of NaH 14 CO $_3$. Incubations were carried out for one hour in an artificial light gradient incubator (Osram HQI-T 250W/D lamp), cooled by circulating surface (-6 m depth) seawater. In order to determine dark fixation, one sub-sample from each sample was placed in the dark inside the incubator, with 4 drops of seawater saturated with DCMU solution (Legendre et al., 1983). The irradiance was measured in each incubation bottle using a 4 π sensor QLS-101 (Biospherical Instruments). After incubation, samples passed through a Whatman GF/F filter. Filtration was carried out as fast as possible in dim light and vacuum was <0.2 atm for all filtration procedures. Filters were acidified with 200 μ l of HCL 0.1 N and after adding 10 ml of Aquasol II scintillation cocktail, they were read within 24 hours from filtration with a Beckman LS 1801 liquid scintillator.

PvsE data were derived from the model by Platt et al. (1980):

$$P^B(E) = P^B_s [1 - \exp(-\alpha E / P^B_s)] \exp(-\beta E / P^B_s)$$

where P^B_s is the potential light-saturated Chl-specific rate of photosynthesis in absence of photoinhibition ($\text{mgC}(\text{mgChl}a)^{-1} \text{h}^{-1}$), α is the initial slope of PvsE curves $\text{mgC}(\text{mgChl}a)^{-1} \text{h}^{-1} (\mu\text{mol photon m}^{-2} \text{s}^{-1})^{-1}$ and β is the index of photoinhibition (same units as α) and E is the irradiance ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$).

The photochemical efficiency of PSII was monitored as the ratio of variable to maximal fluorescence: F_v/F_m (where F_v is the difference between maximal ($F_{m\max}$) and initial fluorescence (F_0) determined using a Fast Repetition Rate Fluorometry) (FRRF).

3. Results and Discussion

Sea ice has strong impacts on ocean biogeochemical cycles and marine ecosystems (Sedwick & DiTullio, 1997; Ducklow et al., 2012; Wang et al., 2014). Phytoplankton blooms are often observed in the MIZ, where there is recent melting of sea ice (Fitch & Moore, 2007; Mangoni et al., 2004). The sea ice represents the most climate change-sensitive ecosystem, while there are strong interannual variations in ice extent and concentration and large regional variations (Oza et al., 2011; Kurtz & Markus, 2012; Parkinson & Cavalieri, 2012; Arrigo et al., 2015; Comiso et al., 2017). During the past few decades from satellite records were reveal the off-shore waters of the Ross Sea essentially free from ice in austral summer (Comiso et al., 2011; Turner & Comiso, 2017).

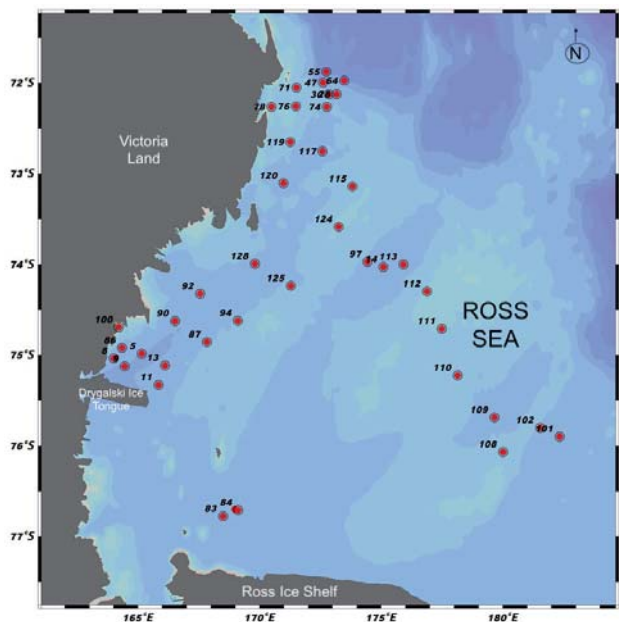


Figure 2. Sampling stations in ice-covered waters of the Ross Sea (Antarctica) during summer 2001.

