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Nutrient utilisation and chlorophyll distribution in the Atlantic sector of the Southern Ocean during Austral summer 1995–96

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Abstract

The chemical fields in the Eastern Bellingshausen Sea, Gerlache and Bransfield Straits were studied for nutrients, apparent oxygen utilisation (AOU) and total inorganic carbon (TIC) in the upper mixed layer of the water column during the FRUELA 95 (December 1995–January 1996) and FRUELA 96 (January–February 1996) cruises. In Bellingshausen Sea area, a strong silicic acid gradient clearly traced the Southern Boundary of the ACC front during the two cruises. In the Bransfield Strait, the lowest concentrations of nutrients, AOU and TIC ($NO_3 < 28\,\mu mol\,kg^{-1}$, $PO_4 < 2\,\mu mol\,kg^{-1}$, $Si(OH)_4 < 80\,\mu mol\,kg^{-1}$, $AOU < 10\,\mu mol\,kg^{-1}$, $TIC < 2170\,\mu mol\,kg^{-1}$) corresponded to transition zonal water with Bellingshausen Sea influence. The southeastern part, which was dominated by transition zonal water with Weddell Sea influence, had the highest levels of these properties. In the Gerlache Strait, the chemical field was marked by low-salinity water in the southwestern extreme, which had low nutrient levels. Though the chemical field strongly reflected the thermohaline field, significant nutrient consumption was observed where there was high chlorophyll *a* and particulate organic matter. During the FRUELA 95 cruise, the highest nutrient consumption in the upper mixed layer was localised in the Gerlache Strait ($\Delta NO_3 = 7 \pm 2\,\mu mol\,kg^{-1}$, $\Delta PO_4 = 0.5 \pm 0.1\,\mu mol\,kg^{-1}$, $\Delta Si(OH)_4 = 6 \pm 3\,\mu mol\,kg^{-1}$, $\Delta AOU = 65 \pm 15\,\mu mol\,kg^{-1}$, $\Delta TIC = 40 \pm 8\,\mu mol\,kg^{-1}$) and in the Southern Boundary of the ACC front ($\Delta NO_3 = 10 \pm 3\,\mu mol\,kg^{-1}$, $\Delta PO_4 = 0.6 \pm 0.2 \mu mol\,kg^{-1}$, $\Delta Si(OH)_4 = 1.9 \pm 1.6\,\mu mol\,kg^{-1}$, $\Delta AOU = 78 \pm 10\,\mu mol\,kg^{-1}$, $\Delta TIC = 69 \pm 17\,\mu mol\,kg^{-1}$), which was associated with high biomass. During FRUELA 96 cruise, the highest nutrient consumption also was observed in the Gerlache Strait ($\Delta NO_3 = 14 \pm 3\,\mu mol\,kg^{-1}$, $\Delta PO_4 = 1.1 \pm 0.2\,\mu mol\,kg^{-1}$, $\Delta Si(OH)_4 = 12 \pm 5\,\mu mol\,kg^{-1}$, $\Delta AOU = 94 \pm 22\,\mu mol\,kg^{-1}$, $\Delta TIC = 70 \pm 16\,\mu mol\,kg^{-1}$), with average chlorophyll *a* of $7 \pm 2\,mg\,m^{-3}$. Using a simple approach, we can ascertain whether the estimated nutrient consumption can account for the observed biomass accumulation during the two cruises. © 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

One of the most characteristic features of the Southern Ocean is its low primary production despite permanently high nutrient concentrations. However, high phytoplankton stocks have been observed in some restricted regions, especially in marginal ice zones (Smith and Nelson, 1986; Comiso et al., 1990; Knox, 1994; Pérez et al., 1994) and in sheltered coastal waters (Smith and Nelson, 1985; Holm-Hansen et al., 1989; Holm-Hansen and Mitchell, 1991). In these regions, vertical stratification has been described as the major driving force for phytoplankton accumulation, as it provides a favourable light regime

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(Mitchell and Holm-Hansen, 1991; Mitchell et al., 1991; Moline and Prezelin, 1997). The demise of phytoplankton stocks can be attributed to several factors: micronutrient availability, grazing, sinking, dispersal by vertical mixing, and other advective processes (Smith and Nelson, 1985; Martin et al., 1991; Holm-Hansen and Mitchell, 1991; Cota et al., 1992; Atkinson and Shreeve, 1995). In contrast, offshore waters of the Southern Ocean have been described as High Nutrient Low Chlorophyll regions (Nelson and Smith, 1991; Comiso et al., 1993). Recent findings from the STERNA program, in the western sector of the Bellingshausen Sea (Turner and Owens, 1995), and from the ANT X/6 cruise, from the ice edge of the eastern Weddell Sea up to the Polar Frontal Zone (Smetacek et al., 1997), also demonstrate the importance of frontal zones in phytoplankton accumulation. High chlorophyll concentrations were found in the region of the Polar Front, whereas unexpected low chlorophyll concentrations were associated with the retreating ice edge during these two programs. These results suggest that a number of factors can limit or enhance phytoplankton stocks in these areas. These observations fit with the Southern Ocean "mosaic of subsystems" theory (Treguer and Jacques, 1992).

There have been few observations of nutrient-depletion in the Southern Ocean with the exception of an ice-edge bloom in the Ross Sea (Nelson and Smith, 1986) and in coastal waters near Palmer Station (Holm-Hansen et al., 1989; Moline et al., 1996). Nevertheless, significant nutrient consumption has been reported for the different subregimes; in the ice-edge zone (Jennings et al., 1984; Pérez et al., 1994; Catalano et al., 1997) and also associated with high phytoplankton stocks in oceanic frontal regions (Goeyens et al., 1991; Bianchi et al., 1992; Whitehouse et al., 1995).

This work presents nutrients, oxygen, inorganic carbon and chlorophyll data collected during the FRUELA 95 and FRUELA 96 cruises in the frame of the Spanish program "Carbon fluxes in an area of high productivity (western basin of the Bransfield Strait and Gerlache Strait)". We begin with a detailed description of the horizontal distributions of these variables in the upper mixed layer (UML) and its relation to the main hydrographic features. We then discuss the relationship between estimated nutrient consumption/oxygen production and biomass accumulation, and examine the ratios between estimated anomalies. Additionally, a simple mathematical approach is applied to assess if the estimated nutrient consumption can justify the biomass measured.

2. Material and methods

2.1. Survey area and analytical details

A detailed description of the survey strategy is explained by Anadón and Estrada (2002). During the FRUELA 95 (3–11 December 1995; Fig. 1a) and FRUELA 96 (18–27 January 1996; Fig. 1b) cruises, the eastern sector of the Bellingshausen Sea, the Gerlache Strait and the western portion of the Bransfield Strait were sampled. An intensive sampling of the Bransfield Strait was also undertaken during FRUELA 95 between 12 and 19 of December 1995 (Fig. 1c). Samples for nutrients, oxygen, pH and alkalinity were taken at selected depths from surface to the bottom. Samples for chlorophyll *a* (Chl *a*) were taken from surface to 100 m, but samples for particulate organic matter were only taken at selected stations (Fig. 1). Sampling depths correspond to the same levels of Chl *a* samples with additional levels from 100 m to the bottom.

Nutrient samples were filtered through 0.45 μm Millipore filters prior to analysis and were analysed within 12 h after collection; and were stored in the refrigerator prior to analysis and in the dark. Nutrient concentrations were determined by segmented flow analysis with Technicon AAII systems, following Hansen and Grasshoff (1983) with some improvements (Mouriño and Fraga, 1985; Álvarez-Salgado et al., 1992). The analytical error was $\pm 0.05\,\mu\text{mol}\,\text{kg}^{-1}$ for nitrate, $\pm 0.05\,\mu\text{mol}\,\text{kg}^{-1}$ for silicic acid, and $\pm 0.01\,\mu\text{mol}\,\text{kg}^{-1}$ for phosphate. Dissolved oxygen was determined by Winkler potentiometric titration. The estimated analytical error was $\pm 1\,\mu\text{mol}\,\text{kg}^{-1}$. Oxygen saturation was calculated following Benson and Krause equation (UNESCO, 1986), and apparent oxygen utilisation (AOU) was calculated as the difference between

