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RESEARCH ARTICLE

Nitrogen uptake by phytoplankton in surface waters of the Indian sector of Southern Ocean during austral summer

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Abstract This study reports the nitrogen uptake rate (using ^{15}N tracer) of phytoplankton in surface waters of different frontal zones in the Indian sector of the Southern Ocean (SO) during austral summer of 2013. The investigated area encompasses four major frontal systems, i.e., the subtropical front (STF), subantarctic front (SAF), polar front-1 (PF1) and polar front-2 (PF2). Southward decrease of surface water temperature was observed, whereas surface salinity did not show any significant trend. Nutrient (NO_3^- and SiO_4^{4-}) concentrations increased southward from STF to PF; while ammonium (NH_4^+), nitrite (NO_2^-) and phosphate (PO_4^{3-}) remained comparatively stable. Analysis of nutrient ratios indicated potential N-limited conditions at the STF and SAF but no such scenario was observed for PF. In terms of phytoplankton biomass, PF1 was found to be the most productive followed by SAF, whereas PF2 was the least productive region. Nitrate uptake rate increased with increasing latitude, as no systematic spatial variation was discerned for NH_4^+ and urea ($CO(NH_2)_2$). Linear relationship between nitrate and total N-uptake reveals that the studied area is capable of exporting up to 60% of the total production to the deep ocean if the environmental settings are favorable. Like N-uptake rates the *f*-ratio also increased towards PF region indicating comparatively higher new production in the PF than in the subtropics. The moderately high average *f*-ratio (0.53) indicates potentially near equal contributions by new production and regenerated production to the total productivity in the study area. Elevation in N-uptake rates with declining temperature suggests that the SO with its vast quantity of cool water could play an important role in drawing down the atmospheric CO_2 through the "solubility pump".

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1 Introduction

Biological sequestration of atmospheric CO_2 to the deep ocean is controlled by the functioning of the 'biological pump' and its spatiotemporal features, which usually differ seasonally due to variations in environmental forcings. Through the biological pump, an estimated 11 to 16 Pg (1 Pg = 10^{15} g) of atmospheric CO_2 is being removed per year from surface waters of the world's oceans; which accounts for 12%–18% of the total carbon sequestration by the ocean (Falkowski et al., 2000). The Southern Ocean (SO) acts as a sink for atmospheric CO_2 via the solubility and biological pumps (Chisholm et al., 2001) and, thus plays a pivotal role in the global carbon cycle and for climatic regulations (Kohfeld et al., 2005; Sigman et al., 2010). In the SO surface waters, nutrients utilization by phytoplankton is incomplete, and it has important implications on glacial/interglacial changes of atmospheric CO_2 (Sigman et al., 2000). It is reported that only 50% of the available nutrients are utilized by the phytoplankton, the rest being transported back into the ocean interior through formation of Antarctic intermediate and bottom waters (Anderson, 2003). As a result, the phytoplankton biomass or chlorophyll *a* (Chl *a*) remains modest and rarely exceeds 1 $mg \cdot m^{-3}$. Thus despite it's nutrient potential for primary production (PP) the SO falls within the high-nutrient low-chlorophyll (HNLC) regions of the world's oceans. Nevertheless, Chl *a* and PP are controlled by several other factors (bottom-up and top-down), indicative of events of phytoplankton blooms and elevated PP close to coastal Antarctica (Fiala et al., 1998; Moore and Abbott, 2000; Uitz et al., 2009; Tripathy et al., 2014). However, due to other complexities (the presence of several frontal features, bottom topography and annual advance and retreat of sea ice), the SO cannot be considered as a single marine ecosystem, and is much more heterogeneous than previously thought (Cochlan, 2008).