Saggiomo and co-workers (2002) report that in off-shore waters and the coastal area of Terra Nova Bay (TNB) the integrated phytoplankton biomass varied between 15 and 102 mg Chl *a* m⁻² and ranged from 41 to 226 mg Chl *a* m⁻² in the 0-100 m layer, respectively (Fig. 3A). Primary production in off-shore waters varied between 124 and 638 mg C m⁻² d⁻¹ and ranged between 620 and 2411 mg C m⁻² d⁻¹ during a typical late summer bloom at TNB. The mean photosynthetic parameters (P_{\max}^B , α , E_k) varied within a limited range of values (Table 1). Phytoplankton communities were characterized by the prevalence of diatoms. These results emphasize that off-shore waters of the Ross Sea were HNLC during the austral summer and then were affected by limiting factors (e.g. Fe) as also reported by several authors (e.g. Bertrand et al., 2007; Feng et al., 2010).

The extensive ice coverage observed in off-shore waters of the Ross sea in 2001 appeared quite anomalous. Based on the data collected in this cruise, our group reported a considerable spatial variability of the phytoplankton biomass, with high concentrations along the southern and eastern ice edges and in the coastal area of TNB (Mangoni et al., 2004). Phytoplankton biomass concentrations, ranging between 25 and 215 mg m⁻² Chl *a* in off-shore waters and from 181 to 237 mg m⁻² Chl *a* in TNB during late summer blooms (Fig. 3B), were higher all over the Ross Sea in 2001 than in 1996 (Mangoni et al., 2004; Saggiomo et al., 2002). Diatoms dominated phytoplankton populations across the entire Ross Sea in both years. Fucoxanthin determined using HPLC analyses was by far the dominant pigment, with Fuco/Chl *a* being generally > 0.5. The results of CHEMTAX analyses for summer 2001 showed

that diatoms were the major contributors to the biomass in the 0-100 m layer (Fig. 4A); they accounted for more than 50% of the phytoplankton community in the entire Ross Sea. On the contrary, the percentage of haptophytes was generally low (Fig. 4B). In both campaigns, macro nutrients were never limiting (Saggiomo et al., 2002; Mangoni et al., 2004).

PvsE experiments (24 stations in 1996, 30 stations in 2001 at 3-4 depths) showed similar photoacclimation index (E_k) and photosynthetic capacity (Table 1). The P_{\max}^B values recorded in 2001 were in sharp contrast with the considerably higher biomass concentrations in the extensive MIZ areas.

Table 1. Mean, maximum, minimum and standard deviation of photosynthetic parameters determined during the austral summer 1996 and 2001 in the Ross Sea (Antarctica).

	P_{\max}^B	α	β	E_m	E_k
1996					
MEAN	1.27	0.073	0.00045	120	23
MIN	0.72	0.024	0.00002	49	3
MAX	2.83	0.132	0.00220	211	55
STD	0.39	0.088	0.00048	32	8
2001					
MEAN	1.34	0.0487	0.00106	136	31
MIN	0.38	0.0082	0.00005	47	8
MAX	3.95	0.1391	0.00521	267	58
STD	0.66	0.0272	0.00091	52	12

