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A geographical and seasonal comparison of nitrogen uptake by phytoplankton in the Southern Ocean

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Abstract

Primary production in the Southern Ocean has been shown to be regulated by light and nutrients (such as silicate and iron) availability. However, the impact of these factors vary seasonally and differ from region to region. The seasonal cycle of primary production in this region is not fully resolved over an annual scale due to the lack of winter in situ measurements. In this study, nitrate and ammonium uptake rates were measured using ^{15}N tracers during a winter cruise in July 2012 and a summer cruise in February/March 2013. In winter, nitrogen uptake rates were measured at 55 % and 1 % of the surface photosynthetically active radiation (sPAR). The summer uptake rates were measured at 4 light depths corresponding to 55, 30, 10 and 3 % sPAR. The integrated nitrate uptake rates during the winter cruise ranged from 0.16–5.20 (average 1.14) mmol N m^{-2} d^{-1} while the ammonium uptake rates ranged from 0.6–32.8 (average 6.72) mmol N m^{-2} d^{-1}. During the summer cruise, the mean integrated nitrate uptake rate was 0.34 mmol N m^{-2} d^{-1} with a range between 0.16–0.65 mmol N m^{-2} d^{-1}. The integrated ammonium uptake rate averaged 5.61 mmol N m^{-2} d^{-1} and ranged from 1.44–11.28 mmol N m^{-2} d^{-1}.

The factors controlling primary production in winter and summer were investigated. During the winter cruise, it was found the different nitrogen uptake regimes were not separated by fronts. Light (in terms of day length) and ammonium concentration had the most influence on the nitrogen uptake regime. In the summer, increases in the mixed layer depth (MLD) resulted in increased nitrogen uptake rates. This suggests that the increases in the MLD could be alleviating nutrient limitations experienced by the phytoplankton at the end of summer.

1 Introduction

In the Southern Ocean, low temperature, low light, strong vertical mixing and iron limitation restrict the uptake of nitrogen and ultimately phytoplankton growth. This results

OSD
11, 1829–1869, 2014

in high nutrients, low chlorophyll (HNLC) conditions despite which the Southern Ocean plays an important role in the global marine carbon cycle. In this region, a combination of the solubility pump and the biological pump regulates the carbon cycle. The solubility pump encompasses the physical processes, such as mixing of surface water masses to the deeper layer, which remove carbon dioxide from the surface. The biological pump is driven by the sinking and subsequent sequestration of organic matter produced by phytoplankton. This combination accounts for about 4 % of global carbon fluxes (Takahashi et al., 2009) and 300 Tg C y^{-1} of export production (Henson et al., 2011; Gruber et al., 2009).

The efficiency of the biological pump in the Southern Ocean is still debated. There is, however, a paucity of observational data in the Southern Ocean, especially for the winter season as most cruises in the Southern Ocean have been confined to spring and summer. As a result, the influences of seasonality on phytoplankton dynamics, nitrogen uptake and consequently the efficiency of the biological pump in the Southern Ocean are still not completely resolved over an annual cycle. Researchers are turning to remote sensing and modelling in order to address global studies (Henson et al., 2011; Vichi et al., 2007) given the logistical constraints of ship-based measurements. Models alone are unable to resolve the various scales such as seasonal variations for the Southern Ocean (Swart et al., 2012) while remote sensing data needs to be calibrated against observational data. These two approaches have their limitations. In the Southern Ocean, satellite observations for the winter season can be limited by the sun angle as well as cloud cover (Vernet et al., 2012). There is little data to compare with results from biogeochemical models which derive primary production from environmental and physical conditions sulch as light availability and nutrient concentrations (Vichi et al., 2007; Bissett et al., 1999). However, the data used to initialise the models is often sparse (Bissett et al., 1999). Biogeochemical models face a number of challenges due to the fact that they are simplified for practical purposes and cannot resolve all the complexity of the marine ecosystem (Doney, 1999; Holt et al., 2014).

OSD
11, 1829–1869, 2014
Seasonal comparison of N uptake in the Southern Ocean
R. Philibert et al.

Furthermore, the influence of the various environmental controls on phytoplankton productivity varies seasonally (Boyd, 2002; Sambrotto and Mace, 2000). However, the Southern Ocean is a complex region with diverse ecological provinces and the effects of seasonality vary from region to region (Boyd, 2002; Boyd et al., 2010; Thomalla et al., 2011a). Understanding these seasonal variations requires in situ data, specially for the winter season.

In this paper, primary production which was estimated using ^{15}N are presented. Nitrate (NO_3^-) and ammonium, (NH_4^+) uptake rates were measured in the Southern Ocean during the austral winter of 2012 and in the late summer of 2013 using ^{15}N tracers. While summer (or early autumn) rates are common, this dataset is a rare instance of primary production rates for winter (Cota et al., 1992). Consequently estimates of nitrogen uptake are presented with the aim of investigating seasonal patterns as well as the significance of primary production in winter. The nitrogen uptake rates from this study are compared to rates measured in winter and other seasons to highlight the fact that nitrogen uptake in winter, while low, is still significant.

Finally, the biogeochemical factors controlling nutrient uptake by phytoplankton are explored. Distinct frontal features, which separate three surface water mass regimes, have been observed in the Antarctic circumpolar current (ACC) (Orsi et al., 1995). These frontal features (from North to South, the subtropical, the subantarctic and the polar fronts) affect the distribution of phytoplankton as well as as other "biogeographical" patterns (Pollard et al., 2002; Sambrotto and Mace, 2000). Furthermore, numerous studies compare nitrogen uptake based on their location with respect to the fronts (Sambrotto and Mace, 2000; Thomalla et al., 2011b; Joubert et al., 2011; Westwood et al., 2011; Cavagna et al., 2011). Given that phytoplankton respond to the biogeochemical setting and that the latter is controlled by the frontal positions, the fronts should play a role in controlling nitrogen uptake by phytoplankton. In this study, the hypothesis that changes in the winter primary production regime are due by the ACC fronts was tested. Using multivariate analyses, the potential factors for the variability in nitrogen uptake rates are explored to determine which ones (nutrients, light, temperature, mixed layer depth) play a more important role in regulating primary productivity. The factors controlling nitrogen uptake during the summer and winter seasons are discussed. This provides for a better mechanistic understanding of factors controlling nitrogen uptake by phytoplankton and can contribute to the development of biogeochemical models.

2 Methods

The present study consists of two cruises which are part of the Southern Ocean Seasonal Cycle Experiment (SOSCEX). The first cruise, referred to as the winter cruise, was undertaken aboard the RV SA Agulhas II from the 10 to 29 July 2012 and consisted of two legs. Leg 1 extended from Cape Town to the ice margin along the Good-Hope Line. Leg 2 stretched from the ice margin to Marion Island (Fig. 1). The summer cruise was conducted on board the RV SA Agulhas from the 15 February 2013 to 11 March 2013. Primary productivity was estimated at 2 stations along the Goodhope line and 2 process stations (A and B) within the Subantarctic zone (SAZ). The sampling locations for the summer cruise are shown in red on Fig. 1. Process Station A was initialised by deploying a float on 25 February 2013 at 42°39′ S 8°41′ E. However, the float was deployed incorrectly and a new float had to be deployed two days later when this station was next occupied. Process Station B did not have a float but was sampled continuously by a glider.

Temperature and salinity were measured by a rosette-mounted Sea-Bird Conductivity Temperature Depth (CTD) sensor. Chlorophyll *a* and oxygen measurements were obtained from calibrated Wetlab sensors attached to the same rosette. During the winter cruise, the CTD was cast three times a day (06:00, 12:00 and 21:00 LT) along the GoodHope Line whereas on the track between the ice-shelf and Marion Island, it was cast at pre-determined locations. Temperature profiles were also obtained from Expendable Bathythermographs (XBT) and Underway CTD (uCTD) deployments at 2 h intervals.

OSD
11, 1829–1869, 2014

The study region was divided into 4 zones based on the temperature criteria of Orsi et al. (1995): the Subtropical zone (north of the Subtropical front), the Subantarctic zone (north of the Subantarctic front), the Polar frontal zone (north of Polar front) and the Antarctic zone (south of the Polar front). The subantarctic zone (SAZ) was the target of the summer cruise while most of the winter stations were found in the Polar frontal zone (PFZ) and the Antarctic zone (AZ).