Nitrogen (N) is generally considered to be the most essential macronutrient for phytoplankton growth, and depending on its availability it can be limiting to PP. The distribution and the mean concentrations of oceanic NO_3^- influence the fertility of the ocean and its consequent exchange of gases with the atmosphere (Sigman et al., 2000). To study this effect, isotopes of nitrogen (^{15}N) are routinely used worldwide to quantify marine PP. Considering the source of nitrogen to the sunlit (euphotic) zone, PP can be subdivided into 'new (export)' and 'regenerated (recycled)' production (Dugdale and Goering, 1967). New production (NP) is the fraction of PP supported by the newly supplied nitrogen (i.e., NO_3^-), either from deep ocean or atmospheric inputs, and regenerated production (RP) is the fraction which is sustained by recycled nutrients (i.e., NH_4^+, $CO(NH_2)_2$) in the euphotic zone. It is important to differentiate between NP and RP while estimating *in toto* marine productivity since, through biological pump, the former is responsible for the sequestration of photosynthetically fixed carbon (Eppley and Peterson, 1979) below the euphotic zone or to higher trophic levels (i.e., export production), whereas the later mostly supports planktonic community maintenance requirements (Tremblay et al., 1979) in the euphotic zone. The ratio of new (NO_3^--based) to total production (sum of NO_3^-, NH_4^+, and $CO(NH_2)_2$) is designated as the *f*-ratio, which theoretically varies between 0 and 1, and can serve as a key variable to assess the strength of export fluxes in nutrient-rich aquatic ecosystem like the SO (Thomalla et al., 2011; Prakash et al., 2015).

The Indian sector represents ~39% (13.1×10^6 km^2) of the SO (Jacques and Fukuchi, 1994). Despite its potential key role in modulating global climate, the SO, particularly the Indian sector, is one of the least studied regions of the world's oceans probably due to logistical reasons. Concerted measurements have been made, during the last decade, to improve our comprehension of the SO biogeochemistry (de Baar et al., 2005; Blain et al., 2007; Boyd et al., 2007). Nevertheless, compared to the Pacific and the Atlantic sector of SO, biogeochemistry studies, especially pertaining to nitrogen uptake (N-uptake hereafter) rates are quite limited in the Indian sector of SO (Collos and Slawyk, 1986; Mengesha et al., 1998; Semeneh et al., 1998; Lucas et al., 2007; Thomalla et al., 2011; Gandhi et al., 2012; Prakash et al., 2015). In SO, it has been shown that, NO_3^- concentrations barely reach limiting levels with strong preference for NH_4^+ accounting for about 50%–95% of the nitrogen demand by phytoplankton (Olson, 1980; Glibert et al., 1982; Probyn and Painting, 1985), whereas Slawyk (1979) have found that the phytoplankton community was mostly based on NO_3^-. This study presents nitrogen uptake rates; measured using the ^{15}N tracer technique, in the surface waters (ca. 0–1 m) of different frontal zones (i.e., regions of enhanced biomass and production) in the Indian sector of the SO during austral summer (January–February) of 2013, to understand the preferential nitrogen uptake by phytoplankton, and the influence of the physical forcings (if any) on this biological response.

2 Materials and methods

2.1 Study area and ship-based sampling

The Indian sector of the SO was investigated during the 7th Indian SO expedition in the austral summer (11 January to 27 February 2013). The study area (Fig. 1) encompasses different frontal regions such as the subtropical front (STF), subantarctic front (SAF), polar front-1 (PF1) and polar front-2 (PF2). STF is one of the major oceanic fronts of the SO, which separates the subtropical surface waters from the subantarctic surface waters and thus acts as the true northernmost boundary of the Antarctic circumpolar current (ACC). The STF is characterized by sharp gradient of temperature and salinity (Orsi et al., 1995), whereas the SAF region is usually associated with the greatest temperature and salinity gradient (Holliday and Read, 1998). The PF plays an important role in biological production and acts as an important biogeochemical divider in the SO (Kemp et al., 2010). Based on the sea surface temperature (SST) criteria the PF is divided into northern (PF1, SST: 4°C –5°C) and southern (PF2, SST: 2°C–3°C) branches between Africa and Antarctica (Holliday and Read, 1998) and it is reported that its physicochemical (Trull et al., 2001) and biological (Pavithran et al., 2012) characteristics vary, perceptibly, on either side of the front. We adopted the criteria of Holliday and Read (1998) for identification of STF (SST: 10.6°C–17.0°C; salinity: 34.05–35.35), SAF (SST: 6.3°C–9.7°C; salinity: 33.85–34.0) and PF (SST: 2.7°C–5.5°C; salinity: 33.7–33.8) in the Indian sector of SO.

