Nitrogen uptake by phytoplankton in the Atlantic sector of the Southern Ocean during late austral summer

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Abstract. As part of the Bonus-GoodHope (BGH) campaign, ¹⁵N-labelled nitrate, ammonium and urea uptake measurements were made along the BGH transect from Cape Town to ∼60°S in late austral summer, 2008. Our results are categorised according to distinct hydrographic regions defined by oceanic fronts and open ocean zones. High regenerated nitrate uptake rate in the oligotrophic Subtropical Zone (STZ) resulted in low f-ratios (f = 0.2) with nitrogen uptake being dominated by urea, which contributed up to 70% of total nitrogen uptake. Size fractionated chlorophyll data showed that the greatest contribution (>50%) of picophytoplankton (<2 µm) were found in the STZ, consistent with a community based on regenerated production. The Subantarctic Zone (SAZ) showed the greatest total integrated nitrogen uptake (10.3 mmol m⁻² d⁻¹), mainly due to enhanced nutrient supply within an anticyclonic eddy observed in this region. A decrease in the contribution of smaller size classes to the phytoplankton community was observed with increasing latitude, concurrent with a decrease in the contribution of regenerated production. Higher f-ratios observed in the SAZ (f = 0.49), Polar Frontal Zone (f = 0.41) and Antarctic Zone (f = 0.45) relative to the STZ (f = 0.24), indicate a higher contribution of NO₃⁻-uptake relative to total nitrogen and potentially higher export production. High ambient regenerated nutrient concentrations are indicative of active regeneration processes throughout the transect and ascribed to late summer season sampling. Higher depth integrated uptake rates also correspond with higher surface iron concentrations. No clear correlation was observed between carbon export estimates derived from new production and ²³⁴Th flux. In addition, export derived from ¹⁵N estimates were 2–20 times greater than those based on ²³⁴Th flux. Variability in the magnitude of export is likely due to intrinsically different methods, compounded by differences in integration time scales for the two proxies of carbon export.

1 Introduction

The Southern Ocean is considered one of the most important ocean sinks of atmospheric CO₂ (Caldeira and Duffy, 2000; Sigman and Boyle, 2000), making it important in understanding the global carbon cycle. Primary productivity in the Southern Ocean plays a key role in the biological uptake of atmospheric CO₂ (Metzl et al., 1999; Takahashi et al., 2002). Phytoplankton biomass typically shows low chlorophyll a (chl-a) (<0.5 mg m⁻³) in open ocean waters of the Southern Ocean (Tréguer and Jacques, 1992; Banse, 1996; Moore and Abbott, 2000), while localised elevated chl-a (>1 mg m⁻³; Moore and Abbott, 2000) are often associated with mesoscale upwelling at hydrographic fronts (Laubscher et al., 1993; Comiso et al., 1993; Moore and Abbott, 2002; Sokolov and Rintoul, 2007), the marginal ice zone (MIZ) (Smith and Nelson, 1986; Sedwick and DiTullio, 1997) and regions of shallow bathymetry around Subantarctic islands (Blain et al., 2001; Pollard et al., 2002; Korb and Whitehouse, 2004; Seeayve et al., 2007; Whitehouse et al., 2008). Under-utilization of available macronutrients by
phytoplankton production results in the prevalent high nutrient low chl-α (HNLC) condition (Chisholm and Morel, 1991) of the Southern Ocean. Despite a high inventory of available macronutrients, low chl-α concentrations are maintained by bottom-up controls of phytoplankton production through light, iron, and silicate limitation (Martin et al., 1990; Bathmann et al., 1997; Boyd et al., 2001, 2002, 2007; Moore and Abbott, 2002; Arrigo et al., 2008), as well as by top-down grazing control (Banse, 1996; Cullen, 1991; Price et al., 1994; Smetacek et al., 2004; Behrenfeld, 2010). These factors regulating primary production all modulate carbon export and thus play a key role in determining the strength of the Southern Ocean biological carbon pump.

Measurements of phytoplankton production throughout the euphotic layer using 15N stable isotopes (Dugdale and Goering, 1967) have often been used to infer carbon export into the ocean interior based on the f-ratio (Eppley and Peterson, 1979; Savoye et al., 2004). The f-ratio differentiates between the uptake of NO3− by phytoplankton which is “new” to the euphotic layer, introduced primarily by seasonal overturning or upwelling and “regenerated” nutrient uptake (NH4+, urea and dissolved organic nitrogen (DON)) which is recycled within the euphotic layer (Eppley and Peterson, 1979). As nitrogen flux into surface waters must ultimately be balanced by equivalent losses, the f-ratio is a measure of that fraction of primary production, which is potentially available for export to the deep ocean or to higher trophic levels; which is surplus to phytoplanktonic community maintenance requirements (Goeyens et al., 1998). NO3− uptake can thus provide an indirect estimate of downward carbon flux when Redfield ratio stoichiometry is inferred or measured (Eppley and Peterson, 1979). This approach to measuring carbon export relies on a number of underlying assumptions which include steady state conditions (uptake flux of NO3− approximately balanced by particulate nitrogen flux out of the surface), no storage of nitrogen in surface waters (Eppley and Peterson, 1979), and minimal euphotic layer nitritification (Bianchi et al., 1996; Yool et al., 2007). In addition, the use of stoichiometric ratios to convert nitrogen uptake (RN) to carbon equivalents may be compromised by non-Redfield behaviour in the cellular response to available light, iron and nutrients (Brzezenski et al., 2003; Arrigo, 2005; Moore et al., 2007). Although nitritification in surface waters is particularly important in oligotrophic ocean regions, this process does not appear to be significant in nitrate replete environments (Yool et al., 2007; Lucas et al., 2007; Clark et al., 2008). Despite its limitations, the f-ratio therefore remains a useful proxy for estimating potentially “exportable production” (Sambrotto and Mace, 2000) in nutrient rich polar oceans.