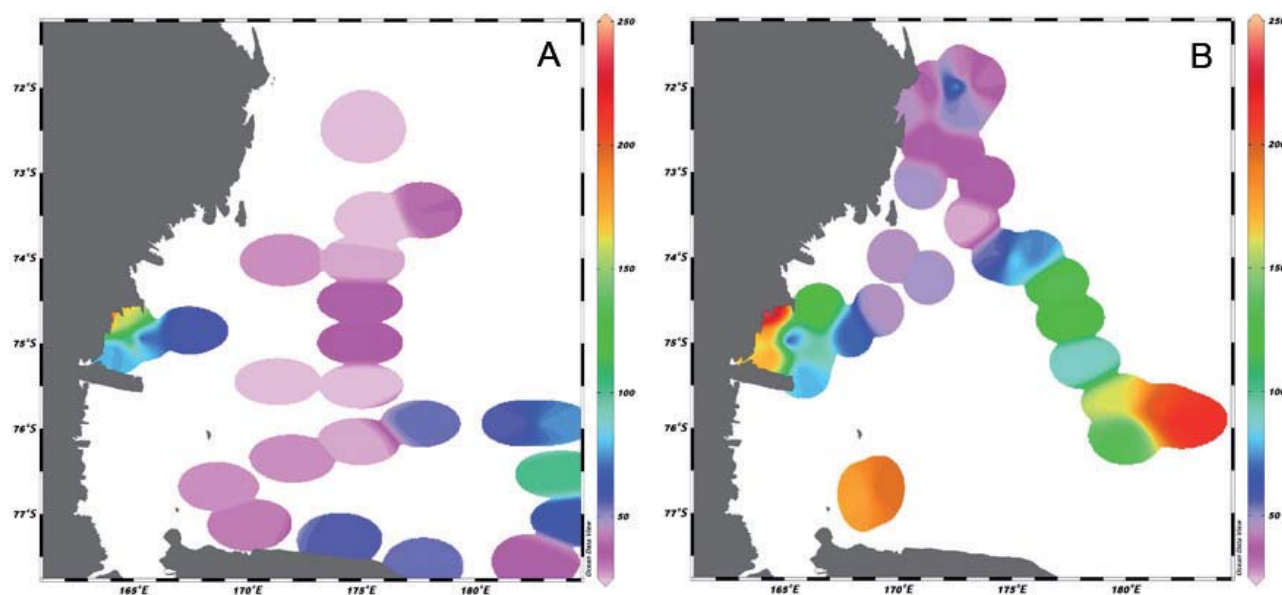


Figure 3. Spatial distribution of integrated total biomass (Chl *a* mg m⁻²) in the 0-100 m layer during summer 1996 (A) and 2001 (B)

The variability in P_{\max}^B across all stations and depths showed high variability in 2001 (Fig. 5). The difference in variations in P_{\max}^B values between two different years may be related to the relatively deep mixed layer in ice-free waters during 1996 (Fig. 3 in Saggiomo et al., 2002) and, as a result of ice melting, the presence of a shallow upper mixed layer (UML) and a strong stratification in 2001 (Fig. 3 in Mangoni et al., 2004). Spatial distribution of

mean values of P_{\max}^B showed similar trend in offshore water above and below the UML; maximum values were recorded in the UML of the Terra Nova Bay polynya (Fig. 6).

The southwestern area is reported as one of the most productive areas in the Ross Sea and this area was furthermore a MIZ in 2001. Replicate sampling over three days showed an increment of phytoplankton biomass coupled with a decrease of primary production in the subsurface