Nutrient concentrations were determined on board: NO_3^- and $Si(OH)_4$ using a Lachat Quick-Chem Flow injection autonalyser; NO_2^- and PO_4^- manually according to methods described by Grasshoff et al. (1983) and NH_4^+ using the fluorometric method described by Holmes et al. (1999) with improvements by Taylor et al. (2007). For the summer cruise, samples for NH_4^+ were frozen and analysed at a later stage.

NO_3^- and NH_4^+ uptake rates were estimated using ^{15}N tracers (Dugdale and Goering, 1967). Water samples were obtained at the early morning CTD stations. During the winter cruise, samples at the CTD stations were taken at the depth of the fluorescence maximum and at the 1 % light depth. Alternatively, on days where the ship did not stop for an early morning CTD cast due to bad weather or sampling plans, samples were taken from the underway water system. Underway samples were collected from 5 m using a mono-pump, which does not damage the phytoplankton cells. For the summer cruise, samples were collected from 4 depths representing 55, 30, 10 and 3 % of surface irradiance. Those light depths were determined during a cast on the afternoon prior to sample collection.

2 L water samples from each depth were amended with $Na^{15}NO_3$ (1 µmol L^{-1}) and $^{15}NH_4Cl$ (0.1 µmol L^{-1} in winter and 0.05 µmol L^{-1}). These values were based on expected ambient nutrient concentrations and kept constant throughout the cruise. The resulting enrichments were between 5 and 160 % for NH_4^+ and 3 and 52 % for NO_3^-. On the winter cruise, the samples were incubated for 24 h on deck under simulated in situ light depths of 1 % and 55 % sPAR. For underway stations, samples were only incubated at the 55 % light depth. On the summer cruise, the samples were incubated for 12 h under the appropriate simulated in situ light depths. During both cruises, the

OSD
11, 1829–1869, 2014
Seasonal comparison of N uptake in the Southern Ocean
R. Philibert et al.

temperature was kept at sea-surface temperature by using a continuous flow of seawater.

Specific and absolute uptake rates for NO_3^- and NH_4^+ were calculated according to the equations described by Gandhi et al. (2012). For each of the CTD stations, the daily nitrogen uptake rate was integrated over the mixed layer. The mixed layer depth (MLD) was identified as the depth where the temperature differed from the surface temperature by more that 0.2°C.

2.1 Statistical analysis

A multivariate statistics approach was employed on this dataset in order to investigate the biogeochemical controls over nitrogen uptake and test the hypothesis that the nitrogen uptake regime in winter was controlled by the fronts in Southern Ocean.

The statistical approach and the interpretation of the results are based largely on material from Borcard et al. (2011). The analysis was done in R using the vegan package. The hypothesis tested here was whether clusters which were derived from the nitrogen uptake rates would be separated by the subtropical (STF), subantarctic (SAF) and polar (PF) fronts. First, a cluster analysis was performed using the physical and biogeochemical variables for each station (temperature, chlorophyll, nutrients) to confirm whether these variables were constrained by the fronts. This cluster analyis was compared with a cluster analysis of the nitrogen uptake rates (response variables). Finally, a redundancy analysis was performed. A redundancy analysis combines a principal components analysis, which identifies the major sources of variations in a dataset, to multiple regressions. The redundancy analysis was done twice for the winter dataset: the first using the CTD stations only and the second using all the stations. Using the CTD stations (where nitrogen uptake was estimated at 2 light depths and for which the mixed layer depths were known) allowed for a quantification of the role of the MLD. When including the underway stations, only the 55 % light depth was used and the MLD was not included as a parameter as it was not available for these stations.

OSD
11, 1829–1869, 2014

For the summer cruise, an RDA on the two process stations was not possible due to the limited number of complete observations. Instead, the correlations between the uptake rates and environmental variables at the two process stations were investigated. The two stations at the PFZ were likely to have different environmental controls (Thomalla et al., 2011a) and were therefore not included in this analysis. These results were also limited by the number of observations and are presented here as a qualitative investigation into the factors controlling nitrogen uptake rates.

3 Results

3.1 Hydrographic data

The first leg of the winter cruise followed the GoodHope line and crossed the STF, SAF and PF. The hydrographic profiles for the winter cruise are not shown here but the frontal positions are indicated on Fig. 1. While the temperatures and salinity decreased with latitude, the transition at the fronts was not sharp. During leg 2, sampling was carried out from the ice edge to Marion Island in a straight line and then around the island in an anti-clockwise direction. There was a sharp temperature transition between station 15N-11 and 15N-13, which indicated the shift between the AZ and PFZ.

For the summer cruise, samples were taken at two process stations within the SAZ as well as two stations within the PFZ. Temperatures through the euphotic zone at Process Station A (Fig. 2) were between 10 and 12 °C. A mixing event occurred between the 3 and 7 March. The mixed layer depth decreased from its shallowest at 37 m to a maximum of 76 m. This brought colder, deeper water to the surface and reduced the average temperature. This was accompanied by a decrease in salinity. Biological activity decreased as shown by a decrease in mean chlorophyll concentration within the euphotic zone (0.70 mg m^{-3} at CTD 4 to 0.42 mg m^{-3} at CTD 15). Process Station B (Fig. 2) showed cooler temperatures (between 9 and 10 °C) than station A. The mixed layer depths were deeper than at Process Station A ranging from 65 to 85 m. The mixed

OSD
11, 1829–1869, 2014

layer deepened between the 28 February and 4 March. Though this did not result in large differences in temperature, salinity and oxygen, there was a clear decrease in mean chlorophyll concentration from 0.51 to 0.39 mg m^{-3} between these two sampling dates.

3.2 Nitrogen uptake rates

This section provides a short description of the nitrogen uptake rates for the two seasons. Specific, absolute and depth-integrated rates are presented here. Specific nitrogen uptake rates (ν) are uptake rates normalised to particulate nitrogen. They allow for comparison of uptake and growth rates independent of biomass. The absolute uptake rates represent the uptake in relation to the particulate nitrogen. This can introduce errors if the PN contains any non-phytoplankton nitrogen. The depth integrated rates allow for estimates of nutrient uptake throughout the water column. It is to be noted that isotopic dilution arising from NH_4^+ regeneration (including nitrification) has not been accounted for. However, the presence of NH_4^+ indicates that regenerative processes were taking place (Semeneh et al., 1998b). Due to environmental constraints, urea concentrations and uptake rates were not measured despite being a potentially important fraction of regenerated primary production (Joubert et al., 2011). These omissions in the regenerated production estimates do not affect the new production estimates but they reduce the usefulness of the f-ratio as an indicator of carbon export. The lack of nitrification rate measurements is a caveat in the estimate of new production. Nitrification has been observed during summer in the Southern Ocean (Bianchi et al., 1997) and DiFiore et al. (2009) have estimated that this process could represent up to 6 % of NO_3^- uptake during this season. Furthermore, the role of nitrification in replenishing nutrients over the winter season has been hypothesised previously (Sanders et al., 2007).

OSD
11, 1829–1869, 2014

3.2.1 Uptake rates for the winter cruise

For the winter cruise, the specific nitrate uptake rates, υ_{NO_3}, ranged between 0.0018 and 0.107 (mean = 0.017 d^{-1}) at the 55 % light depth. At the 1 % light depth, the specific nitrate uptake ranged between 0.003 and 0.03 (mean = 0.009) d^{-1}. Specific ammonium uptake rates, υ_{NH_4}, averaged 0.073 (0.006–0.37) d^{-1} for the 55 % light depth and 0.085 (0.00036–0.42) d^{-1} for the 1 % light depth. The absolute nitrate uptake rates, ρ_{NO_3} averaged 8.897 (1.28–57) nmol L^{-1} d^{-1} and absolute ammonium uptake rates, ρ_{NH_4}, 31 (2.3–58) nmol L^{-1} d^{-1} at 55 % sPAR. At the 1 % light depth, the average ρ_{NO_3} was 5.980 (1.070–36) nmol L^{-1} d^{-1} and the average ρ_{NH_4}, 41 (0.17–160) nmol L^{-1} d^{-1}.

In this dataset, the 55 % light depth nitrate uptake rate at station 6 was much higher than other nitrate uptake rates in the AZ. It was also much higher than the corresponding nitrate uptake rate at the 1 % light depth. It is considered as an outlier for further statistical analyses. However, it cannot be excluded from the dataset as there are no valid experimental reasons to do so. Furthermore, this station was located within the polar front and this could also explain the high uptake rate.