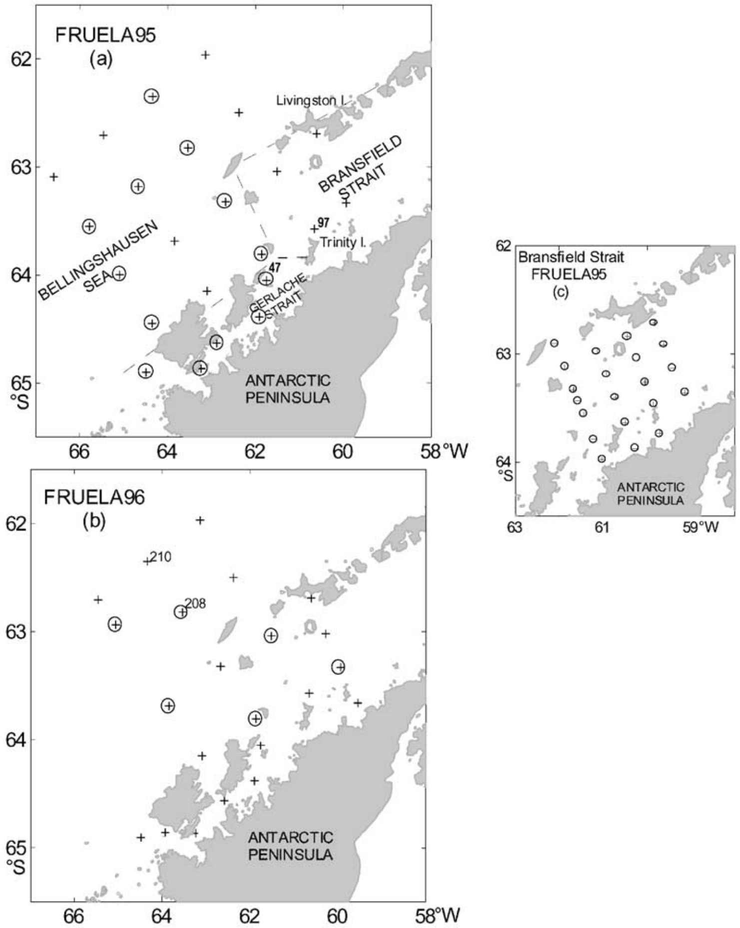

Fig. 1. Map of the chemical stations sampled during FRUELA 95 cruise (a); FRUELA 96 cruise (b); and the intensive sampling of the Bransfield Strait during FRUELA 95 (c). The different domains, Bellingshausen, Bransfield and Gerlache Straits, are demarcated by dashed lines in Fig. 1a. (O) Stations where particulate organic matter samples also were collected. Stns which are also cited in the text are numbered.

saturation oxygen and observed oxygen. pH(NBS) was measured potentiometrically with an error of ±0.005 and normalised to 15°C (Pérez and Fraga, 1987a). Alkalinity was determined by potentiometric titration with HCl to a final pH of 4.4 (Pérez and Fraga, 1987b). The analytical error was $\pm 2\,\mu\text{mol}\,\text{kg}^{-1}$. Total inorganic carbon and partial CO_2 pressure (pCO$_2$) were estimated from pH and alkalinity measurements using the carbonic system equations with the acid constants of Mehrbach et al. (1973) and the solubility constant of Weiss (1974). The estimated error of total inorganic carbon was $\pm 4\,\mu\text{mol}\,\text{kg}^{-1}$. Chl *a* was measured using 90% acetone extraction in a 10,000 R Turner fluorometer (Yentsch and Menzel, 1963). The precision was $\pm 0.05\,\text{mg}\,\text{m}^{-3}$. Particulate organic matter (filtration volume 1 l) was collected on Whatman GF/F filters, and analyses were performed in a PE 2400 elemental analyser, with a precision of $\pm 0.04\,\mu\text{mol}\,\text{kg}^{-1}$ for nitrogen and $\pm 0.1\,\mu\text{mol}\,\text{kg}^{-1}$ for carbon.

2.2. Depth of the upper mixed layer and stability

CTD profiles were used to delimit the depth of the UML. A change of $\sigma_t \geqslant 0.05$ over 5 m depth interval was the criterion used to establish the depth of UML (Z_{UML}) (Mitchell and Holm-Hansen, 1991). The vertical stability E was calculated as $E = 1/\rho(\delta\rho/\delta z)$, where ρ is the density of the seawater and z is the depth in m. The stability maximum immediately below the depth of the UML represents the strength of the pycnocline.

2.3. Estimated anomalies of the chemical variables

Nutrient deficit was calculated as the difference between the winter nutrient concentration (prebloom conditions) and average nutrient concentration for the UML; following Le Corre and Minas (1983). Average nutrient concentration in the UML is the integrated nutrient concentration from the surface down to the depth of the upper mixed layer (Z_{UML}) divided by Z_{UML}. We have considered the winter nutrient concentration as the nutrient concentration at the temperature minimum of Antarctic Surface Water. This temperature minimum of Antarctic Surface Water corresponds to the remnant of the winter mixed layer (Le Corre and Minas, 1983; Pollard et al., 1995). For each station, we have found the depth of the temperature minimum of Antarctic Surface Water based on the CTD profiles, and nutrient values at this depth were calculated by linear interpolation between the bottle nutrient concentrations at the two closest depths. At the easternmost portion of the Bransfield Strait, there is no signature of the temperature minimum associated with Antarctic Surface Water. For these stations, we have taken as a reference concentration the nutrient concentration at $\theta = -1°C$, which corresponds to the upper limit of the Bransfield Deep Water (García et al., 1994). Nutrient decrease due to dilution by melt water was considered following Catalano et al. (1997).

2.4. Corrected chemical variables

In order to remove the influence of the dissolution/precipitation of calcium carbonate in the concentration of TIC, we must introduce the following correction (Broecker and Peng, 1982) as

$$[\mathrm{TIC_{cor}}] = [\mathrm{TIC}] - 0.5(A + [\mathrm{NO_3^-}]),$$

where A is alkalinity and $[\mathrm{NO_3^-}]$ is the nitrate concentration. An average of 23% of the TIC concentration corresponds to the dissolution/precipitation of calcium carbonate in the studied area.

3. Results

3.1. Spatial distributions of nutrients and Chl *a* in the upper mixed layer

The horizontal distribution of the average silicic acid concentration in the UML in the eastern Bellingshausen Sea and Gerlache Strait region in December 1995 is clearly controlled by hydrography (Fig. 2a). There is a southward increase in silicic acid concentrations, with the highest silicic acid levels ($\mathrm{Si(OH)_4} > 80\,\mu\mathrm{mol\,kg^{-1}}$) in the Gerlache Strait. Advection of waters from the Gerlache Strait to the Bransfield Strait is traced by high silicic acid concentrations found close to Trinity Island. In the northwestern part of the Bellingshausen Sea region, there is a strong gradient in silicic acid concentrations, of about $30\,\mu\mathrm{mol\,kg^{-1}}$ in only 70 km. This strong gradient is associated with the Southern Boundary of the ACC front (SbyACC; García et al., 2002). Silicic acid concentrations $<40\,\mu\mathrm{mol\,kg^{-1}}$ are found north of the SbyACC front, which corresponds to Bellingshausen Sea Warm Water.

The horizontal distribution of the average Chl *a* concentration in the UML (Fig. 2b) shows two maximum regions. High values of Chl *a* (Chl $a > 3\,\mathrm{mg\,m^{-3}}$) are found in the Gerlache Strait, with a maximum of $8\,\mathrm{mg\,m^{-3}}$ centred at stn 47, in the northeast part of the Strait. These high Chl *a* concentrations are associated with shallow UML ($Z_{\mathrm{UML}} < 10$ m, Table 1) and relatively high stabilities of the pycnocline ($(1.5 \pm 0.6) \times 10^5\,\mathrm{m^{-1}}$; Table 1; Fig. 2e and f). The Chl *a* concentration integrated to UML is about 60% of integrated Chl *a* to the light compensation depth in the Gerlache Strait (~ 30 m considering 0.1% of photosynthetic available radiation). The other phytoplankton accumulation is localised in the SbyACC frontal region, with Chl *a* levels $> 2\,\mathrm{mg\,m^{-3}}$. In contrast to the Gerlache Strait,