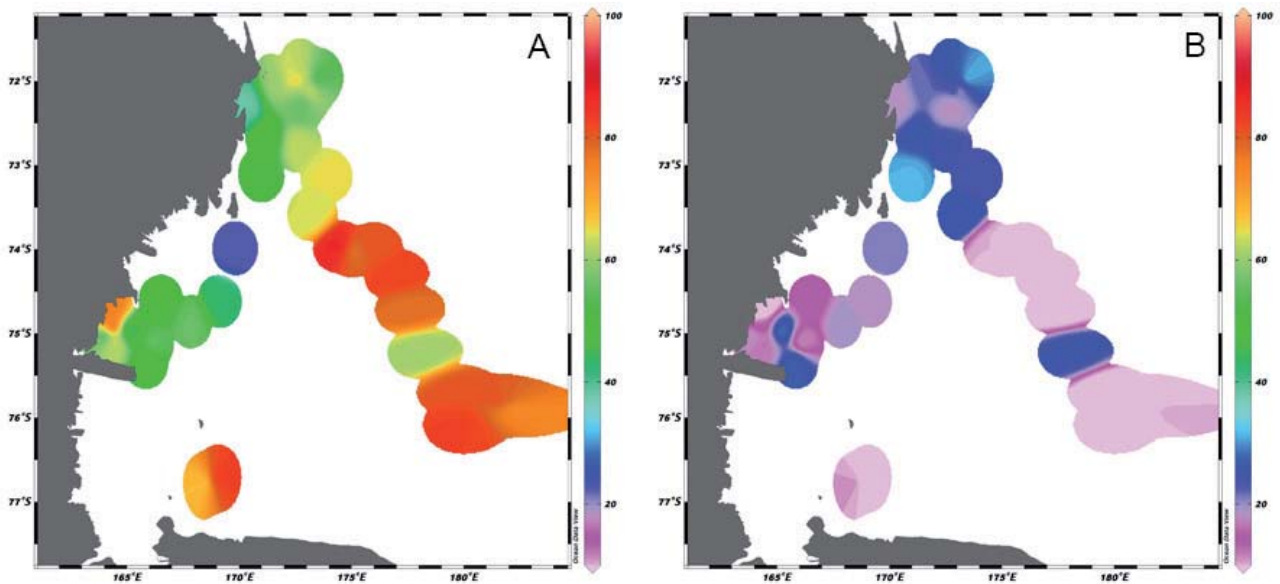


Figure 4. Spatial distribution of the mean percentage contribution of diatoms (A) and haptophytes (B) to phytoplankton community during summer 2001 in the layer 0-100 m

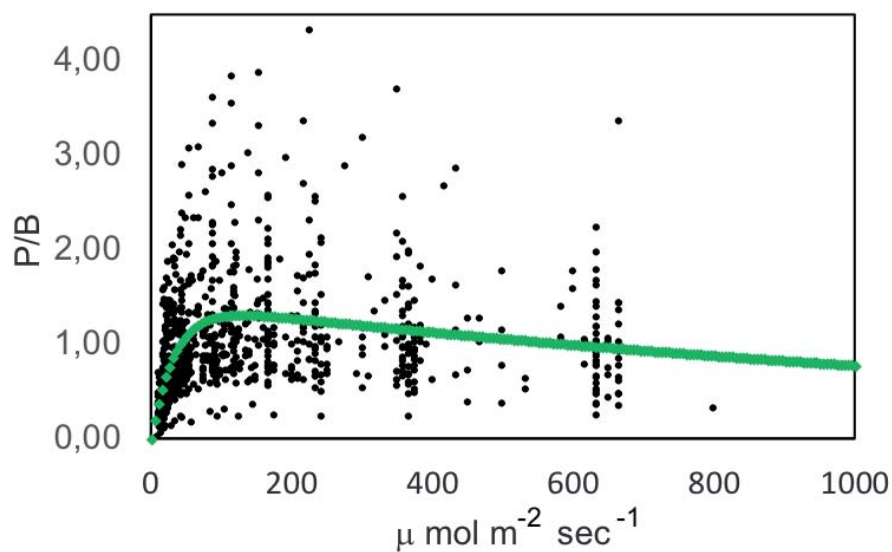


Figure 5. PvsE curves determined at 4 depths of all stations sampled in summer 2001

layers (Fig. 7). P_{vsE} experiments conducted at two days interval showed similar values at surface in the first experiment (P_{max}^B 1.42 at surface and 1.38 $\text{mgC}(\text{mgChl}a)^{-1}\text{h}^{-1}$ at 10 m depth) and a sharp decline of P_{max}^B 0.46 $\text{mgC}(\text{mgChl}a)^{-1}\text{h}^{-1}$ two days later at 10m depth (Fig. 8). Macronutrient concentrations did not change. Unfortunately, micronutrient measurements were not performed but photosynthetic performance F_v/F_m was well below 0.3 in the upper layer of the off-shore MIZ areas (Fig. 7), which indicates iron limitation (Parkhill et al., 2001). In fact, high F_v/F_m values

(0.45-0.65) are in the optimal range reported for the Ross Sea, which suggests the onset of a phytoplankton bloom, not affected by limiting factors (Fragoso & Smith, 2012; Mangoni et al., 2017). High photosynthetic performance ($F_v/F_m > 0.3$) and the highest integrated primary production values were recorded in the coastal area of TNB, where iron limitation does not occur.