Table 3 shows the integrated nitrate uptake rates over the mixed layer for the CTD stations from the winter cruise. Integrated ρ_{NO_3} ranged from 0.1664 to 5.1990 mmol m^{-2} d^{-1} (mean = 1.14 mmol m^{-2} d^{-1}) and integrated ammonium uptake from 0.60 to 32.8 mmol m^{-2} d^{-1}(mean = 6.72 mmol m^{-2} d^{-1}).

3.2.2 Uptake rates for the summer cruise

For the summer cruise, more detailed depth profiles were available (Fig. 3). CTDs 1 and 2 were the two stations outside the SAZ and process study. They showed similar nitrate uptake profiles (Fig. 3a). CTD 2 (which was further north) however has lower subsurface nitrate uptake rates than CTD 1. At Process Station A (Fig. 3c), nitrate uptake increased between the CTD stations conducted on 25 February 2013 (CTD 4) and 5 March 2013 (CTD 14). Between CTD 14 and 15, there was a change in nitrate

OSD
11, 1829–1869, 2014

Seasonal comparison of N uptake in the Southern Ocean

R. Philibert et al.

uptake pattern. CTD 4, 8, 14 all showed a subsurface maximum in terms of nitrate uptake. This maximum value was found at the 10 % light depth for CTD 4 and 14 but was shallower at CTD 8. For CTD 15, the nitrate uptake rate at 20 m (30 % light depth) represented a minimum rate. This rate then surprisingly increased with depth to the 1 % light level. It is possible that nitrate uptake rate through the water column did not differ much and that the differences seen are due to standard errors in the measurements.

At Process Station B (Fig. 3e), two of the stations CTD 7 and 9 showed nitrate uptake rates which decreased with depth. Differences between CTD 7 and 9 were minimal. At the 55 % light depth, nitrate uptake for CTD 13 was very similar to the two other stations. However, nitrate uptake rates at this station were much larger subsurface, with a maximum at 20 m.

At Process Station A, three ammonium uptake profiles were available (Fig. 3d). For CTD 4 and 14, ammonium uptake decreased with depth. At CTD 15, however, ammonium uptake increased with depth. Those patterns were opposite to the nitrate uptake pattern. At Process Station B, ammonium uptake rates were only available for a few points (Fig. 3f). CTD 7 showed a greater ammonium uptake rate than CTD 9 and 13 at the 60 m depth (0.3 % light depth). For CTD 13, like the nitrate uptake, ammonium uptake was maximum at 20 m. As expected, the subsurface maximum in chlorophyll at CTD 14 coincided with the maximum uptake rate. At CTD 4 and 8, the subsurface minimum of chlorophyll was at the subsurface maximum of nitrate uptake.

The integrated summer uptake rates are shown in Table 2. For the summer cruise, the mean ammonium integrated rates was 7.60 with a standard deviation of 2.8 mmol m^{-2} d^{-1} and the mean integrated nitrate uptake rates was 0.384 mmol m^{-2} d^{-1} with a standard deviation of 0.135.

OSD
11, 1829–1869, 2014

3.3 Biogeochemical controls on primary productivity

3.3.1 Winter cruise

A multivariate statistical analysis was performed to determine which one of the environmental variables had the most influence on nitrate and ammonium uptake by phytoplankton.

The first step of the analysis was a cluster analysis. The hypothesis tested here was whether clusters based on the uptake rates are separated by the fronts (STF, SAF and PF). Two cluster analyses were undertaken one based on the environmental variables at the 50 % and 1 % light depths and the other on the uptake rates. The environmental clustering showed clusters which were separated by the fronts. This was an expected result as the location of the fronts and the delineation of the different regons (STZ, SAZ, PFZ and AZ) is based on environmental parameters. In the cluster analysis based on the uptake rates, stations did not follow such clear cut separation across the fronts. Stations, situated far from each other geographically, had similar responses. For example stations 15-N-3 and 15-N-11 were placed in the same cluster. When using only the CTD stations for the cluster analysis, 15-N-2, however, was identified as a SAZ station rather than a STZ station where it was actually located. This could be due to its proximity to the STF. While surface parameters at this station were typical of the STF, the transition was not so clear in deeper waters. For the rest of the analysis, 15-N-2 will be considered as a sub-antarctic station rather than a sub-tropical one.

A redundancy analysis (RDA) was then performed. The RDA combines a principal component analysis and multiple regressions. The process identifies sets of axes along which most of the variation can be explained. As stated previously, in this analysis, station 15-N-6 was considered as an outlier and not used because it had a very high nitrate uptake rate. On the plot, the angle between the blue lines represent the strength of the correlation between the environmental parameters. The length of the arrows shows the significance of the regressions between a particular variable and the response variables. The angle between the blue arrows and red lines shows the

OSD
11, 1829–1869, 2014

correlation between the environmental parameter and each response variable. Finally the distance between the stations on the plots are based on their euclidean distance. This means that stations that have similar responses both in terms of nitrate and ammonium uptake are plotted close to each other.

The controlling factors included in the analysis were the day length and MLD as measures of light limitation, SST and nutrient concentrations ([NO_3^-], [NH_4^+], [NO_2^-]). The $Si(OH)_4$ and PO_4^{3-} were not included in the analysis as they are strongly colinear with the NO_3^- concentrations. Such strong colinearity results in additional variation which is insignificant. While SST and day length were also strongly correlated, they were included in the analysis in order to determine which of the two factors has a larger influence on the uptake rates.

The RDA plot is shown in Fig. 4. The angle between the arrow representing day length and nitrate uptake was smaller than between SST and nitrate uptake. This implies that day length had a more important role in the regulation of nitrate uptake than SST. Ammonium concentration was positively correlated to ammonium uptake and negatively correlated to nitrate uptake. Though the MLD was negatively correlated to nitrate uptake, the length of its representative arrow indicates that it did not contribute significantly to the variation in the uptake rates. Similar results were obtained with an RDA which included all the underway stations and the specific uptake rates and excluded the MLD.

The unadjusted and adjusted R^2 values for the RDA were 0.74 and 0.36 respectively. This gives an indication of the proportion of variance that can be explained through this analysis. A permutation test confirmed (p value 0.0967) that the RDA was significant and that the relationship between the environmental parameters and uptake rates was not random. Given this information, it was possible to perform a "forward selection" of variables (Borcard et al., 2011), which allows to identify the minimum number of environmental variables explaining the maximum variation in the response variables (uptake rates). This process identified day length and ammonium concentration as the two variables which influenced the variation in uptake rates the most. The controlling factors in this RDA explain 36 % (adjusted R^2) of the variation in the uptake rates. This value has to be adjusted as the RDA employs multiple regressions. Each regression is a hypothesis test. At each iteration, the probability of making a type I error (where a relationship that is not significant is seen as significant) increases and this needs to be accounted for. The algorithm used here has been shown to be conservative (Borcard et al., 2011). This would mean that the parameters used here explain more that 36 % of the variation in nitrogen uptake.

3.3.2 Summer cruise

A correlation matrix was done for the summer cruise (Fig. 5). As the mixed layer depth increased, SST decreased as shown by the strong negative correlation between the two parameters. This also corresponded to an increase in the concentration of nitrate, nitrite, ammonium and phosphate concentrations. Silicate concentration was the only nutrient concentration to decrease with deeper vertical mixing. Both ammonium and nitrate uptake increased when the mixed layers were deeper even though the chlorophyll concentrations decreased.

4 Discussion

4.1 Comparison of nitrogen uptake rates with previous studies

Shipboard observations allow for a snapshot view of primary productivity. In order to obtain a more complete image of the seasonal and interannual variability, a comparison with historical data is useful. Figures 6 and 7 compares the absolute nitrate and ammonium uptake rates for the two cruises with historical data. The historical data includes data along the GoodHope Line (Joubert et al., 2011), the Indian sector (Thomalla et al., 2011b) and the three SANAE cruises. SANAE cruises are yearly cruises which take place between December and February in the Atlantic sector of the Southern Ocean.

OSD
11, 1829–1869, 2014

Winter uptake rates from previous winter and autumn studies (Cota et al., 1992; Nelson, 1990) are comparable with the current dataset. As expected, ρ_{NO_3}, υ_{NO_3} and therefore $\int \rho_{NO_3}$ were lower in winter than in summer and spring. The extent of the seasonal difference varied from region to region. In the STZ, nitrogen uptake rates were of similar order of magnitude for both seasons (Thomalla et al., 2011b). Further south, the differences between summer and winter rates increased; winter ρ_{NO_3} along the GoodHope line were between 2–80 times smaller than summer rates measured by Joubert et al. (2011) for similar latitudes and light depths.