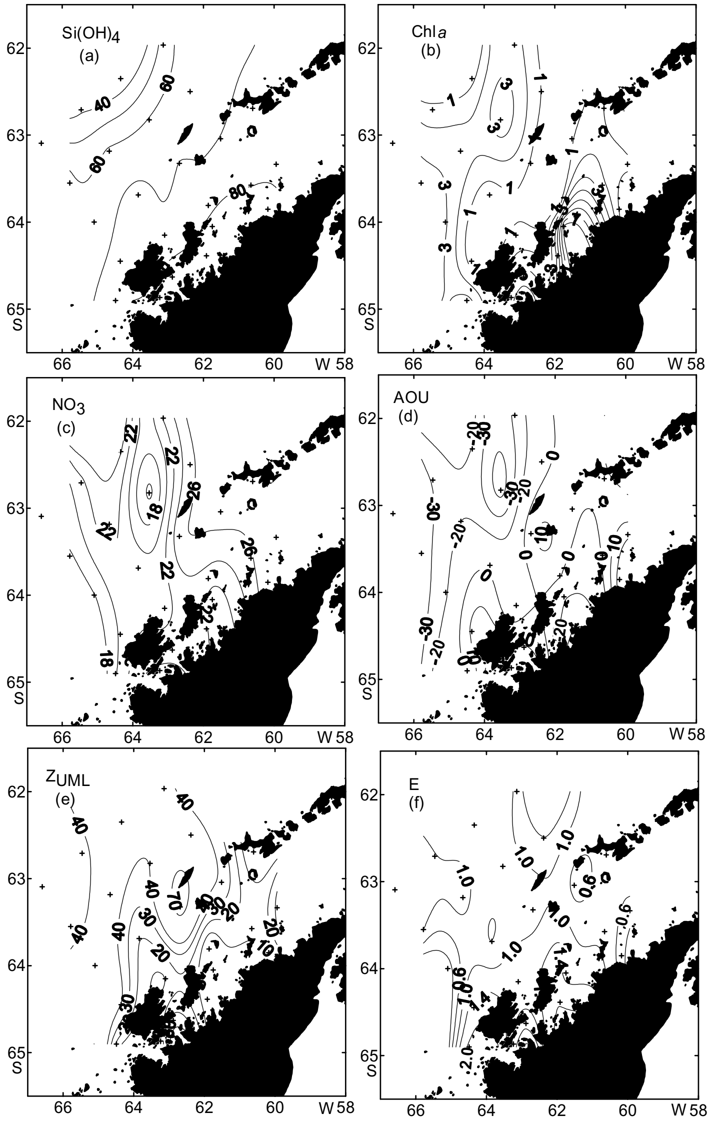

Fig. 2. Horizontal distributions for the UML of average silicic acid (a); average Chl *a* (b); average nitrate (c); average AOU (d); depth (e); and stability (*E*) (f) in December 1995 sampling. Nutrient and AOU concentrations in μmol kg^{-1}; Chl *a* in mg m^{-3}, depth in *m* and stability in m^{-1} ($\times 10^5$).

this biomass accumulation is coupled with deep UML ($Z_{\mathrm{UML}} \sim 40$ m; Table 1) and slightly lower pycnocline stabilities (Fig. 2e and f). Integrated Chl *a* concentration in the UML are 60% of the integrated Chl *a* up to the depth of 0.1% of photosynthetic available radiation ($\sim$49 m), and there is a good correlation between them ($r^2 = 0.70$; $n = 16$).

Unlike silicic acid average concentrations, nitrate and apparent oxygen utilisation (AOU) average concentrations in the UML are strongly affected by phytoplankton utilisation (Fig. 2c and d). Minima of nitrate ($NO_3 < 20\,\mu$mol kg^{-1}), accompanied with minima of AOU ($AOU < -30\,\mu$mol kg^{-1}), correspond to the Chl *a* maxima at the SbyACC frontal region. High nitrate and

Table 1
Average values of depth, stability (E), Chl a, PON and POC of the UML in the different domains[a]

Domain	Z_{UML}	E	Chl a	[PON]	[POC]
Bellingshausen'95	39 ± 19	1.0 ± 0.4	1.7 ± 1.1	2.5 ± 0.7	17 ± 6
Gerlache'95	13 ± 11	1.5 ± 0.6	4.3 ± 1.7	3.6 ± 1.2	19 ± 5
Bransfield'95	25 ± 19	1.0 ± 0.5	2.0 ± 0.9	2.1 ± 0.6	12 ± 3
Bellingshausen'96	38 ± 12	1.8 ± 0.6	0.5 ± 0.2	1.0 ± 0.3	6 ± 1
Gerlache'96	17 ± 7	2.2 ± 1.3	7.1 ± 1.7	n.d.	n.d.
Bransfield'96	12 ± 10	1.4 ± 0.5	1.0 ± 0.3	1.8 ± 0.6	10 ± 3

[a] Note: Depth in m, stability in $10^5\,\mathrm{m}^{-1}$, Chl a in $\mathrm{mg\,m^{-3}}$, PON and POC in $\mu\mathrm{mol\,kg^{-1}}$, n.d. not determined.

AOU concentrations in the easternmost section reflect the presence of transitional zonal water dominated by Weddell Sea features (García et al., 2002). In the Gerlache Strait, nutrient utilisation/oxygen production by phytoplankton is not as evident as in the oceanic frontal region. Oxygen values above oxygen saturation concentration ($\mathrm{AOU} < -10\,\mu\mathrm{mol\,kg^{-1}}$), with relatively low nitrate levels ($\mathrm{NO_3} < 23\,\mu\mathrm{mol\,kg^{-1}}$) are observed in the northeast sector, where the Chl a maximum is found. Higher nitrate ($\mathrm{NO_3} > 22\,\mu\mathrm{mol\,kg^{-1}}$) and AOU concentrations ($\mathrm{AOU} > 20\,\mu\mathrm{mol\,kg^{-1}}$) are observed in the southwestern sector of Gerlache Strait.

During the intensive sampling of the Bransfield Strait in December 1995 (Fig. 1c), the hydrography was defined by the advection of waters with Bellingshausen Sea influence and Weddell Sea influence (García et al., 2002). Waters with Bellingshausen Sea influence dominated the northwestern sector and had silicic acid levels of $< 80\,\mu\mathrm{mol\,kg^{-1}}$ (Fig. 3a) and salinities of > 34.0 (distribution not shown). The highest silicic acid concentrations (maximum of $85\,\mu\mathrm{mol\,kg^{-1}}$ at stn 72 in the Gerlache–Bransfield confluence) are associated with water coming from the Gerlache Strait. This hydrographic situation strongly determined the Chl a distribution in the UML (Fig. 3b). In general, phytoplankton maxima were concentrated at the front between waters with Bellingshausen Sea and Weddell Sea influence and in the Gerlache–Bransfield confluence. Maximum Chl a levels are very similar to those found in the SbyACC frontal region in the Bellingshausen Sea. Chl a concentrations decrease (Chl $a < 2\,\mathrm{mg\,m^{-3}}$) north of the front. The distributions of Z_{UML} and the corresponding pycnocline stability (Fig. 3e and f) show the shallowest UML and more stratified waters in the southeastern part, with no UML in the southernmost stns due to the influence of glacial melt water (Table 1). In spite of this, the highest biomass concentrations are located at the frontal region with deep UML ($Z_{UML} \sim 50\,\mathrm{m}$) and lower pycnocline stabilities. The distributions of nitrate and AOU (Fig. 3c and d) are very similar to each other. The highest nitrate and AOU concentrations are centred at stn 97. Low nitrate and AOU levels concur with the biomass accumulation at the Bransfield Front and in the Gerlache-Bransfield confluence.

The presence of the SbyACC front during FRUELA 96 can be seen clearly from the horizontal distribution of silicic acid (Fig. 4a). In contrast to the situation found during FRUELA 95 cruise (Fig. 2a), silicic acid values lower than $25\,\mu\mathrm{mol\,kg^{-1}}$ are only found at stn 210. There was also, a shift of the SbyACC front (Gomis et al., 2002) which was followed by a shift in the position of the $60\,\mu\mathrm{mol\,kg^{-1}}$ silicic acid isoline. Unfortunately, the westernmost section of the Bellingshausen Sea region sampled in December 1995 was not surveyed again during the FRUELA 96 cruise, due to bad weather conditions. High silicic acid concentrations were also found in the Gerlache Strait, though were slightly lower (average $\mathrm{Si(OH)_4} = 80 \pm 6\,\mu\mathrm{mol\,kg^{-1}}$) than those found during the FRUELA 95 cruise (average $\mathrm{Si(OH)_4} = 84 \pm 3\,\mu\mathrm{mol\,kg^{-1}}$), which probably suggests a greater silicic acid utilisation during the second survey.