In the northern area, the ratio between primary production and Chl*a* (PP/Chl_a) was similar in both years, resulting in primary production values 2.5 times higher than

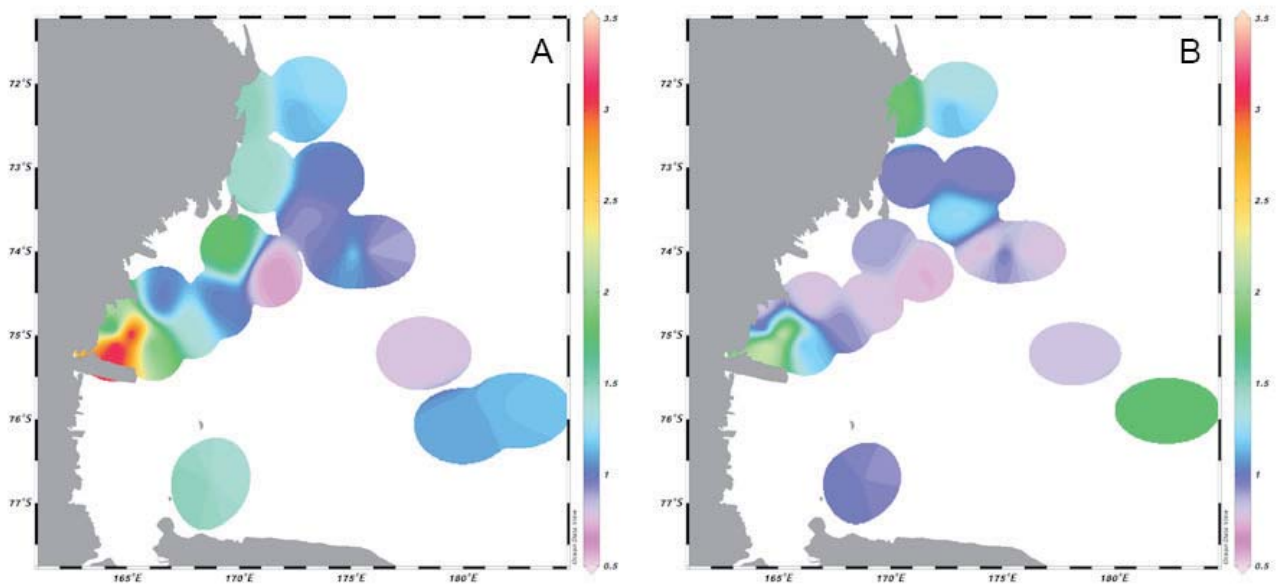


Figure 6. Spatial distribution of mean values of P_{max}^B above (A) and below (B) the UML in summer 2001