The summer nitrate uptake rates presented here were lower than summer rates from most past studies (Table 1). The nitrate uptake rates from the summer cruise were, indeed, very similar to the winter uptake rates (Table 1 and Fig. 6). Most of the summer studies were conducted between December and February. For instance, integrated nitrate uptake in the SAZ from Savoye et al. (2004) were greater than our estimates. While this could be due to longitudinal variations, it is to be noted that the sampling by Savoye et al. (2004) was done in October and December. At that point, it is likely that the phytoplankton were not yet affected by nutrient limitations (e.g iron). While Joubert et al. (2011) sampled at a similar time of the year, their high nitrate uptake rates for SAZ stations were due to an anti-cyclonic eddy in this region at the time of sampling. For Gandhi et al. (2012), sampling extended from December to April and the nitrate concentrations and uptake rates were comparable to the summer uptake in this dataset.

The variations in nitrate uptake are in contrast with ammonium uptake rates which did not vary much seasonally or geographically (Fig. 7). The ammonium uptake for the winter cruise was very weakly correlated to latitude. Rates from the winter and summer cruises were similar to previous studies. A preference for ammonium was observed during the two cruises. Both υ_{NH_4} and ρ_{NH_4} were higher than υ_{NO_3} and ρ_{NO_3} respectively. Such a preference has been observed in winter (Cota et al., 1992), summer (Semeneh et al., 1998b) and autumn (Thomalla et al., 2011b).

OSD
11, 1829–1869, 2014

There are instances, however, where nitrate uptake is preferred. Gandhi et al. (2012) measured higher nitrate uptake than ammonium and urea uptakes during the summer on transects in the Indian Sector of the Southern Ocean. Sambrotto and Mace (2000) observed a shift in preference from nitrate to ammonium between December and February in the Pacific sector of Southern Ocean. Nelson (1990) also observed a preference for nitrate. However, in Nelson's study 1990, as the season progressed from spring into autumn, there was no shift in preferential uptake but a decrease in both uptake rates. Unavailability of nitrate or silicic acid as well as changes within the phytoplankton community structure can lead to a preference for regenerated nutrients. The smaller (seasonal and geographical) variation in NH_4^+ uptake are due to the lower energy requirements of NH_4^+ uptake compared to NO_3^- uptake. The phytoplankton are able to use NH_4^+ even under severe limitations such as low light in winter and decreased nutrients in summer.

4.2 Biogeochemical controls on primary productivity

Given the importance of primary production and nitrogen uptake for the global carbon and nitrogen cycle, it is important to understand the factors which control these processes. This section discusses various controls on primary production for the winter and summer seasons. This was investigated using multivariate statistical analyses (Sects. 2.1 and 3.3).

4.2.1 The fronts

Two cluster analysis (one on the environmental variables, the other on the uptake rates) were undertaken on the winter data to test the hypothesis that the location of the stations relative to the fronts regulated the nitrogen uptake regime. The cluster analysis for the environmental parameters corresponded to the fronts. This was to be expected as the fronts separate waters with different environmental properties. Stations with similar nitrogen uptake regimes, however, were not separated based on their positions

OSD
11, 1829–1869, 2014

relative to the fronts. This shows that the frontal positions cannot be used to distinguish between nitrogen uptake regimes, specially in winter, and that the factors controlling nitrogen uptake are not a simple linear combination of the various environmental variables.

4.2.2 Temperature

Temperature has the same effect on nitrogen uptake by phytoplankton as on photosynthesis. The growth rate is halved for every drop of 10 °C. (Smith Jr. and Harrison, 1991; Tilzer and Dubinsky, 1987). Positive correlations have been observed between nitrate uptake and phytoplankton growth and temperature in the Southern Ocean (Smith Jr. and Harrison, 1991; Reay et al., 2001). At temperatures above zero °C, this relationship was no different to that of temperate phytoplankton and temperature (Smith Jr. and Harrison, 1991). Polar phytoplankton do not seem to have special adaptations to the low temperatures which they encounter in their natural environment (Smith Jr. and Harrison, 1991; Reay et al., 2001; Cochlan, 2008). At low temperatures, nitrate uptake rates are potentially limited by its transport into the cell rather than assimilation rates (Reay et al., 2001; Lomas and Glibert, 1999; Cochlan, 2008), however, the effect of temperature on polar assemblages is not completely understood as a number of culture studies have been done at temperatures which are much higher than the natural ambient temperatures (Cochlan, 2008).

In agreement with previous studies, a positive correlation was shown between temperature and nitrogen uptake during the winter cruise. However, the RDA for the winter cruise showed that the general decrease in ρ_{NO_3} and υ_{NO_3} with latitude, temperature and day length during the winter cruise was more strongly correlated to day length than temperature. This is in line with differences reported between summer and winter rates. When considering summer rates from previous studies, the temperature differences are not large enough to explain the variations in the uptake rates. Furthermore, within the SAZ, temperatures were higher during the summer cruise than the winter one. Nitrogen uptake rates on the other hand were very similar. Furthermore, during

OSD
11, 1829–1869, 2014

the summer cruise nitrate uptake increased when temperature decreased (Fig. 5). This is in agreement with the model developed by Laws et al. (2000). In nutrient limited regions, low temperatures were linked to vertical mixing, which lead to nutrient inputs and enhanced primary production. During the summer cruise, the decreases in temperature corresponded to mixing events by increases in nutrient uptake rates.

As it has been reported for previous studies (Reay et al., 2001; Laws et al., 2000), the correlation between nitrate uptake and temperature was stronger than that between ammonium uptake and temperature during both cruises. The low dependency of ammonium uptake on temperature and the contradictory responses of nitrate uptake to temperature for the summer and winter cruises show that temperature alone cannot explain variations in the nitrogen uptake regimes. Other factors might have more impact through their interactions with each other and with temperature (Tilzer and Dubinsky, 1987; Reay et al., 2001).

4.2.3 Irradiance

The current dataset supports the use of light availability as one of the main drivers of nitrate uptake during the winter (Boyd, 2002; Boyd et al., 2010) but not for ammonium uptake. The amount of light available to phytoplankton is controlled by the time of the year (effectively day length) and the mixed layer depth (Smith Jr. and Harrison, 1991; Cochlan, 2008). The relationship between nitrogen uptake rates and light is similar to that of nitrogen uptake rates and inorganic nitrogen concentrations. It can be described by a Michaelis–Menten type curve, which shows that increasing light (or nutrients) will result in increasing phytoplankton growth up to the point of process saturation. At this maximal growth rate, the system is said to be saturated Smith Jr. and Harrison (1991); Cochlan (2008). However, there are contradictions to this simple relationship. Maximal rates can be found at depths with 1 % and even 0.1 % of the surface irradiance (Cochlan, 2008). For instance, at the summer process station A, one of the nitrate uptake profiles (CTD 15) showed higher nitrate uptake at 60 m rather than at 20 m. Furthermore, subsurface maxima were observed in several of the nitrate uptake profiles.

OSD
11, 1829–1869, 2014

This could be due to photoinhibition of nitrogen uptake (Hoffmann et al., 2008). For the winter cruise, similar uptake rates were observed in samples incubated at simulated 55 % and 1 % light depths. The relationship between irradiance and nitrogen uptake by phytoplankton can also be influenced by a number of other factors such as the bloom stage and phytoplankton community structure (Smith Jr. and Harrison, 1991; Cochlan, 2008).

The use of the mixed layer depth as a determining factor for phytoplankton growth (Sverdrup, 1953) has been a classic tenet of biological oceanography. It assumes that a phytoplankton bloom is not possible if the depth of vertical mixing is deeper than the critical depth. At the critical depth, losses through respiration and other processes exceed growth from photosynthesis. Moreover, with deep vertical mixing, phytoplankton are not exposed to light for long enough to allow nutrient uptake. Consequently, growth would slow down (Mitchell et al., 1991).