The Chl a distribution in the UML during the FRUELA 96 cruise is very different to that observed during FRUELA 95 (Fig. 4b). The phytoplankton stock found in the SbyACC frontal

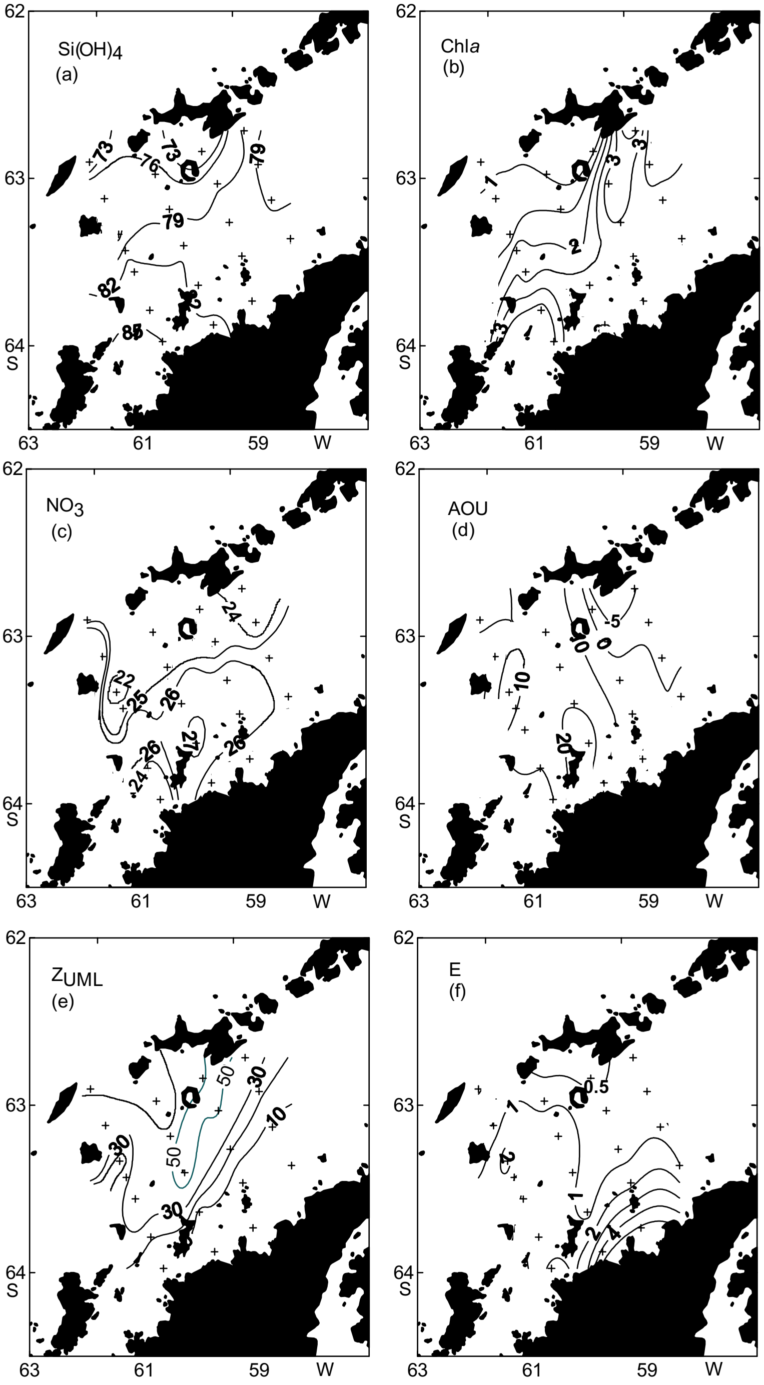

Fig. 3. Horizontal distributions for the UML of average silicic acid (a); average Chl *a* (b); average nitrate (c), average AOU (d); depth (e) and stability (*E*) (f) during the intensive sampling of the Bransfield strait in December 1995. Nutrient and AOU concentrations in μmol kg^{-1}; Chl *a* in mg m^{-3}, depth in *m*, and stability in m^{-1}(× 10^5).

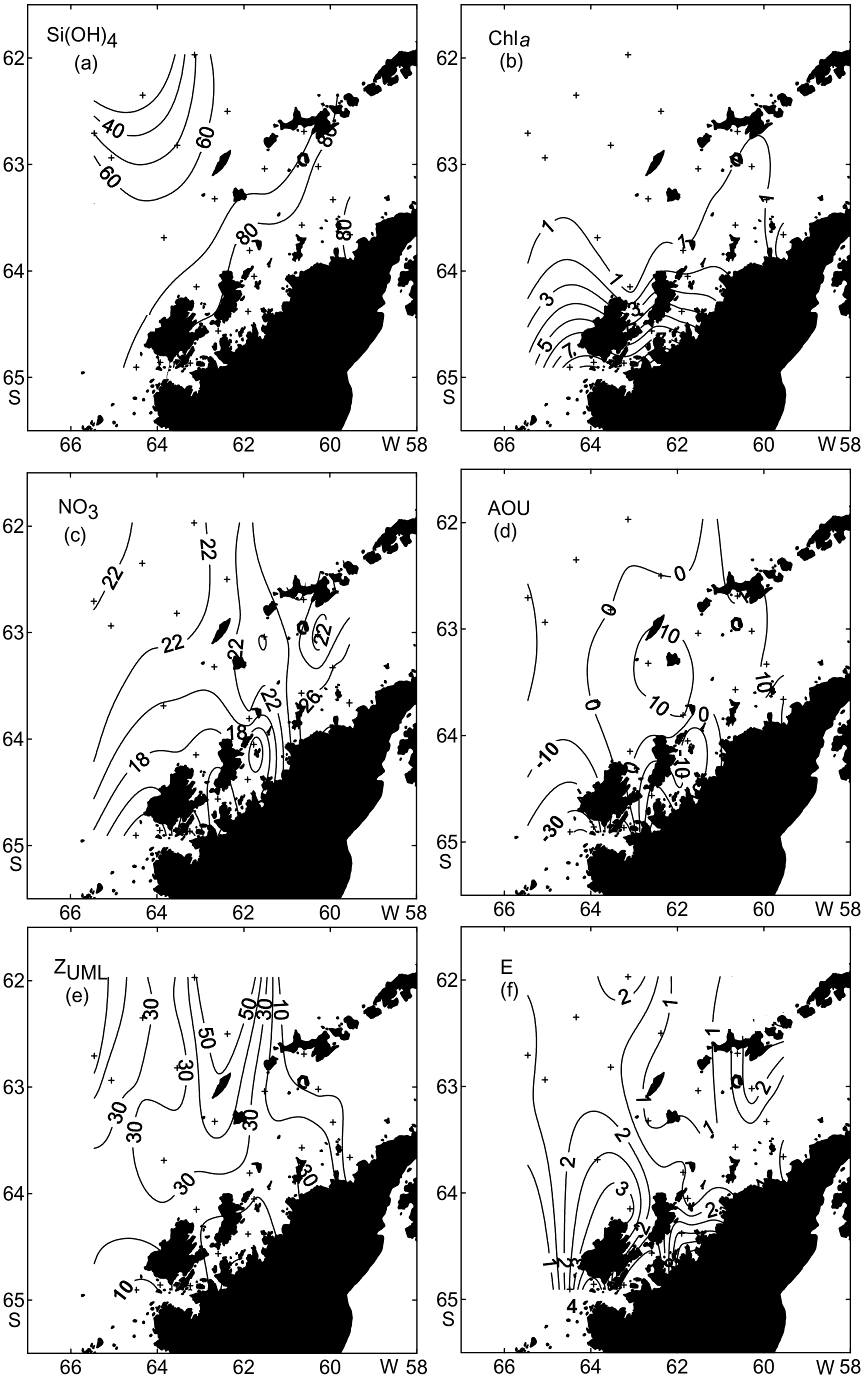

Fig. 4. Horizontal distributions for the UML of average silicic acid (a); average Chl *a* (b); average nitrate (c); average AOU (d); depth (e); and stability (E) (f) in January 1996. Nutrient and AOU concentrations in μmol kg^{-1}; Chl *a* in mg m^{-3}, depth in *m* and stability in m^{-1}($\times 10^5$).

region during the first survey (Fig. 2b) has completely disappeared during the FRUELA 96 cruise, and average Chl *a* concentration has decreased from $2\pm1\,\mathrm{mg\,m^{-3}}$ to $0.5\pm0.2\,\mathrm{mg\,m^{-3}}$ (Table 1). However, UML depths have not changed and pycnocline stability has increased (Table 1; Fig. 4e and f). Chl *a* maxima are again found in the Gerlache Strait, reaching an average of $7\pm2\,\mathrm{mg\,m^{-3}}$. These maxima are associated with shallow UMLs and the strongest stratification during the cruise (Table 1).

The horizontal distributions of average nitrate and AOU in the UML (Fig. 4c and d) are very similar for the three large transects. Nitrate levels $>25\,\mu\mathrm{mol\,kg^{-1}}$ and $\mathrm{AOU}>10\,\mu\mathrm{mol\,kg^{-1}}$ in the region of the Bransfield Strait are associated with the advection of transitional zonal waters with Weddell Sea influence. The lowest nitrate and AOU concentrations ($\mathrm{NO_3}=16\pm3\,\mu\mathrm{mol\,kg^{-1}}$ and $\mathrm{AOU}=-17\pm18\,\mu\mathrm{mol\,kg^{-1}}$) are localised in the Gerlache Strait. Chemical parameter concentrations are lower than during the FRUELA 95 cruise coupled with higher Chl *a* levels in the Strait (Table 1).