Carbon export estimates are also possible using 234Th/238U disequilibrium (e.g. Buesseler, 1992). Lower activities of particle-reactive 234Th relative to its conservative parent 238U in surface waters are associated with sinking particles. Particulate Organic Carbon (POC) export is calculated as the product of the ratio of POC/234Th on set-
2 Methods

2.1 Sampling and cruise track

The sampling cruise on board the R/V Marion Dufresne was conducted from 8 February–18 March 2008. The cruise transect (Fig. 1) started on the shelf outside Cape Town (South Africa) at the 200 m isobath and followed the GoodHope–A21 transect in a south-westerly direction to the 0° meridian, then continued south to 58° S. A total of 79 sampling stations were completed, 12 of which were targeted for ρN incubations using 15N tracer techniques (Slawyk and Collos, 1977; Dugdale and Wilkerson, 1986).

2.2 Hydrography

Water mass characteristics of the section sampled were determined from temperature, salinity measured with a CTD (SEABIRD 911plus) mounted on a SEABIRD rosette. On-board thermostalinograph (SEABIRD SBE21) data were collected in continuous mode at 5 m below sea level. Thermostalinograph data was validated with daily water sampling followed by on-board analysis. Mixed layer depths were determined using the temperature criteria (ΔT < 0.2°C in reference to the temperature at 10 m depth, de Boyer-Montégut et al., 2004).

2.3 Nutrient analyses

Ambient concentrations of NH4+ and urea-N were determined manually by the colorimetric method of Grasshoff et al. (1983), scaled to 5 ml samples. Ambient NO3− and Si(OH)4-Si concentrations were analyzed on a Bran and Lomb AAIII autoanalyser, as described in Tréguer and Lecoré (1975).

2.4 Chlorophyll-a

Total chl-a samples were collected in the upper 300 m at 6 depths from all CTD stations and 10 depths at all the ρN experiment stations. The samples were filtered onto 25 mm Whatman GF/F filters, extracted in 6 ml Acetone prior to fluorometric determination on a Turner Designs AU-10 fluorometer (Strickland and Parsons, 1972). Phaeopigments were determined by reading the fluorescence after acidification with 2–3 drops of 10% hydrochloric acid. Size-fractionated chl-a determinations were collected opportunistically from surface water sampling. Size-fractionated chl-a concentrations were determined by screening samples through a 200 µm mesh (<200 µm fraction), and a 20 µm mesh (<20 µm fraction), followed by filtration onto Whatman GF/F filters. The <2 µm fraction was obtained by filtering a sample through a 2 µm Nuclepore membrane filter and thereafter collecting the filtrate on a Whatman GF/F filter. Microphytoplankton (20–200 µm) were determined by subtracting the <20 µm fraction from the <200 µm fraction; nanophytoplankton (2–20 µm) by subtracting the <2 µm fraction from the <20 µm fraction, while picophytoplankton were represented by the <2 µm fraction. Chl-a and phaeopigment concentrations of each fraction were determined as above.

2.5 POC and PON

Particulate organic carbon (POC) and nitrogen (PON) were determined by filtering 11 samples onto pre-ashed 25 mm Whatman GF/F filters that were frozen at −20°C until analysis ashore. Samples were then oven-dried at 45°C, acid fumed with sulphuric acid to drive off inorganic carbon and pelleted into tin cups (8 x 5 mm) prior to analysis on a Thermo Scientific Flash EA1112 elemental CHN analyser.

2.6 Nitrogen uptake measurements

To determine depth integrated nitrogen uptake (∫ρN, samples were collected at 5 underwater irradiance levels (100%, 50%, 25%, 10% and 1%) measured using an underwater PAR (400–700 nm) sensor attached to the CTD rosette. Three bulk samples (21 each) from each light level were pre-screened through a 200 µm plankton mesh to exclude zooplankton grazers and transferred into borosilicate glass Schott bottles. Aliquots of 200 µl stock solutions of K15NO3 (1 µmol/100 µl), 15NH4Cl (0.1 µmol/100 µl) and CO2(15NH2)2 (0.1 µmol/100 µl) were added, one to each of the three bottles from all light depths for ρN incubations. The 15N enrichment was aimed at ∼10% for each nutrient, assuming an average ambient NO3− concentration of 10 µmol l−1, and 1 µmol l−1 for NH4+ and urea. The inoculum was kept constant throughout the cruise and resulted in NH4+ enrichments that were greater than 10% of ambient concentrations (10–30%). Incubation bottles were placed inside a Perspex tank covered with neutral density filters to recreate the appropriate light environment. Temperature was maintained at sea surface temperature (SST) by circulating surface water through the incubation tanks. Samples were incubated for 24 h and terminated by filtration onto ashed 47 mm Whatman GF/F filters, which were then dried at 45°C before later isotopic analyses.