The winter data shows a negative correlation with the nitrate uptake as expected (as MLD decreases, nitrate uptake increases) but not with ammonium uptake. However, the MLD appears to play a limited role. The length of each arrow (representing a variable) on the RDA plot indicates its relative contribution to explaining the variability of the dataset. The MLD arrow here was very short. It is possible that changes in MLD during the days preceding sampling have a more important effect than the MLD at the time of sampling. The effect of vertical mixing is not always instaneous. For instance, Venables et al. (2013) have shown that the depth of mixed layer during winter on the Western Antarctic Peninsula could influence phytoplankton growth during the following summer. Furthermore, they also showed that at the time of sampling, incoming irradiance – a function of day length – was a more important control than MLD. This is because the critical depth depends on incoming irradiance – the higher the incoming irradiance, the deeper the critical depth. This is also seen in the winter dataset where day length was very strongly correlated to nitrate uptake. Day length was also one of the two factors explaining most of the variation in nitrogen uptake regime during the winter cruise. This is in agreement with the model by Vernet et al. (2012) who showed a strong correlation

OSD
11, 1829–1869, 2014

between the seasonal cycle of day length and primary production close to the Antarctic Peninsula.

Light limitation also changes the responses of phytoplankton to other factors. For example, Tilzer and Dubinsky (1987) showed that the light : dark ratio modulated the responses of phytoplankton to low temperatures. Photosynthesis (dominant in light periods) and respiration (dominant in dark periods) have differential temperature dependencies. Therefore, when temperature changes, the amount of daylight required to maintain a balance between growth from photosynthesis and losses from respiration also changes.

In addition, light limitation can lead to a decoupling of carbon and nitrogen uptake (Smith Jr. and Harrison, 1991). Under low light conditions, nitrogen uptake saturates first leading to an increased C : N ratio. Such increased C : N ratios were not observed in our dataset. The C : N ratio was on average 6.75, which is very close to the classic Redfield C : N ratio (6.6).

This could be due to the fact that the light periods during the winter cruise, when one would expect light limitation, were still significant. The station furthest south was located at −56.92° N and had a day length of 7.6 h. This is located far from positions where periods of total darkness are experienced much closer to the Antarctic Peninsula (Vernet et al., 2012). During the summer cruise, the day length for all stations were very similar and this was therefore not considered as a major factor affecting the variability in uptake rates. Nitrogen uptake rates increased when mixed layer depth increased in contradiction with the idea that shallow mixed layers would reduce light limitation and enhance primary production. This shows that the changes in vertical mixing impacts controls other than light availability and that depending on the season or stage of bloom, factors such as nutrient availability might become more important than light.

4.2.4 Nutrients

While increased vertical mixing is purported to create unfavourable light conditions for phytoplankton growth, it can promote growth by alleviating nutrient limitations. In this

OSD
11, 1829–1869, 2014

section, the role of iron, silicic acid and ammonium for the nitrogen uptake regime are discussed. The potential effects of iron on the nitrogen uptake as discussed here are purely conjectural as the iron concentrations were not available for the two cruises. Nitrate concentrations were not limiting throughout the two cruises. In the winter, there is a negative correlation between nitrate uptake and nitrate concentration. The high nitrate concentrations could be due to low nitrate uptake rates and the inability of the phytoplankton to deplete this nutrient. Phytoplankton community structure is strongly influenced by the nutrient limitations (Hutchins et al., 2001; Sedwick et al., 2002; Hoffmann et al., 2008). This will not be discussed in detail here as no data on the size or species distribution were available for these two cruises.

Iron

Within the SAZ during the summer cruise, nitrate uptake, which is thought to be more dependent on iron than ammonium uptake, was very low. As the vertical mixing increased, nitrate uptake increased. The deeper mixed layers resulted in enhanced nutrient availability and consequently increased nitrate uptake. As nitrate concentrations were not limiting, other macro- and micro- nutrients are responsible for this enhanced nitrate uptake rate. Iron is the most likely candidate given its well-established role in regulating primary productivity within the Southern Ocean (Van Oijen et al., 2004; Strzepek et al., 2012; Sanders et al., 2007; Moore et al., 2007; Falkowski et al., 1998; Cochlan, 2008; Boyd et al., 2010; Boyd, 2002). However, in winter, iron limitation by itself is unlikely to be a major control. The deep vertical mixing brings up a constant supply of nutrients (Boyd, 2002; Boyd et al., 2010; Thomalla et al., 2011b). Furthermore, in iron-limited systems, islands can be a source of iron which will enhance primary production and nitrate uptake (Sanders et al., 2007). The stations closer to Marion island would show higher nitrogen uptake than stations further away in the PFZ. This would have been reflected in the cluster analysis as a separate cluster for stations around Marion Island. No such difference was observed supporting the contention that low iron supply was not limiting at this time of year. However, during

OSD
11, 1829–1869, 2014

this season, an iron-light colimitation, in which light might play a more important role than iron, is plausible (Moore et al., 2007; Van Oijen et al., 2004; Strzepek et al., 2012). In autumn, when mixed layers have started deepening and nutrient supply increased, Van Oijen et al. (2004) observed no changes in uptake rates after iron additions. Strzepek et al. (2012) found in laboratory experiments that the effects of iron addition on phytoplankton growth were less pronounced under light limitation. They also suggest that the relationship between iron and light utilisation by Southern Ocean phytoplankton might be different from that in temperate phytoplankton. Iron limitation affects the nitrogen uptake regime as it influences the phytoplankton community structure (Hutchins et al., 2001; Sedwick et al., 2002; Hoffmann et al., 2008). This also results in changes in the interactions with the cycling of Si.

Silicic acid

During the winter cruise, Silicic acid, $Si(OH)_4$, concentration was low north of the Polar front. This corresponds to observations from previous studies (Tréguer and Jacques, 1993). The minimum $Si(OH)_4$ concentration was 1.7 µmol L^{-1}. At this concentration, $Si(OH)_4$ is not limiting if the assemblage is dominated by non-diatom phytoplankton (Sedwick et al., 2002). Notwithstanding, phytoplankton communities can be limited by low $Si(OH)_4$ concentration. A number of studies have shown co-limitations of iron and silicate (Hutchins et al., 2001; Sedwick et al., 2002; Hoffmann et al., 2008). In those studies, growth rates increased to a greater extent when both Si and Fe were added together than when either nutrient was added alone. Increases in Si can also shift the community structure from dinoflagellate dominated to diatom dominated (Hutchins et al., 2001). This results in changes to the nitrogen uptake regime – the preference for ammonium and other non-nitrate nitrogen sources is reduced. During the winter cruise, however, $Si(OH)_4$ and NO_3^- concentrations were positively correlated and both increased with latitude. Nitrate uptake rates decreased with latitude indicating that $Si(OH)_4$ was not a limiting nutrient. However, its influences on the community structure during this cruise is unknown. For the summer cruise, $Si(OH)_4$ was the only nutrient

OSD
11, 1829–1869, 2014

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀◀ ▶▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

to decrease with increased vertical mixing and to be negatively correlated to nitrogen uptake. The silicate concentration profiles show that there was an increase below 60 m following a similar pattern to nitrate. However, there is no correlation between nitrate and silicate concentration within the euphotic zone. This could indicate a decoupling between the Si and N cycles. This arises when the recycling of nitrogen is high as opposed to the slow recycling of silicic acid (Tréguer and Jacques, 1993).

Ammonium

The RDA plot for the winter data (Fig. 4) shows that when ammonium is present, phytoplankton exhibit a preference for ammonium. Ammonium concentration was identified as one of the factors explaining the most of the variance in the dataset (Sects. 2.1 and 3.3). The presence of ammonium has two reported effects on the nitrogen uptake regime: it can either inhibit nitrate uptake or increase the specific ammonium uptake rate (Goeyens et al., 1995; Whitehouse et al., 2011; Cochlan, 2008; Smith Jr. and Harrison, 1991). The question remains as to which of the two is more effective at shifting the uptake regime from one which is mainly fuelled by nitrate to one fuelled by regenerated nutrients. Inhibition of nitrate uptake by ammonium has been reported in a number of studies (Goeyens et al., 1995; Smith Jr. and Harrison, 1991; Reay et al., 2001; Semeneh et al., 1998a), but the concentration at which this inhibition effect starts is controversial. Goeyens et al. (1995) synthesised data from 9 studies and observed the changes in nitrate depletion and ammonium availability over a full seasonal cycle. Higher ammonium availability was observed when nitrate assimilation decreased. Nitrate assimilation usually decreases after a period of sustained phytoplankton growth. Following such a bloom, the particulate organic matter is remineralised to regenerate ammonium (Goeyens et al., 1995). From our winter data, there was no correlation between ammonium and chlorophyll concentrations. There might be a lag between the peak in nitrate uptake and the remineralisation of particulate organic matter. In this case, ammonium concentrations would be more likely to correlate with chlorophyll concentrations from some preceding period rather than chlorophyll concentrations at the

OSD
11, 1829–1869, 2014

time of sampling. In the summer dataset, a negative correlation is observed between chlorophyll and ammonium concentrations, but this cannot be attributed to an accumulation of ammonium due to remineralisation of particulate organic matter. Mixing events during the course of the study could be responsible for entraining the organic matter and bringing ammonium formed in a different location to the process station.