3.2. Spatial distributions of nutrients and AOU anomalies

Nutrient anomalies were obtained by the method described in Section 2. Only the nitrate, AOU and silicic acid anomalies distributions are presented (Figs. 5–7). Phosphate and $\mathrm{TIC_{cor}}$ anomalies followed a similar pattern to nitrate, (see following section). The distributions of nitrate, AOU and silicic acid anomalies in the eastern Bellingshausen Sea during December 1995 are shown in Fig. 5. Nitrate anomalies distribution is akin to the AOU anomalies distribution and significantly correlates with the average Chl *a* of the UML (Fig. 2b) ($r^2=0.69$ and $r^2=0.75$ $n=11$; for nitrate vs Chl *a* and AOU vs Chl *a* respectively). The highest nitrate consumption/oxygen production is located in the region of the SbyACC front (maxima $\Delta\mathrm{NO_3}=14\,\mu\mathrm{mol\,kg^{-1}}$ and $\Delta\mathrm{AOU}=95\,\mu\mathrm{mol\,kg^{-1}}$) and in the Gerlache Strait with a maximum in the Gerlache–Bransfield confluence ($\Delta\mathrm{NO_3}=8.3\,\mu\mathrm{mol\,kg^{-1}}$ and $\Delta\mathrm{AOU}=84\,\mu\mathrm{mol\,kg^{-1}}$). However, in the horizontal distribution of silicic acid anomalies (Fig. 5c), we observe the highest anomalies ($\Delta\mathrm{Si(OH)_4}>15\,\mu\mathrm{mol\,kg^{-1}}$) north of the SbyACC frontal region and south of the Shetland Islands. High silicic acid anomalies ($\Delta\mathrm{Si(OH)_4}>10\,\mu\mathrm{mol\,kg^{-1}}$) also are reached in the SW portion of the Gerlache Strait dominated by diatoms (Varela et al., 2002), whereas there is no silicic acid consumption in the NE sector of the Strait, where cryptomonad populations prevailed (Varela et al., 2002).

Nutrient anomalies and oxygen production in the Bransfield region were not so high as in the Bellingshausen area (Table 3). However, the slope of the regression (model II; Sokal and Rolhf, 1995) between particulate organic carbon (POC) and particulate organic nitrogen (PON) ($\mathrm{C:N}=5.0\pm0.2$; Table 2) suggests that phytoplankton biomass is actively growing. This phytoplankton biomass represents about 68% of the particulate organic matter in the UML, obtained by multiplying the slope of the regression of POC vs. Chl *a* by the Chl *a* average and dividing by the POC average (Table 1). The horizontal distributions of nitrate and AOU anomalies (Fig. 6a–b) show maximum values located in the region of high Chl *a* concentration. One maximum is in the region of the Gerlache–Bransfield confluence and the other in the Bransfield Front. The horizontal distribution of silicic acid anomaly is slightly different from the other two (Fig. 6c). Silicic acid anomalies $<1\,\mu\mathrm{mol\,kg^{-1}}$ are obtained in the southern part, and are associated with criptomonad populations (Varela et al., 2002). The highest silicic acid anomalies are found in the domain of the transitional zonal waters with Bellingshausen Sea influence.

In the Bellingshausen area during the FRUELA 96 cruise, relatively high nutrient consumption/oxygen production (Fig. 7a–c; Table 3) is found but the Chl *a* concentration is low (average Chl $a=0.5\pm0.2$; Table 1). The positive intercept of the regression between POC and Chl *a* (Table 2) suggests that approximately 59% of POC is comprised of microheterotrophs and detritus material, which contrasts the situation found during December 1995 where autotrophic material prevailed (Pedrós-Alió et al., 2002). The low slope of the POC vs PON regression (Table 2) indicates

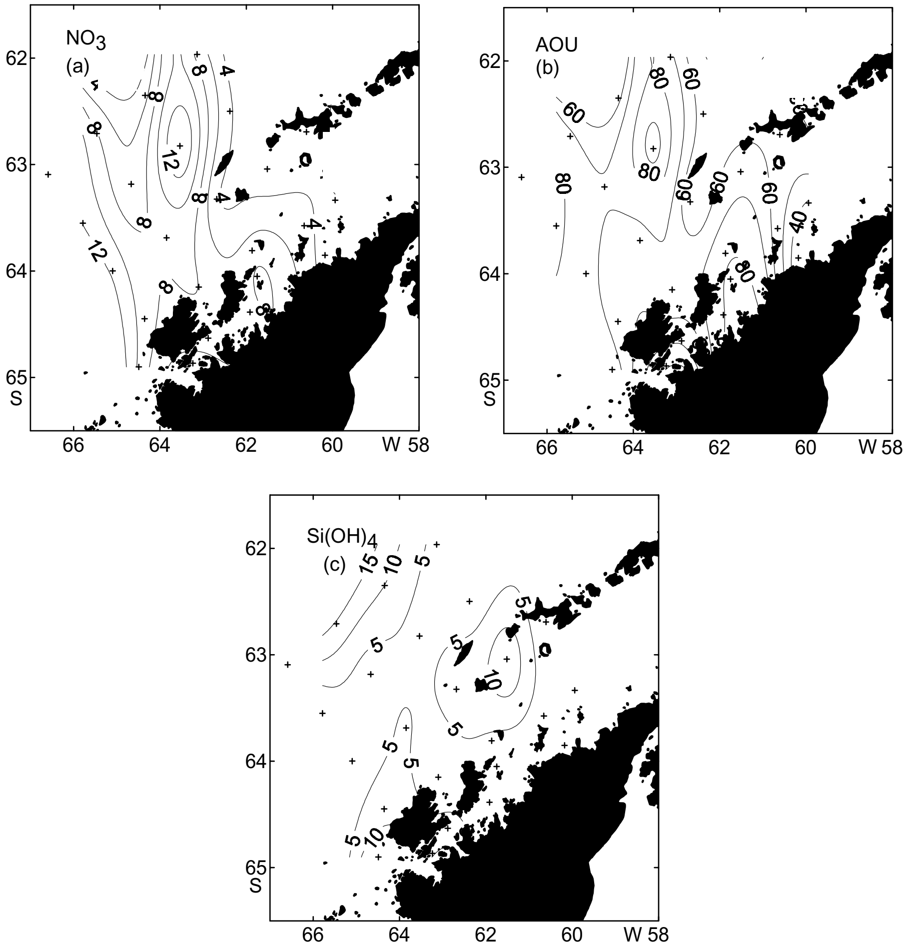

Fig. 5. Horizontal distributions for the UML of estimated nitrate (a); AOU (b); and silicic acid (c) consumptions in December 1995. Units in $\mu mol\,kg^{-1}$.

that phytoplanktonic populations are still growing. Average silicic acid anomaly for the Bellingshausen area ($\Delta Si(OH)_4 = 11 \pm 8\,\mu mol\,kg^{-1}$) is higher than that recorded during the FRUELA 95 cruise ($\Delta Si(OH)_4 = 5 \pm 4\,\mu mol\,kg^{-1}$; Table 3). The highest silicic acid anomalies ($\Delta Si(OH)_4 > 20\,\mu mol\,kg^{-1}$) are located in the SbyACC frontal region (Fig. 7c). By comparison, high silicic acid anomalies ($\Delta Si(OH)_4 > 20\,\mu mol\,kg^{-1}$), associated with high nitrate and AOU anomalies ($\Delta NO_3 > 10\,\mu mol\,kg^{-1}$; $\Delta AOU > 100\,\mu mol\,kg^{-1}$; Table 3), are encountered in the Gerlache Strait, where Chl *a* concentrations reach maximum values (Fig. 4b; Table 1). Nutrient anomalies are higher than in the first transect along this Strait during the FRUELA 95 cruise. Unfortunately, we do not have particulate organic matter data for Gerlache Strait during FRUELA 96 cruise, but high rates of primary production were measured (Varela et al., 2002).