2.7 Isotope analyses

Particulate matter collected on the Whatman GF/F filters were pelleted and placed 8 x 5 mm into tin capsules prior to isotopic analysis. Analyses were carried out on a Delta V Plus stable light isotope mass spectrometer interfaced to a Thermo Scientific Flash EA1112 Elemental Analyser. Natural abundance for nitrogen was 0.3663 atom % 15N, were used to calculate the isotopic enrichment of the nitrogen additions. Values were scaled upwards to reflect the proportion of the sub-sampled area relative to the total filtered area. Sulphanilamide and urea were used as calibration standards for carbon and nitrogen determinations. Specific uptake rates
3 Results

3.1 Hydrography

The BGH meridional cruise track crossed all the major hydrographic fronts and open ocean regions commonly recognised in the Southern Ocean (Orsi et al., 1995) (Fig. 1). The frontal positions during the cruise were determined using potential temperature criteria (Speich et al., 2011) (Fig. 2). The region north of the STF was defined as the Subtropical Zone (STZ) where SST exceeded 14°C and salinity exceeded 35 psu (Fig. 2). The Sub-Antarctic Zone (SAZ) was located across the STF (42.2°S) and the SAF (44.2°S), where SST fell in the range 9–14°C, and surface salinity between 34–35 psu. In this zone, an intense anticyclonic eddy (“anticyclone M”; Arhan et al., 2011) of Indian Ocean origin was observed (at 42.9°S to 44.5°S) over the Agulhas Ridge (Fig. 2). The Polar Front Zone (PFZ) extended from the SAF to the PF (Pollard et al., 2002) at 50.1°S, where SST decreased from 10–5°C and surface salinity was <34 psu (Fig. 2). The Antarctic Zone (AZ) was found south of the PF where temp was <3°C and salinity was ~34 psu. The following results are presented according to the four zones defined above (STZ, SAZ, PFZ and AZ).

3.2 Nutrients

Nutrient concentrations shown in Fig. 3a, b are from the upper 200 m of the BGH cruise track (LeMoigne et al., 2011). In the STZ, surface nutrient concentrations (Fig. 3a, b) showed typical oligotrophic conditions, with surface NO$_3^-$ concentrations <0.05 µmol l$^{-1}$ (Fig. 3a), while surface Si(OH)$_4$ concentrations were typically <2 µmol l$^{-1}$ (Fig. 3b). Surface NH$_4^+$ concentrations were depleted (<0.1 µmol l$^{-1}$), while urea concentrations were variable, ranging from 0.22–1.51 µmol l$^{-1}$ (Table 2). In the AZ, a gradual increase in surface NO$_3^-$ concentrations was observed ranging from 5–15 µmol l$^{-1}$, but reaching 20 µmol l$^{-1}$ below 100 m depth (Fig. 3a, Table 2). Si(OH)$_4$ concentrations were depleted (<2 µmol l$^{-1}$) throughout the surface 250 m (Fig. 3b). NH$_4^+$ concentrations were <0.25 µmol l$^{-1}$, but reached concentrations of up to 0.4 µmol l$^{-1}$ between 40–70 m depth (Table 2), while urea concentrations ranged from 1–1.5 µmol l$^{-1}$ (Table 2). In the PFZ, surface NO$_3^-$ concentrations reached >20 µmol l$^{-1}$ (Fig. 3a), while Si(OH)$_4$ concentrations remained <2 µmol l$^{-1}$ in the upper 100 m of the water column (Fig. 3b). From north to south, surface NH$_4^+$ concentrations (above 100 m) gradually increased from <0.25 to >1.0 µmol l$^{-1}$ (Table 1). Urea concentrations were higher than in the STZ and ranged from ~1 µmol l$^{-1}$ to a maximum of 3.27 µmol l$^{-1}$ (at ~60 m, station S3). Universally high nutrient concentrations were observed in the AZ. NO$_3^-$ concentrations exceeded 30 µmol l$^{-1}$ in the surface ~100 m and continued to increase to a maximum of ~40 µmol l$^{-1}$ with depth (Fig. 3a). Si(OH)$_4$ concentrations showed a steep north-south gradient from <2 µmol l$^{-1}$ north of the PF to >60 µmol l$^{-1}$ at the southern margin of the region (Fig. 3b). NH$_4^+$ and urea concentrations in the AZ reached 0.8 and 2 µmol l$^{-1}$ in the euphotic layer.
Fig. 3 (a, b) Profiles of nitrate and silicate in the upper 500 m along the Bonus Goodhope cruise track (taken from LeMoigne et al., 2011). It shows increasing surface nutrient concentrations with increasing latitude. Frontal positions are indicated by the white vertical dotted lines.

Fig. 3 (c, d) Profiles of chlorophyll-α and phaeopigments in the upper 200 m of the water column along the Bonus Goodhope cruise track (taken from Beker et al., 2011). Elevated pigment concentrations were observed equatorward of the Sub-Antarctic Front. Frontal positions are indicated by the white vertical dotted lines.

Fig. 3 (e, f) Profiles of particulate carbon and nitrogen in the upper 200 m of the water column along the Bonus Goodhope cruise track. Highest concentrations were observed equatorward of the Sub-Antarctic Front. Frontal positions are indicated by the white vertical dotted lines.