Given the role of ammonium, it was important to verify that the addition of ^{15}N tracer did not impact the ammonium uptake rates. The specific ammonium uptake rates, υ_{NH_4}, was plotted against ^{15}N tracer concentration as a percentage of ambient concentration (referred here as the "percentage spike"). This data was fitted to a exponential curve ($r^2 = 0.44$, RMSE = 0.0775). This does not deviate from a Michaelis–Menten type curve. The tracer concentrations were kept constant throughout the cruise. At low ammonium concentrations, the "percentage spike" was high but the ammonium uptake rate remained low as expected from concentration effects. This also confirms that the shift of preference to ammonium is at least partly due to increased concentrations of ammonium. In contradiction to studies which have observed a fairly constant nitrate uptake in the presence of ammonium (Whitehouse et al., 2011), the winter dataset shows that nitrate uptake decreases when ammonium concentration increases. This indicates that inhibition of nitrate uptake could also be contributing to shifting the nitrogen uptake regime.

5 Conclusions

The seasonality of primary production in the Southern Ocean was investigated. Two cruises were conducted: one in winter (July–August 2012) along the Goodhope line and one in late summer within the SAZ (February–March 2013). Nitrate uptake rates were similar for both cruises, but ammonium uptake rates were generally greater during the summer cruise. These nitrate uptake rates were, however, lower than rates measured in other cruises undertaken in spring and early summer. Primary production was mainly driven by ammonium during both seasons. During the winter cruise, nitrogen

OSD
11, 1829–1869, 2014

uptake rates decreased southwards and seemed to be limited by light rather than by nutrients. During this season, the presence of ammonium was shown to shift the nitrogen uptake regime towards increased ammonium uptake. This was a result of both inhibition of nitrate uptake by ammonium as well as concentration effects increasing ammonium uptake. During the summer, on the other hand, nutrient availability seemed to be the most important control. With increased vertical mixing and increased nutrients, nitrogen uptake rates increased even though deepening mixed layers mean that the light conditions are less favourable. Wider observational studies are required to be able to resolve the seasonality behind nutrient fluxes and phytoplankton biogeochemistry as shipboard measurements offer only a snapshot view. It is recommended that winter cruises along the GoodHope line are more frequent in the future and that this dataset is the first of a time-series which will contribute to the improvement of biogeochemical models for the Southern Ocean.

Author Contribution

R. Philibert and H. Waldron conducted the field experiments during the winter cruise. R. Philibert performed the data processing and statistical analyses. R. Philibert wrote the manuscript with inputs from all the authors.

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OSD
11, 1829–1869, 2014

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11, 1829–1869, 2014
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OSD
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OSD
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OSD
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Seasonal comparison of N uptake in the Southern Ocean

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OSD
11, 1829–1869, 2014

Table 1. Overview and comparison of integrated nitrogen uptake rates (mmol N m^2 d^{-1}). Average rates and the range are presented here.

Integrated ρ_{NO_3}		Integrated ρ_{NH_4}			
mean	range	mean	range	season	reference
0.34	0.16–0.65	5.605	1.44–11.28	Late summer (Mar)	SOSCEX
1.14	0.16–5.20	6.72	0.6–32.8	Winter (Jul)	Winter
3.01	1.75–6.58	1.06	0.55–2.18	autumn (Mar)	Nelson and Smith (1990)
0.78	0.27–1.78	2.09	0.89–5.07	Late autumn/winter (Apr–May)	Waldron (unpublished)
3.33	0.79–8.63	14.5	2.65–39.17	autumn (Apr)	Thomalla (2011)
1.49	0.80–2.48	3.6	0.35–10.55	Summer (Feb)	Sambrotto and Mace (2000)
4.37	1.32–8.86	2.3	1.62–2.91	Spring (Oct)	Savoye (2004)
5.25	1.85–9.26	4.63	1.51–10.06	spring (Nov)	Nelson and Smith (1990)
10.43	0.90–34.94	12.63	2.84–23.19	spring (Nov)	Waldron (1995)
6.10	1.90–12.59	5.65	3.03–8.80	Summer (Dec)	Sambrotto and Mace (2000)
1.50	0.30–4.10	1.1	0.8–1.6	Summer (Dec–Apr)	Gandhi (2012)
4.07	(3.63–4.55)	1.37	(0.98–1.91)	Spring (Dec)	Savoye (2004)

OSD
11, 1829–1869, 2014

Seasonal comparison of N uptake in the Southern Ocean

R. Philibert et al.

OSD
11, 1829–1869, 2014

Table 2. Summer depth integrated ρ_{NO_3}, ρ_{NH_4}, new production, total primary production, chlorophyll concentration and associated SST, MLD, $[NO_3]$ and $[NH_4]$. $[NO_3]$ and NH_4 are given for the 50 % light depth only.

Process station	date	Lat	Long	$[NH_4]$	$[NO_3]$	SST	MLD	Depth integrated chlorophyll	Depth integrated ρ_{NH_4}	Depth integrated ρ_{NO_3}
–	–	°N	°E	$\mu mol\,L^{-1}$	$\mu mol\,L^{-1}$	°C	m	$mg\,m^{-2}$	$mmol\,N\,m^2\,d^{-1}$	$mmol\,N\,m^2\,d^{-1}$
A	26 Feb 2013	−42.645	8.6	0.05	6.7	12.2	57	40.1	3.6	0.23
A	01 Mar 2013	−42.7412	8.8		9.5	11.3	54	26.0		0.26
A	03 Mar 2013	−42.7758	9.2	0.31	9.0	11.2	37	16.8	NA	0.30
A	05 Mar 2013	−42.6436	9.4	0.93	13.1	10.7	69	31.7	11.4	0.54
A	07 Mar 2013	−42.6153	9.6	0.34	12.7	10.3	76	32.3	8.30	0.39
B	28 Feb 2013	−43.5064	7.2	0.30	13.1	10.0	65	34.7	NA	0.34
B	02 Mar 2013	−43.4233	7.2		12.9	10.0	82	31.4	NA	0.36
B	04 Mar 2013	−43.5178	7.1	0.41	12.5	10.0	85	33.5	7.08	0.65

Table 3. Winter Depth integrated ρ_{NO_3}, ρ_{NH_4}, new production, total primary production and f ratio from ^{15}N estimates and associated SST, MLD, $[NO_3]$, $[NH_4]$. $[NO_3]$ and NH_4 are given for the 50 % light depth only.

Station number	Zone	SST °C	MLD m	$[NO_3]$ µmol L^{-1}	$[NH_4]$ µmol L^{-1}	Depth integrated: Chlorophyll mg m^{-2}	Depth integrated: ρ_{NO_3} mmol N m^{-2} d^{-1}	Depth integrated: ρ_{NH_4} mmol N m^{-2} d^{-1}
15N-2	STZ	14.6	236	3.1	0.25	33.22	1.02	13.12
15N-3	SAZ	10.3	206	9.3	1.7	33.091	0.34	32.86
15N-4	PFZ	6.9	200	16.6	0.06	22.302	1.31	1.70
15N-5	PFZ	5.4	151	18.2	0.35	30.779	0.61	8.32
15N-6	AZ	2	178	22.9	0.19	22.732	5.20	0.60
15N-7	AZ	0.88	142	28.5	0.1	17.396	0.22	1.70
15N-8	AZ	−1	126	25.6	0.46	13.216	0.45	2.13
15N-11	AZ	0.4	165	20	1.79	18.572	0.21	8.03
15N-13	PFZ	5.4	59	16.4	0.07	12.949	0.17	0.81
15N-15	PFZ	4.95	180	16.1	below dl	19.914	0.57	2.00
15N-16	PFZ	5.39	206	16.7	below dl	24.794	2.46	2.73