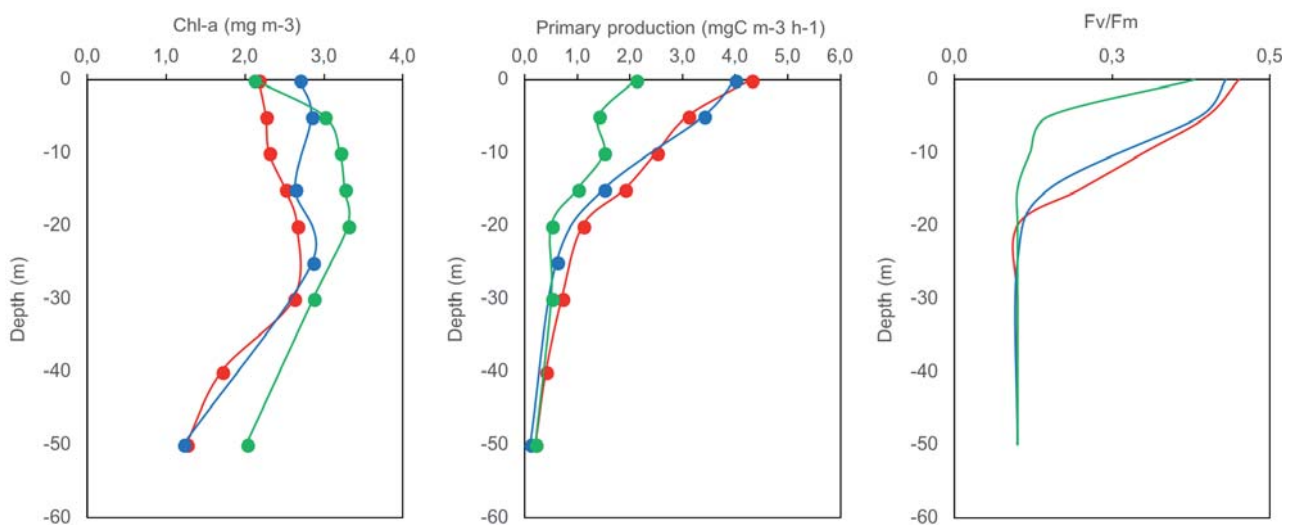


Figure 7. Replicate vertical profiles of Chl*a*, primary production and F_v/F_m in the southwestern Ross Sea area during summer 2001 (Jan. 30, Jan. 31, Feb. 1)

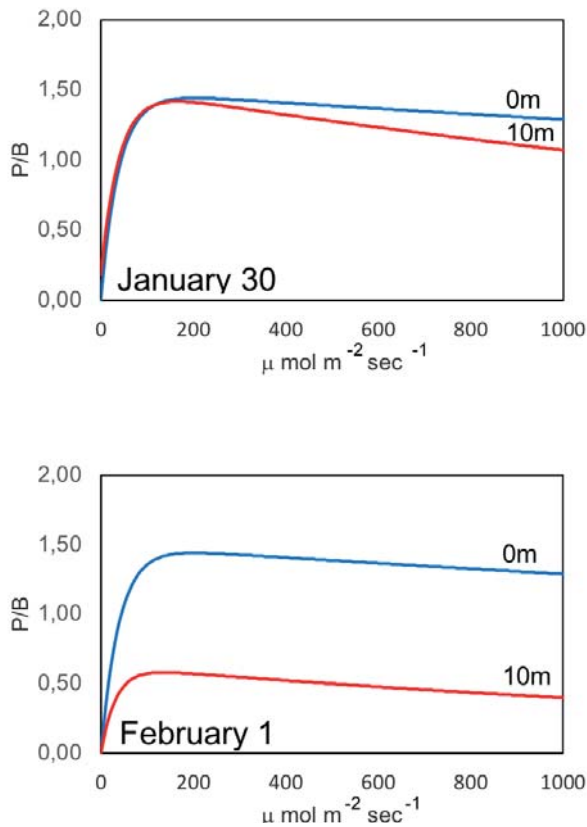


Figure 8. Replicate PvsE experiments at two depths (0 and 10m) in the southwestern Ross Sea area during summer 2001

those recorded in 1996 (Table 2). In all other areas, the PP/Chla ratio was lower in 2001 and minimum growth capacity was recorded in the southwestern ice edge area. Only minor differences were observed in the coastal area, that indicates non-limiting conditions.

Table 2. Mean values of integrated primary production ($\text{mgC m}^{-2} \text{d}^{-1}$) of different areas in the Ross Sea during austral summer 1996 and 2001.

	North	Southwest	Southeast	Coastal water (BTN)
Summer 1996	188	200	600	1410
Summer 2001	479	707	1100	1562

The data collected during austral summer 1996 and 2001 in different environmental conditions (ice-free and ice-covered waters) emphasize that the off-shore waters

of the Ross Sea represent the classic ecological Antarctic paradox with limiting factors such as micronutrients. The magnitude, extent and timing of phytoplankton blooms are likely affected by the timing of sea ice disappearance, prevailing wind speed and wave action. In contrast with this scenario, in the latest 10 years relevant changes in the abundance of phytoplankton in off-shore waters of the Ross Sea have been verified during austral summer in ice-free waters (Hatta et al., 20017; Kohut et al., 2017).