3.3 Chlorophyll-α

In the STZ, euphotic zone chlorophyll-α concentrations were highest, exceeding 0.4 μg l⁻¹ with a sub-surface chlorophyll-α maximum (>0.5 μg l⁻¹) at 30–40 m (Fig. 3c; see also Beker et al., 2011). A similar sub-surface maximum was observed for phaeopigments, although slightly deeper in the water column at 40–60 m (Fig. 3d). Size-fractionated chlorophyll-α showed that pico-pytoplankton (<2 μm) contributed 50.4% to total chlorophyll-α (Fig. 4b). In the SAZ, chlorophyll-α concentrations in the surface ~40 m exceeded 0.4 μg l⁻¹ (Fig. 3c), whereas a sub-surface maximum in phaeopigments (>0.3 μg l⁻¹) was observed at ~50 m (Fig. 3d). Size-fractionated chlorophyll-α indicated that nano-(2–20 μm) and pico-pytoplankton contributed 60.2% and 39.8% respectively to total chlorophyll-α concentrations, while no microplankton (20–200 μm) were measured (Fig. 4) in the SAZ. In the PFZ, chlorophyll-α concentrations of ~0.3 μg l⁻¹ were found in the upper 70 m (Fig. 3c). Phaeopigments typically exceeded 0.1 μg l⁻¹ in the upper 50 m of the water column, and remained <0.1 μg l⁻¹ below this depth (Fig. 3d). Size-fractionated chlorophyll-α in surface samples was dominated by nanophytoplankton (54.3%) throughout this region (Fig. 4), followed by picophytoplankton (30.6%) and microphytoplankton (15%). Chlorophyll-α concentrations in the AZ between the PF and the SAZ, as well as south of the SBdy, ranged from 0.2 to 0.3 μg l⁻¹, while a band of low chlorophyll-α (~0.2 μg l⁻¹) was evident between the SAZ and the SBdy (Fig. 3c). Phaeopigments appeared completely absent in this region (Fig. 3d). In the AZ, nanoplankton comprised 61.9% of the phytoplankton community, while micro and picoplankton comprised 18.9 and 19.2% respectively (Fig. 4).

3.4 POC and PON

Maximum concentrations of POC (14.1 μmol l⁻¹) and PON (1.9 μmol l⁻¹) were found in the STZ just north of the STF (Fig. 3e, f) and confined to the upper 25 m. Average PON concentrations over the euphotic layer of the STZ were 1.0 ± 0.6 μmol l⁻¹, with a mean euphotic zone C:N ratio of 7.16 ± 2.29. In the SAZ, POC and PON concentrations in the surface 40 m reached a maximum of 7.7 and 1.5 μmol l⁻¹ respectively (Fig. 3e, f, modified from Beker et al., 2011), with a mean euphotic zone C:N ratio of 6.0 ± 0.7. In the PFZ, POC and PON averaged 5.3 ± 0.5 μmol l⁻¹ and 0.7 ± 0.2 μmol l⁻¹ respectively in the upper 60 m of the water column (Fig. 3e, f), with both decreasing below this depth. The average C:N ratio in the euphotic zone was 8.2 ± 1.7. In the AZ, POC and PON were typically <4 μmol l⁻¹ and <0.5 μmol l⁻¹ respectively (Fig. 3e, f) in the euphotic zone, with a mean C:N ratio of 7.4 ± 2.7.
Table 2. List of data at each sampling station (including latitude positions) during the BGH cruise (MLD; m, sample depth; m, chl-α, µg l⁻¹; POC and PON, µmol l⁻¹; nutrients, µmol l⁻¹; ρN, nmol l⁻¹ d⁻¹). The five sample depths at each station represent, with increasing depth, the 100 %, 50 %, 25 %, 10 % and 1 % light depths. nd indicates no data.

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<td>0.76</td>
<td>27.81</td>
<td>0.61</td>
<td>1.68</td>
<td>47.5</td>
<td>20.0</td>
<td>29.3</td>
<td>0.49</td>
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<tr>
<td>(57.6°S)</td>
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</table>

3.5 Nitrogen uptake

In the STZ (n = 3), urea dominated \( f \rho N \) by \( \sim 80 \% \) (Table 3), reaching a maximum rate of 347 nmol l\(^{-1}\) d\(^{-1}\) at 40 m at station S1 (Table 2). Urea was on average 8 times greater than \( \rho NO_3^- \) or \( \rho NH_4^+ \) yielding a mean \( f \)-ratio of 0.24 ± 0.22 (Table 3). Specific uptake of urea (\( V_{urea} \)) was on average 10 times greater than that of nitrate (\( V_{NO_3^-} \)) or ammonium (\( V_{NH_4^+} \)) (Fig. 5). In the SAZ (n = 1) \( \rho NO_3^- \) and urea reached maximum rates at 5 m of 157.3 and 197.2 nmol l\(^{-1}\) d\(^{-1}\) respectively (Table 2). These values decreased to 54.7 and 46.4 nmol l\(^{-1}\) d\(^{-1}\) respectively at the 1% euphotic depth. \( f \rho N \) was 10.3 mmol m\(^{-2}\) d\(^{-1}\), with the highest contribution from \( f \rho NO_3^- \) (49.4 %) followed closely by \( f \rho urea \) (43 %) (Table 3). The depth-integrated \( f \)-ratio for this station was 0.47 (Table 3). Specific uptake rates of nitrate (\( V_{NO_3^-} \)) and urea (\( V_{urea} \)) over the euphotic zone were 0.12 ± 0.05 d\(^{-1}\) and 0.13 ± 0.08 d\(^{-1}\) (Fig. 5), while \( V_{NH_4^+} \) was lower (0.02 ± 0.02 d\(^{-1}\)). In the PFZ (n = 5), euphotic zone \( \rho NO_3^- \), urea and \( \rho NH_4^+ \) remained below 50 nmol l\(^{-1}\) d\(^{-1}\) (Table 2) and were typically lower than uptake rates in the STZ and SAZ. Station S3 exhibited the highest \( \rho N \) rates, compared to adjacent stations to the north or south. At station S3, \( \rho NO_3^- \) decreased from 124.0 nmol l\(^{-1}\) d\(^{-1}\) in the surface to 22.2 nmol l\(^{-1}\) d\(^{-1}\) at the base of the euphotic zone (Table 2). Conversely, \( \rho urea \) increased from 13.0 nmol l\(^{-1}\) d\(^{-1}\) in the surface to 108.5 nmol l\(^{-1}\) d\(^{-1}\) at depth. Average \( f \rho N \) for the PFZ was 5.26 ± 2.2 mmol m\(^{-2}\) d\(^{-1}\) (Table 2), with the majority being due to \( f \rho NO_3^- \) (1.94 ± 0.46 mmol m\(^{-2}\) d\(^{-1}\)) and \( f \rho urea \) (2.13 ± 1.78 mmol m\(^{-2}\) d\(^{-1}\)), while \( f \rho NH_4^+ \) averaged 1.16 ± 0.41 mmol m\(^{-2}\) d\(^{-1}\), resulting in a mean \( f \)-ratio of 0.41 ± 0.11 (Table 3). Average euphotic zone \( V_{NO_3^-} \), \( V_{NH_4^+} \) and \( V_{urea} \) were 0.07 ± 0.07, 0.03 ± 0.1 and 0.04 ± 0.03 d\(^{-1}\) respectively (Fig. 6). In the AZ (n = 3), \( \rho NO_3^- \), \( \rho NH_4^+ \) and urea also remained below 50 mmol l\(^{-1}\) d\(^{-1}\) (Table 1), with up to 50 % being derived from \( f \rho NO_3^- \) (3.43 ± 2.68 mmol m\(^{-2}\) d\(^{-1}\)) (Table 3). Mean \( f \)-ratio in the AZ was 0.45 ± 0.11 (Table 3). Specific nitrogen uptake rates in the AZ were similar to those observed in the PFZ (Fig. 5).