3.3. *Ratios between estimated nutrient consumption/oxygen production*

High correlations were found between nitrate, phosphate, TIC_{cor} and AOU anomalies (Table 4). However, silicic acid anomalies did not follow a

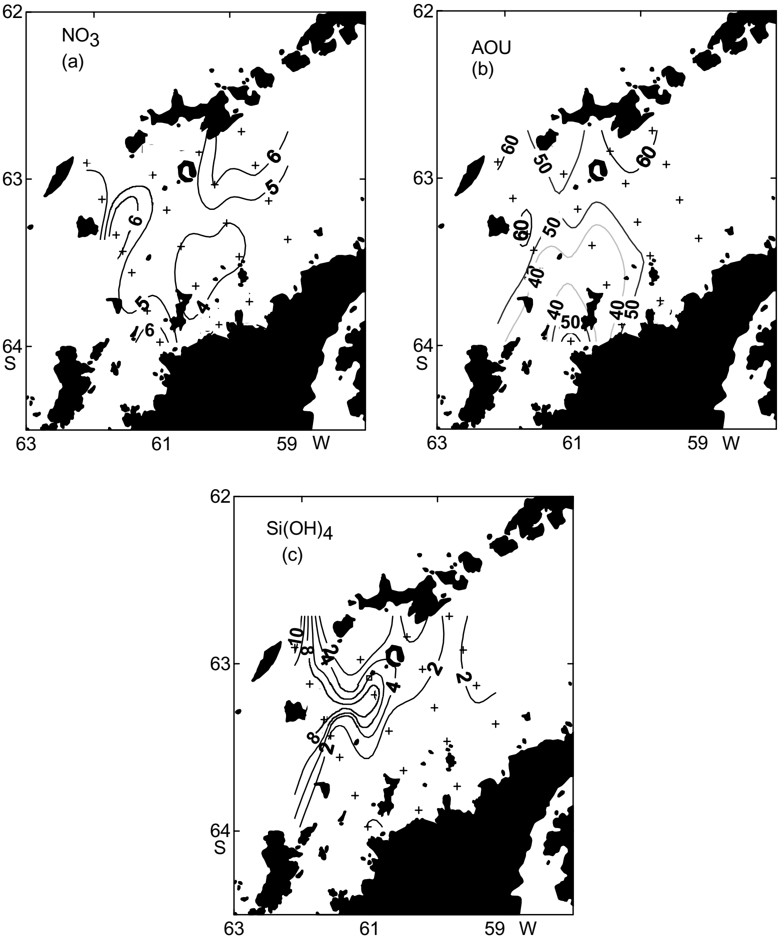

Fig. 6. Horizontal distributions for the UML of estimated nitrate (a); AOU (b); and silicic acid (c) consumptions during the intensive sampling of the Bransfield Strait in December 1995. Units in μmol kg^{-1}.

closed pattern to the other chemical parameters as it was mentioned before.

The $\Delta NO_3:\Delta PO_4$ ratios are similar or slightly lower than the classical Redfield ratio of 16:1 (Redfield et al., 1963). Our results are similar to the rather low $N:P \sim 14$ assimilation ratios reported for surface Antarctic waters (Martin et al., 1991; de Baar et al., 1997), which reflects a preferential P-assimilation regarding to nitrogen, for Antarctic phytoplankton (Catalano et al., 1997).

Silicic acid anomalies did not correlate with the anomalies of the other chemical properties. Averages $\Delta Si(OH)_4:\Delta NO_3$ range from 0.8 to 1.9, and are within the values reported by Copin-Montegut and Copin-Montegut (1978) from the particulate organic matter analysis for Antarctic cruises (Si : N range from 0.1 to 2.3). Higher Si : N ratios have been obtained for the Southern Ocean (between 0.8 and 13 (Le Jehan and Treguer, 1983); 4.55 (Minas and Minas, 1992)), which is related to the high need of the Antarctic diatoms, high sedimentation rates, and low dissolution of biogenic silica (Le Jehan and Treguer, 1983).

The $\Delta TIC_{cor}:\Delta NO_3$ ratios range from 5.0 to 6.4, and are similar to the C : N ratio derived from the particulate organic matter (Table 2), but are lower than those deduced in a similar manner by

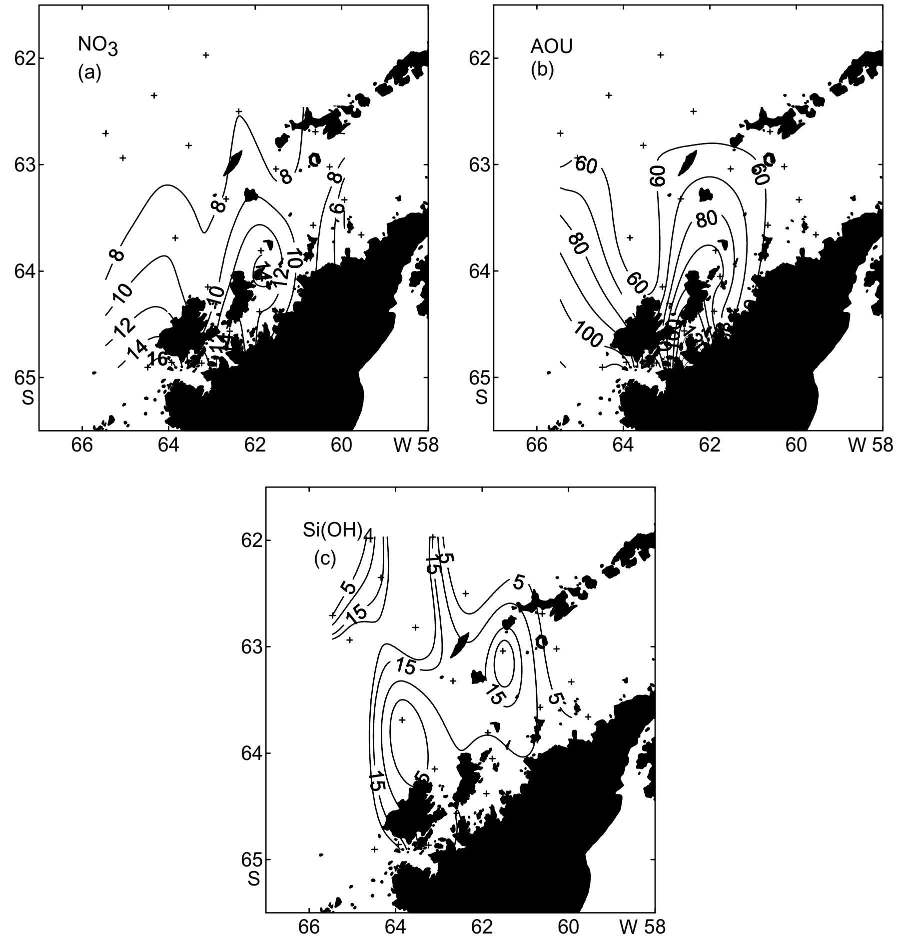

Fig. 7. Horizontal distributions for the UML of estimated nitrate (a); AOU (b); and silicic acid (c) consumptions in January 1996. Units in μmol kg^{-1}.

Codispoti et al. (1991) for high-latitude areas (>9) and Sambrotto et al. (1993) for the Gerlache Strait ($C:N=11$). In addition, if we take into account that a fraction of the estimated nitrate and TIC_{cor} deficits are transformed to dissolved organic matter, characterised by high C : N ratios (Sambrotto et al., 1993; Chen et al., 1996), we would expect higher $\Delta C:\Delta N$. Unfortunately, we do not have dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) measurements for all the FRUELA stns to evaluate the contribution of this pool. A simple estimate can be obtained with the available data in the following manner. We can consider the excess of DOC in the upper mixed layer compared to the DOC concentration at the temperature minimum of Antarctic Surface Water as the DOC due to phytogenic material (Doval et al., 2002). This DOC excess is between 0.5 and 1.5 times higher than the POC concentration in the upper mixed layer. Thus, with this ratio between DOC excess and POC and a DOC : DON ratio of 12 (Sambrotto et al., 1993; Chen et al., 1996), the estimated $\Delta C:\Delta N$ could increase between 8–34%.

In the same way, we also have to consider ammonium contribution. Ammonium measurements were only undertaken at the Bransfield and Gerlache Straits in December 1995 and January 1996 respectively. The average ammonium concentration to the nitrate deficit ratio was

0.06 ± 0.04, which increases the $\Delta C:\Delta N$ ratios by only 6%. One possible factor responsible of these low C : N ratios could be the air–sea exchange of CO_2. In our estimated TIC_{cor} deficits, we do not include any corrections due to the air–sea fluxes. Álvarez et al. (2002) found that the study area acts as a sink of CO_2 during the two cruises with the exception of the Bransfield Strait in December 1995. Consequently, TIC_{cor} deficits and $\Delta C:\Delta N$ ratios are probably underestimated. An estimate of the atmospheric input of CO_2 can be obtained based on CO_2 air–sea fluxes (Álvarez et al., 2002; see Table 1), upper mixed-layer depths (Table 1) and an integration time of 30 and 75 days since the pre-bloom conditions for FRUELA 95 and FRUELA 96 cruises, respectively. Applying this correction, $\Delta C:\Delta N$ ratios could increase between 10% for the Bellingshausen'95 domain to 95% in the case of the Gerlache'96 domain.

Our average $\Delta AOU:\Delta NO_3$ and $\Delta AOU:\Delta TIC_{cor}$ agree with the Redfield ratios (Table 4), though for the Bransfield'95 domain, $\Delta AOU:\Delta TIC_{cor}$ is significantly higher than 1.4 (Laws, 1991). This would probably be related with the high influx of oxygen from the atmosphere in this region (see Table 1, Álvarez et al., 2002). These authors found the highest ratio of oxygen flux regarding to CO_2 flux in this region.