Water samples were collected, onboard *ORV-Sagar Nidhi*, along the 57.5°E meridian transect (regular track of the Indian SO expedition) covering at least one station as representative of each frontal regions (i.e., STF, SAF, PF1, and PF2). Figure 1 shows the 12 sampling locations visited during the cruise. Surface as well as water column sampling was carried out by 10 L Niskin bottles mounted on a conductivity-temperature-depth (CTD, SBE 911 +) carousel (General Oceanics Inc., USA) and sub-sampled for further analyses.

2.2 Physicochemical parameters, light and chlorophyll *a*

Measurement of SST (±0.2°C) was conducted using a bucket thermometer (Theodor Friedrichs & Co, Germany); sea surface salinity (SSS) was measured using an onboard

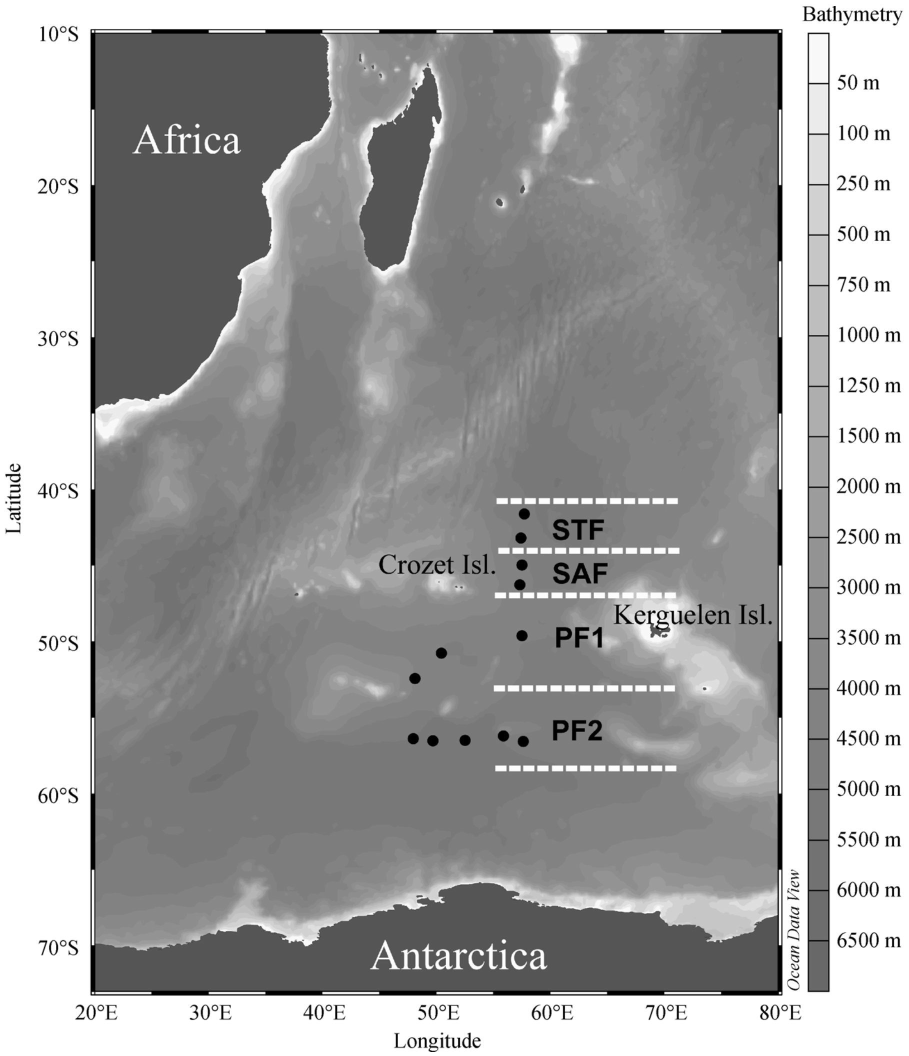


Fig. 1 Sampling locations (12 filled circles) across different frontal zones of the Indian sector of Southern Ocean. The hydrographic fronts, subtropical front (STF), subantarctic front (SAF) and polar front (PF1 and PF2) are indicated by dotted white lines overlaid on bathymetry.

Salinometer (Guildline 8400A, Canada). Both SST and SSS data were verified with simultaneous measurements obtained from onboard thermosalinograph. 100 mL of samples were collected for analyzing nutrients (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, and SiO_4^{4-}) by an onboard segmented flow analyzer (SKALAR) adopting standard methodology for analysis of seawater (UNESCO, 1994). The detection limit (precision) for NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, and SiO_4^{4-} were ±0.06 (±0.07), ±0.006 (±0.01), ±0.01 (±0.04), ±0.003 (±0.004), and ±0.06 (±0.04) µM, respectively. Incident photosynthetically active radiation (PAR) at sea surface ($\mu E \cdot m^{-2} \cdot s^{-1}$) was continuously recorded using quantum scalar irradiance sensor (QSL-2100, Biospherical Instruments Inc.) mounted onboard the vessel, and integrated over the photoperiod to get daily PAR($E \cdot m^{-2} \cdot d^{-1}$). Measurement of phytoplankton biomass or chlorophyll *a* (Chl *a*, $mg \cdot m^{-3}$) was carried out fluorometrically (AU-10, Turner Designs, USA) following overnight extraction using 47 mm GF/F filters (Whatman) in 10 mL of AR grade 90% acetone (Strickland and Parsons, 1972).