4 Discussion

In this section we discuss nitrogen uptake dynamics across four different hydrographic regions in the Atlantic sector of the Southern Ocean. We highlight regional differences in uptake rates, \( f \)-ratios and community size structure and investigate how these change in relation to MLD, temperature, nutrients and surface dissolved iron concentrations. We compare our data with other \(^{15}\)N estimates of production in the Southern Ocean, as well as with \(^{234}\)Th based estimates of carbon export measured during the BGH cruise.

4.1 Regional comparisons of nitrogen uptake

4.1.1 The Subtropical Zone

Relatively high \( f \rho N \) in the STZ (8.18 ± 6.8 mmol m\(^{-2}\) d\(^{-1}\)) was dominated by \( f \rho urea \) (~79 %), with \( V_{urea} \) being ten times higher than \( V_{NO_3^-} \) or \( V_{NH_4^+} \) (Fig. 5), indicating significant regenerated production, as reflected by low \( f \)-ratios (0.24 ± 0.22). It is however unlikely that all the urea uptake is through phytoplankton production, as urea is easily assimilated by heterotrophic bacteria (Kirchman,
Fig. 6. Comparison between $^{234}$Th carbon export (at 100 m) (grey bars) and “new production” estimates (black triangles) in units mmol C m$^{-2}$ d$^{-1}$ during BGH. $f$-ratio is indicated in brackets. New production calculated from $\int \rho$NO$_3$ and the C:N ratio. It shows the difference in magnitude of these proxies of carbon export. $^{234}$Th data from Planchnon et al. (2011). Latitudes for the different zones are STZ (34.2–42.2° S), SAZ (42.2–44.2° S), PFZ (42.2–50.1° S) and the AZ (50.1–57.5° S).

2000) which can contribute up to 25 % of nitrogen uptake (Fouilland et al., 2007). Low new production rates in this region are likely due to limiting surface NO$_3$ concentrations ($<$0.05 µmol l$^{-1}$). Phytoplankton community structure was consistent with a typically regenerated-based community (Tremblay et al., 2000) with picophytoplankton dominating by ~51% (Fig. 4). This is consistent with previous results of low $f$-ratios in the Indian ($f = 0.07 \pm 0.03$) (Thomalla et al., 2011) and Pacific basins (Sambrotto and Mace, 2000) (Table 2). These results imply that this region of the Southern Ocean is dominated by urea re-cycling within the microbial loop, with little carbon export, little atmospheric CO$_2$ “draw-down”, and conservation of nitrogen in surface waters (LeFevre et al., 1998; Smetacek et al., 2004).

### 4.1.2 The Subantarctic Zone

Station S2 in the SAZ exhibited only slightly higher total $f$ $\rho$N rates compared to those observed in the STZ, however this station showed a greater contribution of $\rho$NO$_3$ (49.4 %), which increased the $f$-ratio from 0.24 to 0.49 (Table 3). $V_{NO_3}$ (0.12 d$^{-1}$) at this station was double that observed in other regions (Fig. 5) along with the highest concentrations of chlorophyll a ($>0.5$ µg l$^{-1}$), POC ($>7$ µmol l$^{-1}$) and PON ($>1$ µmol l$^{-1}$) (Fig. 3c, e, f). Specific uptake rates are known to provide information on the potential for macronutrient, light or iron limited growth, with higher values being characteristic of faster growth rates in nutrient and light replete environments. These high $V_{NO_3}$ values thus suggest possible alleviation of iron stress (Lucas et al., 2007), along with sufficient light availability (MLD = 45.2 ± 17.1). It has been shown for oligotrophic regions that new production is enhanced within mesoscale eddy activity through the vertical injection of nutrients into the euphotic layer (Strass et al., 2002; Greenwood, 2007; Levy et al., 2009). This station was on the edge of a mesoscale hydrographic feature, “anticyclone M” (Arhan et al., 2011), observed just north of the SAF (Fig. 2). The proposed mechanism for the enhanced production and higher $f$-ratios at this station is enhanced vertical nutrient injection (including iron) at the edges of the anticyclone (Levy et al., 2009) along with an improved light environment associated with persistent shallow and stable mixed layers associated with the warm core eddy (Llido et al., 2005). Mesoscale eddies such as these provide important areas for local but significant POC export and biological CO$_2$ draw-down in an overall HNLC Southern Ocean. $\rho$N rates in the SAZ of the Atlantic measured in this study (10.3 mmol m$^{-2}$ d$^{-1}$) were slightly higher than those measured in the Australian sector in late spring/early summer (4.4 ± 0.3 mmol m$^{-2}$ d$^{-1}$) (Savoye et al., 2004) and were comparable to the Indian sector in late summer (12.7 ± 7.9 mmol m$^{-2}$ d$^{-1}$) observations (Thomalla et al., 2011) (Table 3).