OSD
11, 1829–1869, 2014

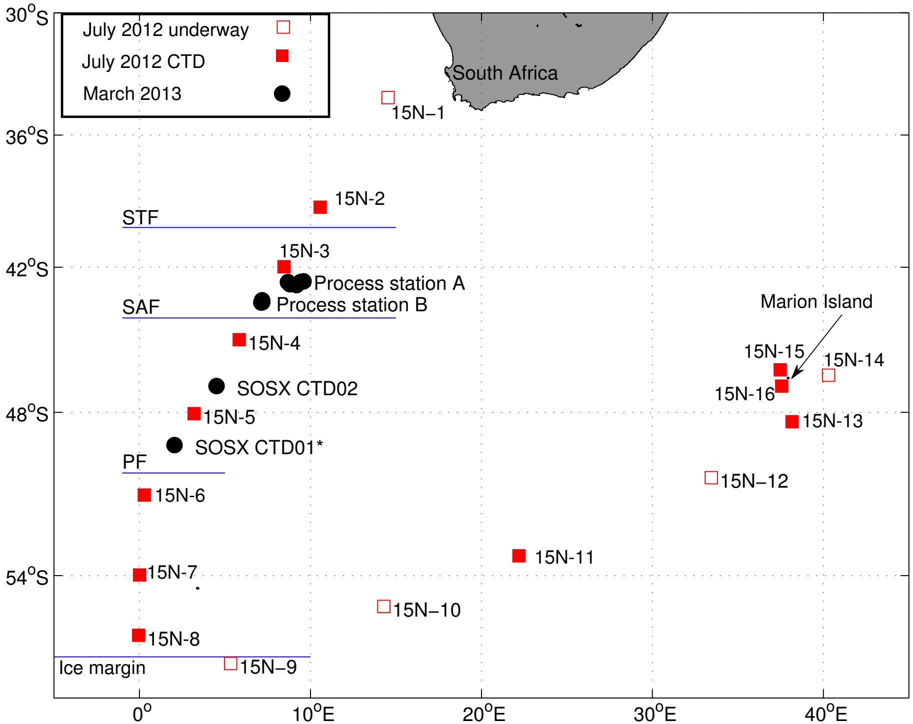

Figure 1. Cruise track for the two cruises. Leg 1 of winter cruise extended from Cape Town to the ice margin 58° S and Leg 2 from the ice margin to Marion Island. The winter frontal and ice margin positions are indicated by the blue lines.

OSD
11, 1829–1869, 2014

Seasonal comparison of N uptake in the Southern Ocean

R. Philibert et al.

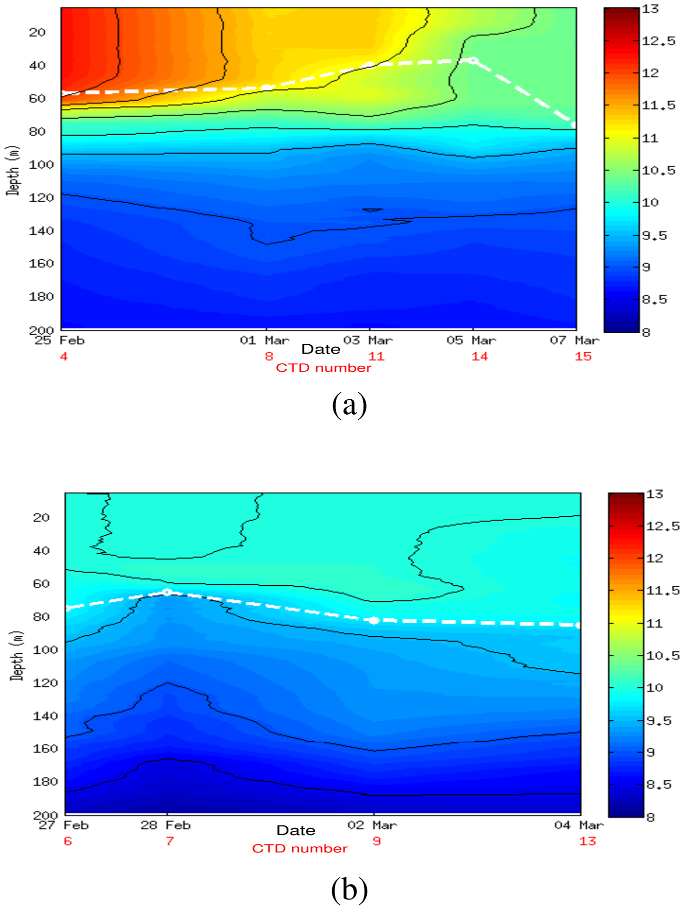

Figure 2. Temperature (°C) profiles for the summer cruise. **(a)** Process station A **(b)** Process Station B. The horizontal axis shows the dates in black and the corresponding CTD numbers in red. The white line represents the MLD.

OSD
11, 1829–1869, 2014

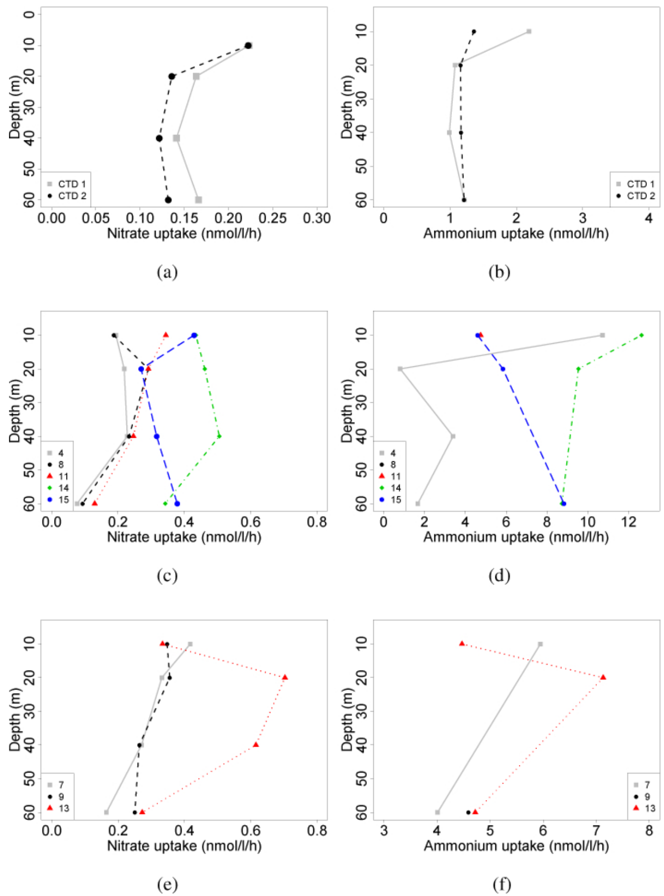

Figure 3. Nitrate and ammonium uptake rates profiles for the summer cruise. (**a**, **c** and **e**) Show the nitrate uptake profiles for the PFZ stations, Process Station A and B. (**b**, **d** and **f**) Show the ammonium uptake profiles for the PFZ stations, Process Station A and B.

OSD
11, 1829–1869, 2014

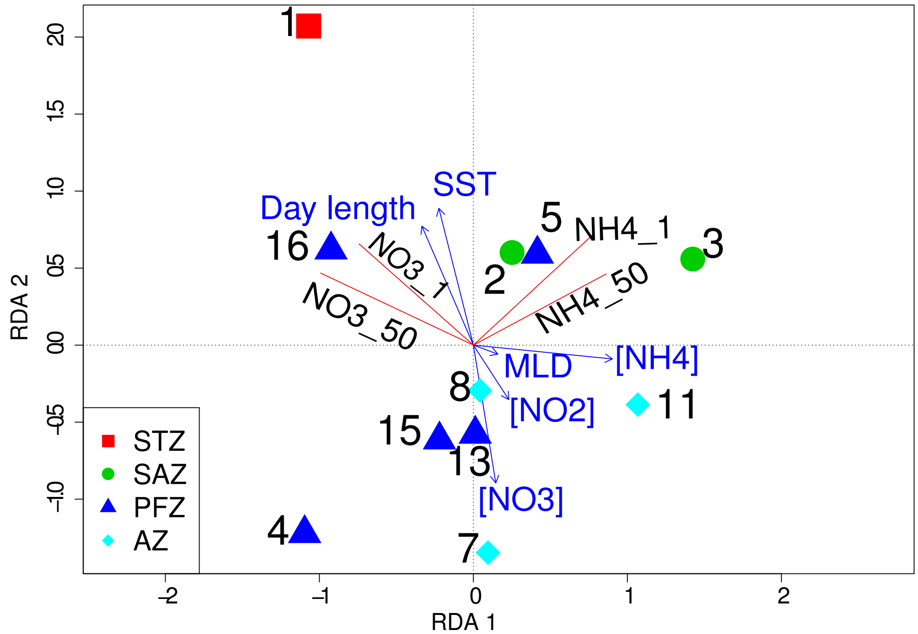

Figure 4. RDA triplot. The blue arrows represent the environmental parameters. The red line are the response variables. The stations are labelled based on the zone in which they are located. NO3_1, and NO3_50 represent ρ_{NO_3} at the 1 % and 55 % light depths respectively and NH4_1 and NH4_50 the ρ_{NH_4} at the same light depths. The uptake rates were log-transformed. SST is the sea-surface temperature, $[NO_2]$, $[NO_3]$ and $[NH_4]$ the concentrations of nitrite, nitrate and ammonium. The numbers for each station are the 15-N station numbers.