Table 2
Intercept (*A*), slope (*B*), correlation coefficients (*r*), and number of samples (*n*) of POC vs Chl *a* and POC vs PON for the samples corresponding to the UML in the different domains. Chl *a* in mg m^{-3}, PON and POC in μmol kg^{-1}

Domain		POC vs Chl *a*	POC vs PON
Bellingshausen'95	$A\pm err_A$	4 ± 3	-3 ± 1
	$B\pm err_B$	6 ± 1	7.7 ± 0.5
	$r(n)$	0.66 (16)	0.97 (16)
Gerlache'95	$A\pm err_A$	-1 ± 5	2 ± 1
	$B\pm err_B$	5 ± 1	4.5 ± 0.3
	$r(n)$	0.83 (8)	0.98 (8)
Bransfield'95	$A\pm err_A$	3.8 ± 0.9	0.6 ± 0.4
	$B\pm err_B$	3.9 ± 0.4	5.0 ± 0.2
	$r(n)$	0.76 (43)	0.97 (43)
Bellingshausen'96	$A\pm err_A$	4.1 ± 0.4	1.3 ± 0.5
	$B\pm err_B$	4.9 ± 0.6	4.6 ± 0.3
	$r(n)$	0.89 (17)	0.95 (17)
Bransfield'96	$A\pm err_A$	1.0 ± 0.7	0.3 ± 0.3
	$B\pm err_B$	8.2 ± 0.7	5.4 ± 0.2
	$r(n)$	0.99 (5)	0.99 (5)

4. Discussion

The data presented provide additional evidence of the emerging view of the Southern Ocean as a "mosaic of subsystems" (Treguer and Jacques, 1992; Robins et al., 1995), supporting the importance of frontal regions as productive zones in the Southern Ocean (Bianchi et al., 1992; Turner and Owens, 1995; Smetacek et al., 1997).

During the FRUELA 95 and FRUELA 96 cruises, the highest biomass accumulation (average of 4 ± 2 and 7 ± 2 mg Chl *a* m^{-3} during FRUELA 95 and FRUELA 96 cruises, respectively) were registered in the sheltered Gerlache Strait, associated with relatively shallow UMLs and high water column stability (Table 1). However, an-

Table 3
Average values of estimated nutrient, AOU, and TIC_{cor} anomalies of the UML for the different domains[a]

Domain	ΔNO_3	ΔPO_4	$\Delta Si(OH)_4$	ΔAOU	ΔTIC_{cor}
Bellingshausen'95	8 ± 3	0.5 ± 0.2	5 ± 4	69 ± 11	52 ± 20
Gerlache'95	7 ± 2	0.5 ± 0.1	6 ± 5	65 ± 15	40 ± 8
Bransfield'95	5 ± 1	0.3 ± 0.1	3 ± 4	51 ± 10	23 ± 9
Bellingshausen'96	8 ± 1	0.5 ± 0.1	11 ± 8	55 ± 9	40 ± 5
Gerlache'96	14 ± 3	1.1 ± 0.2	12 ± 5	94 ± 22	70 ± 16
Bransfield'96	7 ± 2	0.4 ± 0.1	6 ± 9	54 ± 9	37 ± 9

[a] Note: Units in μmol kg^{-1}. Integrated nutrient, AOU, and TIC_{cor} anomalies for the UML can be obtained multiplying this value for Z_{UML} (Table 1).

Table 4
Average (Avg), standard deviation (SD) and correlation coefficients (*r*) of estimated anomalies ratios for the different domains[a]

		Bellings'95	Gerlache'95	Bransf'95	Bellings'96	Gerlache'96	Bransf'96
$\Delta NO_3:\Delta PO_4$	Avg±SD	15.1±1.6	13.0±1.6	15.7±2.4	16.2±0.9	12.4±1.4	15.7±1.1
	r	0.98	0.92	0.88	0.93	0.86	0.99
$\Delta TIC_{cor}:\Delta NO_3$	Avg±SD	6.4±0.9	5.7±0.3	5.04±1.1	5.2±0.6	5.2±0.8	5.42±0.06
	r	0.96	0.94	0.78	0.45	0.73	0.99
$\Delta AOU:\Delta NO_3$	Avg±SD	9±2	9±1	10±2	8±1	6.9±0.9	8±1
	r	0.92	0.68	0.71	0.00	0.82	0.66
$\Delta AOU:\Delta TIC_{cor}$	Avg±SD	1.4±0.4	1.6±0.3	2.2±0.6	1.4±0.1	1.3±0.1	1.5±0.3
	r	0.96	0.59	0.77	0.80	0.69	0.92
$\Delta Si(OH)_4:\Delta NO_3$	Avg±SD	0.8±0.8	1.9±0.6	0.7±0.6	1.6±1.3	0.87±1.23	0.85±0.25
P:N:C:O		1:15:97:139	1:13:74:116	1:16:79:165	1:16:84:121	1:12:64:86	1:16:85:130

[a] Note: Units in $\mu mol\,kg^{-1}$. Bellings: Bellingshausen Sea; Bransf: Bransfield Strait.

other striking Chl *a* maximum was observed in the SbyACC frontal region, with deep UML (~40 m), during the FRUELA 95 cruise. Chl *a* levels (~3 mg m^{-3}) were similar to those previous reported for frontal zones in the Southern Ocean and also extended to deep levels of the water column (Chl *a* of 0.5 mg m^{-3} at about 80 m). This suggests that phytoplankton cells were adapted to low-light regime, as has been observed in other open-ocean blooms in the Southern Ocean (Boyd et al., 1995; Smetacek et al., 1997; Figueiras et al., 1998). However, this high Chl *a* stock at the SbyACC frontal region completely disappeared during the FRUELA 96 cruise (40 days later). The demise of phytoplankton stock cannot be attributed to changes in hydrographic conditions; average Z_{UML} is very similar for the two cruises, and the stability of water column has increased due to seasonal heating (Table 1). On the other hand, nutrient levels are sufficiently high during the second cruise to sustain high biomass stock. Therefore, other factors such as light limitation, grazing pressure and micronutrient availability (Fe limitation) or a combination of these, may explain the demise of the phytoplankton (Anadón and Estrada, 2002).

In contrast, during the STERNA (26 October to 18 December 1992) and ANT X/6 (13 October to 11 November 1992) expeditions, open-ocean large phytoplankton blooms were maintained for about 40–50 days (Turner and Owens, 1995; Smetacek et al., 1997). From our data, we can not ascertain the duration of the phytoplankton bloom observed during the FRUELA 95 cruise. It is possible that during this cruise, we had sampled a late stage of diatom-dominated phytoplankton bloom, as high C:N and C:Chl *a* ratios suggest (Table 2). Consequently, the situation found during the FRUELA 96 cruise, dominated by nanoplankton, can be considered as an advance stage of the phytoplankton succession (Varela et al., 2002). There are no time series studies of phytoplankton development in these oceanic regions of the Southern Ocean, probably due to sampling difficulties. Seasonality has been documented in coastal habitats of the Southern Ocean (Clarke, 1988; Huntley et al., 1991; Karl et al., 1991; Moline and Prezelin, 1997) with an intensive spring bloom that starts in November and lasts till January. Also measurements of nitrate and ammonium uptake and ammonium regeneration rates with ^{15}N techniques during FRUELA 95 point to a final stage of this phytoplankton bloom (Bode et al., 2002).

The situation found during the intensive sampling of the Bransfield Strait in December 1995 also provides additional evidence of the important role of frontal regions, with deep-extending maxima of Chl *a* in the region of the Bransfield Front. As during the RACER cruises (Holm-Hansen and Mitchell, 1991), we found a maxima in the region of Gerlache-Bransfield confluence but not in the SE end of the Bransfield Strait, where the highest stratification was encountered (Fig. 3; Table 1). The bloom observed in this study (average Chl *a* of 2.0±0.9 mg m^{-3} with average Z_{UML} of 25±19 m) was not as massive as that reported for the December RACER cruise, where average Chl *a* was $8\pm2\,\mathrm{mg\,m^{-3}}$ and average Z_{UML}; $12\pm2\,\mathrm{m}$ (Holm-Hansen and Mitchell, 1991; Mitchell and Holm-Hansen, 1991).

Although no nutrient limitation was found, nutrient distributions were strongly controlled by the phytoplankton biomass. The imprint of biological consumption was more clearly discerned in nitrate distributions, mirrored in oxygen production, than in silicic acid distributions. Phosphate and $\mathrm{TIC_{cor}}$ anomaly distributions for the UML (see Álvarez et al., 2002) followed a similar pattern to nitrate distributions, as the high correlations indicate ($r^2 = 0.91$ and $r^2 = 0.83$ for phosphate and $\mathrm{TIC_{cor}}$, respectively for FRUELA 95 data set and $r^2 = 0.93$ and $r^2 = 0.91$ for phosphate and $\mathrm{TIC_{cor}}$, respectively for FRUELA 96 data set).