### 4.1.3 The Polar Front Zone

Total $f$ $\rho$N rates in the PFZ were the lowest of the four regions (Table 3), with low $f$-ratios of 0.41 ± 0.11. $\rho$urea and $V_{urea}$ were substantially lower than in the STZ and SAZ to the north (Fig. 5). High concentrations of ammonium and urea (Table 2) were observed in the PFZ indicating very active regeneration processes. Dilution of the isotopic $^{15}$NH$_4$ and $^{15}$N-urea uptake due to high regenerated nutrients released by bacteria and zooplankton grazers can potentially lead to an underestimation of the uptake rates of these substrates and consequently an overestimation of the $f$-ratio. Early work in the Scotia Sea showed that ammonium uptake can be underestimated by a factor of 2–3 in summer (Glibert et al., 1982). Although no $NH_4^+$ regeneration experiments were conducted during the cruise, one can expect that underestimation of regenerated uptake would further reduce the $f$-ratio’s presented here. Although our cruise was in late austral summer, deep mixed layers in this region (MLD = 68.7 ± 18.9 m) relative to the 1% light depths (61 ± 11 m) make light a potentially limiting factor to primary production and to NO$_3^-$ uptake in particular considering its high light demand in comparison to $NH_4^+$ and urea uptake (Lucas et al., 2007; Cochlan, 2008). In addition, low surface Fe concentrations <$0.2$ nmol l$^{-1}$ (Chever et al., 2010) likely limit new production (Timmermans et al., 1998) promoting the dominance of small cells as size enforces a competitive advantage for nutrients at low concentrations (Lehnart et al., 2004). Smaller cells are however more susceptible to grazing by microzooplankton (Raven, 1986), which controls their biomass and at the same time contributes to potential regenerated production through $NH_4^+$ excretion (Glibert and Garside, 1992). Size-fractionated chlorophyll concentrations showed the PFZ to be dominated by nanophytoplankton (54 %, Fig. 4).

Several authors have found an increase in diatom concentration to be associated with the PF and attribute this
to an increase in Si(OH)$_4$ (Laubscher et al., 1993; Bathmann et al., 1997; Smetacek et al., 1997; Tremblay et al., 2002). Although it is possible for diatoms to fall within the nanophytoplankton size range, substantial increases in Si(OH)$_4$ were only found south of the SACCFF (Fig. 3b). Thus, although the percentage of microphytoplankton increased from 0% in the SAZ to 15% in the PFZ, the continued dominance by nanophytoplankton (54%) was likely due to Si(OH)$_4$ limitation of diatom growth and low surface Fe concentrations (<0.2 mmol l$^{-1}$, Chever et al., 2010) favouring smaller cells. Similarly, low Si(OH)$_4$ concentrations have been shown to play an important role in regulating nitrate uptake (Dugdale and Wilkerson, 1998; Sambrotto and Mace, 2000) such that the low Si(OH)$_4$ concentrations in this region may have contributed to the low NO$_3^-$ uptake rates (1.97 mmol m$^{-2}$ d$^{-1}$) and $f$-ratios found here. Our $f\rho$N rates in the Atlantic PFZ (5.26 mmol m$^{-2}$ d$^{-1}$) were similar to those in the Australian sector (5.6 mmol m$^{-2}$ d$^{-1}$) and the HNLC Crozet sector (6 mmol m$^{-2}$ d$^{-1}$), but lower than the bloom region associated with naturally Fe fertilized Crozet (30.1 mmol m$^{-2}$ d$^{-1}$) and Kerguelen (11.9 mmol m$^{-2}$ d$^{-1}$) Islands (Table 3). High concentrations of regenerated nutrients, low $f$-ratios and nanophytoplankton dominated communities implies an inefficient biological pump for this region which appears to be controlled by nutrient (Fe and Si(OH)$_4$) and light co-limitation and microzooplankton grazing.