OSD
11, 1829–1869, 2014

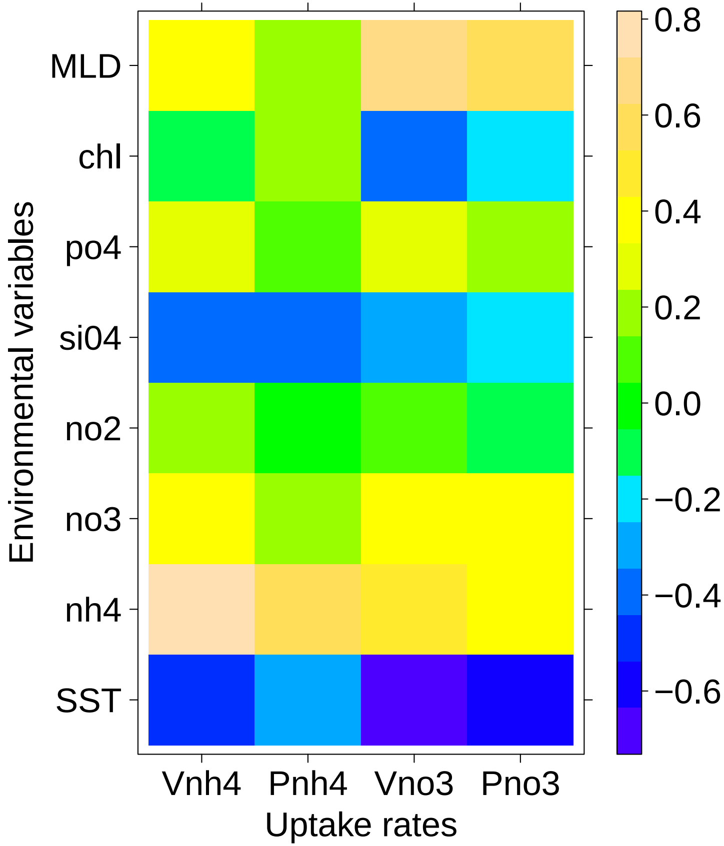

Figure 5. Correlation matrix of uptake rates and environmental variables for the summer cruise. Vnh4 and Vno3 are the specific ammonium and nitrate uptake rates while Pnh4 and Pno3 are the absolute uptake rates. SST is the sea-surface temperature and MLD the mixed layer depth. nh4, no3, no2, siO4, po4 and chl are the concentrations of ammonium, nitrate, nitrite, silicate, phosphate and chlorophyll.

OSD
11, 1829–1869, 2014

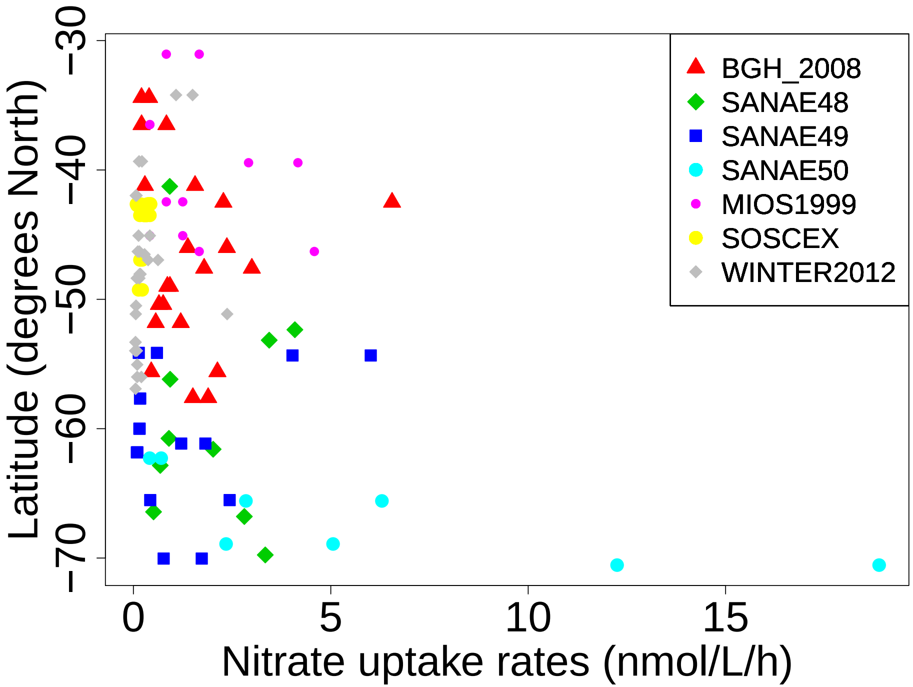

Figure 6. Comparison of nitrate uptake rates from the summer cruise (SOSCEX) and the winter cruise (WINTER2012) and previous cruises. The data includes both the 50 % and 1 % light depths where available for each cruise. The data shown here includes data from Joubert et al. (2011) (BGH2008), the SANAE cruises in 2009, 2010 and 2011 (SANAE48,49,50) and Thomalla et al. (2011b) (MIOS1999).

OSD
11, 1829–1869, 2014

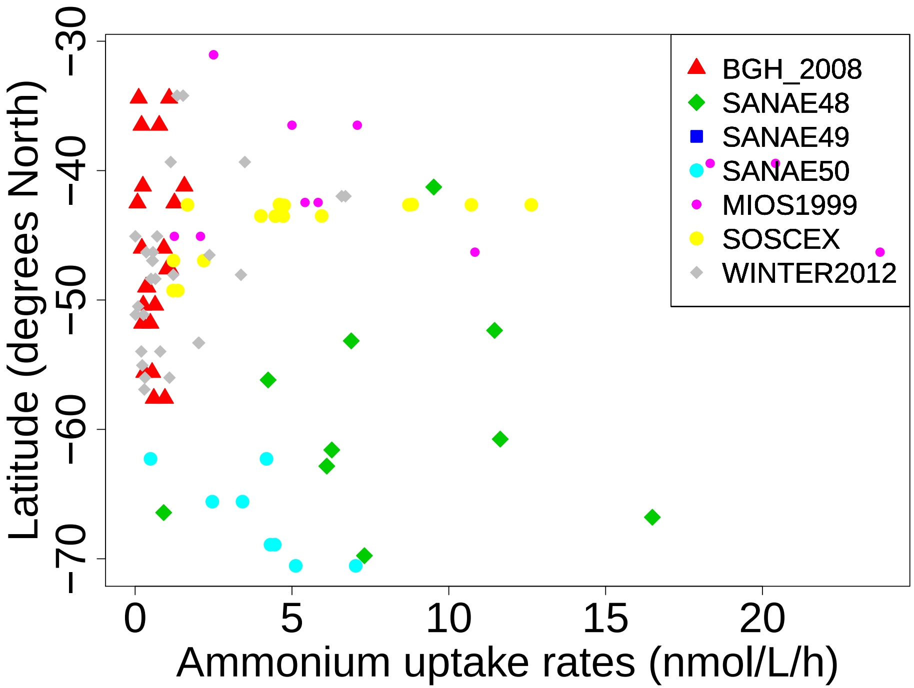

Figure 7. Comparison of ammonium uptake rates from the summer cruise (SOSCEX) and the winter cruise (WINTER2012) and previous cruises. The data includes both the 50 % and 1 % light depths where available for each cruise. The data shown here includes data from Joubert et al. (2011) (BGH2008), the SANAE cruises in 2009, 2010 and 2011 (SANAE48,49,50) and Thomalla et al. (2011b) (MIOS1999).

OSD
11, 1829–1869, 2014

Seasonal comparison of N uptake in the Southern Ocean

R. Philibert et al.