Overall, our estimated nutrient consumptions (Table 3) were of the same magnitude as nutrient depletions measured for other pelagic regions in the Southern Ocean. Jennings et al. (1984) estimated nutrient deficits of $6\,\mathrm{mmol\,N\,m^{-3}}$, $0.54\,\mathrm{mmol\,P\,m^{-3}}$ and $17\,\mathrm{mmol\,Si\,m^{-3}}$ for a station in the eastern Weddell Sea in January 1973. Goeyens et al. (1991) also found the highest nitrate depletion ($\sim 10\,\mathrm{mmol\,N\,m^{-3}}$) at the southern part of the Weddell–Scotia Confluence during November–December of 1988 over 1 to 1.5° latitude. Whitehouse et al. (1995) presented data for a section in the eastern Bellingshausen Sea ($\sim 85°$W) from the marginal ice zone to the Southern Polar Front during austral spring. They also encountered substantial nutrient depletion at the frontal region (average of 7.7 ± 0.2, 0.66 ± 0.03, $15\pm1\,\mathrm{mol\,m^{-3}}$ for nitrate, phosphate and silicic acid, respectively), associated with the highest biomass accumulation. Minas and Minas (1992) reported lower nutrient deficits (average of 2.5, 0.22 and $11.7\,\mathrm{mol\,m^{-3}}$ for nitrate, phosphate and silicic acid, respectively) for a section in the Antarctic Indian sector along 65°E from 40° to 62°S at the end of the austral summer.

In order to assess if the estimated nutrient consumption can account for the biomass accumulation observed, we applied a simple mathematical approach, in which biomass accumulation through time is given by

$$[\mathrm{Chl}\ a]_t = [\mathrm{Chl}\ a]_0 \mathrm{e}^{(\mu-l)t}$$

where $[\mathrm{Chl}\ a]_t$ is Chl *a* biomass at time *t*, $[\mathrm{Chl}\ a]_0$ is Chl *a* at the pre-bloom situation and μ and l are the specific growth and loss rate. The specific loss rate encompasses the losses due to grazing, sinking and respiration. Therefore, the time rate of change of nitrate due to phytoplanktonic consumption is given by:

$$\mathrm{d}[\mathrm{NO_3}]_t/\mathrm{d}t = -\mu(\mathrm{PON} : \mathrm{Chl}\,a)\,[\mathrm{Chl}\ a]_t$$

from the two equations, nutrient consumption can be calculated as:

$$\delta\mathrm{NO_3} = [\mathrm{NO_3}]_0 - [\mathrm{NO_3}]_t = (\mathrm{PON} : \mathrm{Chl}\ a)\,(\mu/(\mu - 1))([\mathrm{Chl}\ a]_t - [\mathrm{Chl}\ a]_0).$$

If we consider that the pre-bloom Chl *a* concentration was $0.1\,\mathrm{mg\,m^{-3}}$ following Mitchell and Holm-Hansen (1991), we can estimate nutrient consumption taking into account measured PON : Chl *a* ratios (Table 2) and specific growth and loss rates of phytoplankton biomass (Table 5; Varela

Table 5
Specific growth (μ) and loss (l) rates ($\mathrm{d^{-1}}$) of phytoplankton with the percentage of nutrient consumption due to the biomass accumulation compared to the estimated nutrient consumption $\delta\mathrm{NO_3}:\Delta\mathrm{NO_3}$ and considering the DON excess in the UML (($\delta\mathrm{NO_3}$ + DONexc) : $\Delta\mathrm{NO_3}$) for the different domains. n.d. not determined

Domain[a]	μ	L	$\delta\mathrm{NO_3}\ \Delta\mathrm{NO_3}$	$\delta\mathrm{NO_3}$ + DONexc $\Delta\mathrm{NO_3}$
Bellingshausen'95	n.d	n.d	45	70
Gerlache'95S	0.27	0.28	52	75
Gerlache'95N	0.77	1.14	n.d	n.d
Bransfield'95	0.47	0.23	68	79
Bellingshausen'96	0.36	0.025	55	n.d
Bransfield'96	0.28	0.048	90	n.d

[a] Gerlache'95S and Gerlache'95N correspond to the northern and southern part of Gerlache Strait respectively.

et al., 2002; Anadón et al., 2002). For the Bellingshausen'95 area, we have to assume an average μ of $0.47\,d^{-1}$ and l of $0.3\,d^{-1}$ according to Mitchell and Holm-Hansen (1991). For the northern part of the Gerlache Strait, we cannot apply this approach, as specific growth rates are lower than specific loss rates.

In Table 5, we show average percentage of δNO_3 in relation to estimated nitrate consumption (ΔNO_3) for all domains. For the FRUELA 96 data, we have added the previous estimated nutrient consumption (δNO_3) for the FRUELA 95 cruise. Calculated ΔNO_3 can account for the phytoplankton consumption estimated with this approach (δNO_3). If we consider the excess of dissolved organic nitrogen, calculated from the excess of DOC (Doval et al., 2002) and a C:N ratio of 12 for the dissolved organic matter, we can explain between 70% and 80% of ΔNO_3. The difference between δNO_3 and ΔNO_3 can be due to several factors. In this calculation, we have considered constant values for the growth and loss rates for the periods from the pre-bloom until FRUELA 95 and for the 40 days between the two cruises. We can argue that some changes may also occur through diffusion and advection. We therefore estimated the vertical diffusion of nitrate from Flux $=K_z\Delta NO_3 : \Delta z$; using an eddy diffusivity coefficient (K_z) of $0.5\,cm^2\,s^{-1}$ (Gordon et al., 1984), and estimating the gradient between the Z_{UML} and 100 m, where the maximum gradient in the nitrate profiles has been found. Below 100 m, the gradient decreases rapidly. The eddy diffusive flux of nitrate ranges from 0.003 to $0.01\,mmol\,m^{-2}\,d^{-1}$. Considering a time period of 30 days, from the pre-bloom conditions until FRUELA 95 cruise, this only amounts to about 2–9% of the biological utilisation. For Chl *a* vertical exchange ranges from 0.001 to $0.006\,mg\,m^{-2}\,d^{-1}$, only about 1–6% of Chl *a* in the UML. For the Bellingshausen area, the maximum Chl *a* change due to horizontal advection occurs in the SbyACC frontal region ($0.02\,mg\,m^{-3}\,d^{-1}$), considering a Chl *a* horizontal gradient of $0.003\,mg\,m^{-3}\,km^{-1}$ and an average velocitiy of $5.2\,km\,d^{-1}$ in this area (Gomis et al., 2002). This value represents a net input of about 15% of Chl *a* in the UML. For the Bransfield Strait, there is a net offshore transport of $0.01\,mg\,m^{-3}\,d^{-1}$, approximately 9% of Chl *a* in the UML. Vertical advection is negligible due to the low vertical velocities obtained (Gomis et al., 2002). Consequently, with the exception of positive advection input of Chl *a* in the Bellingshausen'95 domain, the other contributions are not significant.

Finally, it is possible that nutrient gain in the UML occurs due to remineralisation processes. In fact, taking into account that the estimated nutrient anomaly encompasses the nutrient consumption since the pre-bloom conditions, higher nutrient anomalies must be expected for the FRUELA 96 cruises. Average values of estimated nitrate and phosphate anomalies for the two cruises in the Bransfield and Bellingshausen area, are similar and contrast silicic acid. These results point to an increase of nitrate and phosphate with respect to silicic acid, due to remineralisation processes. A shorter residence time of biogenic silica in the photic layer compared to nitrogen and a higher dissolution of opaline silica below the main thermocline is expected (Broecker and Peng, 1982).

The biomass accumulation observed for the Bellingshausen and Bransfield domains can be explained by in situ growth, when we take into account the calculated nutrient consumption. Additional supply of cells by advection seems not to be important, with a maximum advection of 15% in the Bellingshausen'95 domain. These results contrast with the situation observed during the STERNA cruises (Boyd et al., 1995; Savidge et al., 1995).

5. Conclusions

The following conclusions can be drawn from this study:

(1) Although no nutrient limitation was found during FRUELA cruises, significant nutrient consumption was observed. In general, the highest nutrient anomalies were associated with the regions of the highest biomass accumulation. These regions corresponded to the sheltered waters of the Gerlache Strait and also to frontal zones; the Bransfield Front and

the SbyACC frontal region. In this sense, the situation found during the FRUELA cruises points to the importance of oceanic frontal regions in the annual production budget of the Southern Ocean.

(2) The phytoplankton demise in the SbyACC frontal region during the FRUELA 96 cruise can not be attributed to nutrient limitation. Nutrient levels were sufficiently high to sustain phytoplankton during the cruise.

(3) Calculated nutrient anomalies can account for the biomass accumulation, defining a time-scale of 30 days since pre-bloom conditions. These results support an in situ development of the phytoplankton bloom observed during the FRUELA cruises.

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