### 4.1.4 The Antarctic Zone

A slight increase in $f\rho$N was observed in the AZ (7.5 mmol m$^{-2}$ d$^{-1}$) relative to the PFZ (5.3 mmol m$^{-2}$ d$^{-1}$). The contribution of $f\rho$NO$_3^-$ to total $f\rho$N increased with a simultaneous increase in $f$-ratios to 0.45 indicating a slightly higher potential for carbon export. As with the SAZ, high ambient regenerated nutrient concentrations (Table 2) imply active regeneration processes occurring in the surface, however a decrease regenerated uptake rates, particularly urea uptake (Fig. 5) were observed relative to regions further north. An underestimation of the regenerated production in this region, could thus lead to an overestimate of the $f$-ratio. Although Si(OH)$_4$ concentrations increase south of the SACCFF (Fig. 3b), lowest chlorophyll concentrations are found in the region between the SACCF and the SBdy and it is only south of the SBdy that chlorophyll concentrations increase (Fig. 3c). Although the mixed layer tends to deepen (MLD = 93.9 ± 14.7 m) in the AZ, so too does the 0.1% light depth (96 ± 12 m), making inadequate light the unlikely primary contributor to limited production. More likely, low surface Fe concentrations (Chever et al., 2010) characteristic of the late summer season are limiting phytoplankton growth despite sufficient irradiance (see also Boyd et al., 2001; Lucas et al., 2007). $f\rho$N from this study (7.5 mmol m$^{-2}$ d$^{-1}$) was in a similar range to the $f\rho$N (9.6 mmol m$^{-2}$ d$^{-1}$) of the permanently open AZ in the Australian sector (Savoye et al., 2004). As expected however, these open ocean $f\rho$N rates are up to 60% lower than those observed during bloom.

### Table 3. Comparison of depth integrated values of $^{15}$N uptake (mmol m$^{-2}$ d$^{-1}$) by phytoplankton in various regions of the Southern Ocean.

<table>
<thead>
<tr>
<th>Region/Description</th>
<th>$f\rho$NO$_3$</th>
<th>$f\rho$NH$_4$</th>
<th>$f\rho$Urea</th>
<th>$\Sigma f\rho$N</th>
<th>$f$-ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic Sector (Summer 2008, BGH)</td>
<td>1.01 (0.3)</td>
<td>0.69 (0.3)</td>
<td>6.47 (6.7)</td>
<td>8.18 (6.8)</td>
<td>0.24 (0.22)</td>
</tr>
<tr>
<td>STZ (34–41° S)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAZ (42–44° S)</td>
<td>5.11</td>
<td>0.92</td>
<td>4.31</td>
<td>10.34</td>
<td>0.49</td>
</tr>
<tr>
<td>PFZ (45–50° S)</td>
<td>1.97 (0.5)</td>
<td>1.16 (0.4)</td>
<td>2.13 (1.8)</td>
<td>5.26 (2.2)</td>
<td>0.41 (0.11)</td>
</tr>
<tr>
<td>AZ (51–57° S)</td>
<td>3.39 (1.9)</td>
<td>1.27 (0.6)</td>
<td>2.86 (1.6)</td>
<td>7.51 (3.5)</td>
<td>0.45 (0.11)</td>
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<tr>
<td>Australian Sector (Spring 2001, CLIVAR-SR3)</td>
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<tr>
<td>SAZ/STF (49–51.0° S)</td>
<td></td>
<td></td>
<td></td>
<td>4.4 (0.3)</td>
<td>0.53 (0.26)</td>
</tr>
<tr>
<td>PFZ (54–57° S)</td>
<td></td>
<td></td>
<td></td>
<td>5.6 (0.1)</td>
<td>0.56 (0.02)</td>
</tr>
<tr>
<td>AZ (61–65° S)</td>
<td></td>
<td></td>
<td></td>
<td>9.6 (2.2)</td>
<td>0.61 (0.08)</td>
</tr>
<tr>
<td>Bellinghausen Sea</td>
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<tr>
<td>SIZ (56–64° S)</td>
<td>1.8 (1.2)</td>
<td>10.9 (3.9)</td>
<td>9.9 (0.4)</td>
<td>18.0 (11.9)</td>
<td>0.1 (0.01)</td>
</tr>
<tr>
<td>Indian Sector (CROZEX, Summer 2004)</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Crozet-M3 bloom</td>
<td>20.3 (5.7)</td>
<td>3.6 (1.3)</td>
<td>6.1 (2.0)</td>
<td>30.1 (7.5)</td>
<td>0.67 (0.08)</td>
</tr>
<tr>
<td>Crozet-South of Plateau (HNLC)</td>
<td>1.8 (0.8)</td>
<td>3.2 (0.5)</td>
<td>1.1 (0.2)</td>
<td>6.0 (1.5)</td>
<td>0.28 (0.07)</td>
</tr>
<tr>
<td>Indian Sector (Summer 1994, ANTARES3)</td>
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<tr>
<td>Kerguelen Plateau (PFZ, Stn A18; 49° S)</td>
<td>5.7</td>
<td>3.5</td>
<td>2.8</td>
<td>11.9</td>
<td>0.48</td>
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<td>Kerguelen Plateau (PFZ, Stn A16; 52° S)</td>
<td>7.7</td>
<td>2</td>
<td>1</td>
<td>10.7</td>
<td>0.72</td>
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<tr>
<td>Indian Sector (late Summer 1999, MIOS-4)</td>
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<tr>
<td>STZ (31–40° S)</td>
<td>3.76 (4.2)</td>
<td>19.83 (15.0)</td>
<td>22.30 (17.8)</td>
<td>46.07 (33.5)</td>
<td>0.07 (0.03)</td>
</tr>
<tr>
<td>SAZ (41–46° S)</td>
<td>0.94 (0.2)</td>
<td>5.26 (2.3)</td>
<td>6.48 (5.4)</td>
<td>12.67 (7.9)</td>
<td>0.09 (0.04)</td>
</tr>
<tr>
<td>Pacific Sector (Summer 1997, US-JGOFS)</td>
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</tr>
<tr>
<td>PFZ (57–61° S)</td>
<td>2–5 (2.3)</td>
<td>0.05–0.48</td>
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</table>
conditions in the Seasonal Ice Zone (SIZ) of the Bellingshausen Sea (18.0 ± 11.9 mmol m⁻² d⁻¹) (Table 3). Lower open ocean $\rho$N rates compared to the SIZ can be ascribed to the lack of dissolved iron inputs from melting ice (Sedwick and DiTullio, 1997; Gao et al., 2003; Grotti et al., 2005) and a less favourable light environment through deep mixed layer depths (93.9 ± 14.7 m) (Smith and Nelson, 1986). Although there is a slight increase in production and $f$-ratios in the AZ, relative to the PFZ, the ice free regions of this sector appear to have a relatively low potential for carbon export particularly in the late summer season due predominantly to Fe limitation.