2.3 Nitrogen uptake measurements

Nitrate ($Na^{15}NO_3$), ammonium ($^{15}NH_4Cl$) and urea ($CO(^{15}NH_2)_2$) uptake by phytoplankton were measured using the ^{15}N tracer technique (Dugdale and Goering, 1967). Water samples (in triplicates) were collected in pre-cleaned polycarbonate bottles (Nalgene®), added with ^{15}N enriched (99 atom %) $Na^{15}NO_3$, $^{15}NH_4Cl$, and $CO(^{15}NH_2)_2$ tracers (Sigma Aldrich, USA) for measurement nitrogen uptake rates. The amount of $Na^{15}NO_3$ tracer added corresponded to < 10% of the ambient NO_3^- concentration. Ambient NH_4^+ and $CO(NH_2)_2$ concentrations could not be measured due to logistical limitation, therefore, assuming 1 µM is the ambient concentration, a fixed amount (i.e., 0.1 μM) of $^{15}NH_4Cl$ and $CO(^{15}NH_2)_2$ tracers was added to the samples. Following addition of the tracers, short time (4 h; symmetrical to local noon i.e., 1000 to 1400 h) simulated *in situ* incubation was conducted, since longer incubation times might lead to increased regeneration of NH_4^+ and $CO(NH_2)_2$, which may also be taken up along with NO_3^- (UNESCO, 1994). The samples were kept in an on-deck incubator equipped with surface seawater flowing facility to maintain the temperature. Immediately after the incubation period samples were filtered under low vacuum (< 75 mm Hg or 0.1 MPa) to retain particulate materials on pre-combusted (4 h @ 400°C) 25 mm GF/F filters, which were dried (@ 60°C over night), sealed and stored in low temperature (–20°C) for subsequent analysis by mass spectrometer. For each incubated sample, aliquots were taken to measure initial (before incubation) and final (after incubation) NO_3^-, NH_4^+, and $CO(NH_2)_2$ concentrations.