To identify the mechanisms that modulate phytoplankton blooms and the consequent fate of organic materials produced by the blooms during austral summer in the Ross Sea, an oceanographic cruise was conducted in 2014 (Mangoni et al., 2017; Misic et al., 2017; Rivaro et al., 2017). Mangoni and co-workers (2017) reported that the distribution of the main functional groups showed significant incongruities with the past. Diatoms (in different physiological status) were the dominant taxon. The high percentage of diatoms appears to be independent from the thickness of the UML. In our opinion, it is relevant that the presence of large diatoms in a wide UML contradicts the classic paradigm of Antarctic diatom accumulation in highly stratified waters (Smith & Nelson, 1985, Arrigo et al., 1998). In addition, *P. antarctica* colonial bloom occurs in an area and in a season that are usually characterized by the prevalence of diatoms. The considerable phytoplankton biomass observed, in agreement with the recent literature (e.g. Kohut et al., 2017), suggests relevant alterations in the Ross Sea summer productivity. Moreover, our findings show an uncoupled increase in large diatoms and primary consumers independent from the phase of the bloom. The low Pheapigment/Chla ratios and the presence of senescent (instead of grazed) phytoplankton cells suggest the presence of a relatively scarce trophic efficiency. The considerable increases in phytoplankton biomass and large size structure (micro-fraction accounting for 75% of the total biomass on average, independent from the functional groups) suggest that the Ross Sea could now be extremely productive in summer (Mangoni et al., 2017). The phytoplankton features in summer 2014 were more similar to typical spring conditions, as characterized by the dominance of micro-phytoplankton fractions along the ice edge, which sustains the energy transfer through the Antarctic short trophic chain “diatoms-euphausiids- whales” (Xavier et al., 2016).

The comparison between conditions observed during summer 2014 and those reported for previous years reveals considerably different ecological assets that may result from current climate changes. Yet the magnitude and nature of changes remain unclear (Massom & Stammerjohn, 2010; Constable et al., 2014; Ainley et al., 2015; Turner et al., 2015). It is unclear what are the environmental factors that drive these extraordinary changes in primary production processes during austral summer and the prevalence of

different functional groups. Probably, a modification of the Ross Sea hydrography is having a key role in reducing the limiting factors and as a consequence in modifying the primary production processes. Hatta and co-workers (2017) suggested that these changes are driven by modifications of the circumpolar deep water circulation and variations of the benthic sources which supply iron to the system.

Recent information coming from the sampling cruise carried out during austral summer 2017 by our group highlights an extraordinary increase of flagellates in the composition of phytoplankton communities but the factors that drove changes in the functional groups are unclear. Other studies reported that the cobalamin (vitamin B₁₂) and iron availability can simultaneously increase the percentage of diatoms, suggesting that vitamin B₁₂ may help govern rates of primary production as well as phytoplankton species composition (Croft et al., 2005; Bertrand et al., 2007; 2015).

4. Conclusions

Antarctic marine ecosystems have been changing, in response to increasing ocean temperatures and changes in the extent and seasonality of sea ice. The magnitude and direction of these changes vary between regions around Antarctica that could see populations of the same species changing differently in diverse regions. The analysis of our data and the recent literature clearly show that some paradigms of functioning in polar ecosystems must necessarily be reviewed in light of new knowledge. The changes that are occurring in polar environments impose different approaches, a new era of study and their global function not only in terms of climate regulations but also in terms of resources and acquisitions of new knowledge. The dynamics of sea ice will probably not change drastically in the coming years and we will see even more interannual variability and different responses of the biotic communities. Climate change effects (Fe?) on algal community structure and carbon and nutrient cycles are difficult to predict, due to the need for multivariate approaches to address synergistic and antagonistic interactions.

There is no new set-up of the ecological dynamics of the polar systems, but the need to increase the studies on these areas that play a key role in the future asset of the planet. Some of the open questions are listed below:

- Could the present ecological asset of the Ross Sea during austral summer affect not only the Ross Sea itself, but probably the entire Southern Ocean ecology, and consequently have an impact at a global scale?
- Could recurrent blooms of un-grazed *Phaeocystis antarctica* during austral spring and summer play an important role in driving CO₂ drawdown?
- Could the imbalance between phytoplankton standing stocks and primary consumers, independently from

the phase of the bloom, dramatically alter the fate of the summer primary production and the C export in the Ross Sea?

- Could the changes in the phytoplankton composition to determine a new asset of the food web in the Ross Sea?

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