### 4.2 $^{15}$N estimates and $^{234}$Th export flux

Carbon export derived from $^{234}$Th deficits at 100 m revealed a north-south gradient, with the highest export fluxes (up to 6 mmol C m⁻² d⁻¹) found south of the APF (Fig. 6, Planchnon et al., 2011). Although the latitudinal trend in $f$-ratio estimates of carbon export were not as clear, with high export being associated with the eddy in the SAZ, there was a similar tendency for carbon export to increase with latitude (Fig. 6). New production estimates of carbon export were however 2–20 times greater in magnitude (Fig. 6) than $^{234}$Th derived estimates. Reasons for this are numerous. Firstly, the two methods used to estimate carbon export are not intended to measure the same process. Although the rates are expected to be comparable in a steady state system or when averaged over large enough time and space scales, there is otherwise no a priori reason why the rates should be identical, bearing in mind $f$-ratio estimates of new production is potentially overestimated as the $f$-ratio is only estimated from $\rho$NO$_3$. Stable isotope incubations measure NO$_3$ uptake at a discrete site over 12–24 h in the euphotic layer (typically <60 m) and may therefore not be representative of mesoscale averages. $^{234}$Th deficit derived estimates of carbon export (at 100 m) on the other hand encompass large spatial scales of 10 s to 100 s of kilometres (Buesseler et al., 1992) and a time period of ~31 days. Hence, in this instance $^{234}$Th derived carbon fluxes more than likely represents a considerable averaging of episodically lower fluxes when compared to the short-term $^{15}$N incubations. Furthermore, $^{234}$Th carbon flux estimates are derived by considering the POC/$^{234}$Th ratio of particles >50 µm and may well ignore a significant export flux within the <50 µm fraction. During BGH however, the POC/$^{234}$Th ratios of particles >50 µm and <50 µm were not very different. New production estimates, on the other hand do not discriminate on a size basis and represents the potential export of both dissolved and particulate material. This is consistent with other observations in both the Indian (Mengesha et al., 1998) and Pacific sector (Savoye et al., 2004) of the Southern Ocean and highlights the important role of this ocean in the global carbon cycle.

### 5 Conclusions

This paper presents $^{15}$N-labelled nitrogen uptake measurements in the Atlantic Southern Ocean in late austral summer, 2008. $\rho$N in the oligotrophic STZ was dominated by $\rho$urea, resulting in low $f$-ratios ($f = 0.24$). Size fractionated chl-a data is dominated by picophytoplankton (>50 %) and also indicative of a community based on regenerated phytoplankton production. It is unlikely that the measured NH$_3$ and urea uptake rates reflect only regenerated production in the STZ, given that the uptake estimates based on $^{15}$N uptake does not account for heterotrophic bacterial activity. This probably results in an overestimation of urea uptake and underestimation of the $f$-ratio in the STZ. However, given the low concentrations of NO$_3$ in the surface waters of the STZ (<0.05 µmol l⁻¹) and the dominance of urea recycling within the microbial loop, with little carbon export. The greatest $f$-$\rho$N was observed in the SAZ and ascribed to enhanced nutrient supply and favourable light conditions associated with an anticyclonic eddy. Higher $f$-ratios were observed in the SAZ ($f = 0.49$), Polar Frontal Zone (PFZ, $f = 0.41$) and Antarctic zone (AZ, $f = 0.45$) relative to the STZ ($f = 0.24$) and indicate a higher contribution of $\rho$NO$_3$ relative to total $\rho$N and higher export potential in regions further south. New production estimates of carbon export (calculated from $\rho$NO$_3$ and the C:N ratio) were lowest in the STZ (7.3 ± 0.43 mmol C m⁻² d⁻¹), compared to 30.4 mmol C m⁻² d⁻¹ in the SAZ, 16.3 ± 1.03 mmol C m⁻² d⁻¹ in the PFZ and 28.2 ± 25.8 mmol C m⁻² d⁻¹ in the AZ. These carbon export estimates are comparable to observations carried out in the other sectors of the Southern Ocean (Waldron et al., 1995; Sambrotto and Mace, 2000; Savoye et al., 2004; Lucas et al., 2007). Increasing trends in ambient water column nutrient and surface iron concentrations corresponded with higher $f$-$\rho$NO$_3$ rates. Higher $f$-ratios south of the SAF reflects this, however, we suspect this to be an overestimation of the $f$-ratio given the elevated regenerated nutrient concentrations which indicate active regeneration processes assuming regeneration of nitrate in the euphotic layer. The relatively low total $\rho$N rates are ascribed to late summer season sampling when nutrients are depleted prior to the winter resupply. Comparison of our $f$-ratio based estimates of carbon export with those from $^{234}$Th data collected during the cruise revealed a similar tendency for carbon export to increase with latitude but no clear correlation was observed. In addition, new production estimates were 2–20 times greater in magnitude and likely the result of the different integration time scales for the two different methods.

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