The ^{15}N (nitrogen isotope) abundance of the particulate material was measured by stable isotope ratio mass spectrometry (Isoprime Ltd.) in continuous-flow mode, coupled with an EA (Isoprime, Vario Isotope Cube). The external precision on $\delta^{15}N$ was ± 0.12 ‰ (1σ standard deviation) obtained by repeatedly running cellulose (IAEA-CH-3) and ammonium sulphate (IAEA-N1) standards. $\delta^{15}N$ values were reported with respect to air N_2. The reference standard used for normalizing to V-PDB and air N_2 scale are cellulose (IAEA-CH-3) and ammonium sulphate (IAEA-N1). N-uptake rates (for $Na^{15}NO_3$, $^{15}NH_4Cl$ and $CO(^{15}NH_2)_2$) were calculated according to Dugdale and Wilkerson (1986), which accounts for the presence of detrital nitrogen on the filter and is also insensitive to simultaneous uptake of labeled and unlabeled nutrients. Daily N-uptake rates were calculated by multiplying hourly values by 12 (Dugdale et al., 1992). The total N-uptake rate represents the sum of $Na^{15}NO_3$, $^{15}NH_4Cl$ and $CO(^{15}NH_2)_2$ uptake rates; whereas *f*-ratio indicates the ratio of $Na^{15}NO_3$ uptake (new production) to the total N-uptake (new + regenerated production).

In this study, only surface (ca. 0–1 m) water samples, which are expected to experience the strongest seasonal variation, were collected for quantifying nitrogen uptake rates. Thus, even though vertical profiles of other oceanographic variables were recorded simultaneously, discussion of their distribution/variation will be restricted to surface layer only to ensure their usefulness in explaining variation in nitrogen uptake data in the study area.

3 Results and discussion

3.1 Hydrography and nutrients variability

The physical conditions encountered during the cruise were typical of the area and season and was well within the designated criteria (Orsi et al., 1995; Holliday and Read, 1998) for identification of fronts in the study area. SST decreased southward from 13.2°C to 2.0°C (6.03±4.09°C). Steep decline in SST was observed between 43.12–44.59°S (~2.9°C) and between 46.15–49.36°S (~3.4°C) and thereafter it decreased gradually till PF2. The observed changes in SST across the different fronts (STF, SAF, PF1, and PF2) were almost analogous to those reported before (Holliday and Read, 1998). A sharp decrease in SSS (34.98 to 33.68 (33.91±0.34)) was noticed from northernmost station in STF to the next station, coinciding with the southern boundary of the STF, and it remained less variable from there until the PF2 region (Fig. 2(a)). The abrupt decline in salinity towards SAF could be associated with the subtropical convergence, where the warm subtropical water meets subantarctic water. The subantarctic surface water is often located near the southern boundary of the subantarctic frontal zone and is characterized by lower temperature (9°C) and salinity (< 34.0) (Park et al., 1993). During this study, colder and fresher (SST and SSS is < 5°C and < 34.0, respectively) water was encountered while approaching the PF region from the subtropics, implying the presence of Antarctic surface water (Anilkumar et al., 2006, 2015).

Nutrient concentrations showed latitudinal variations (Fig. 2(b)) and were analogous to those reported previously (Jasmine et al., 2009; Gandhi et al., 2012; Tripathy et al., 2015) during austral summer. Concentrations of NO_3^- and SiO_4^{4-} ranged between ND-25.86 (16.62±8.78 μM) and 2.34–36.6 (14.81±13.48 μM), respectively, and increased southward from STF to PF. Whereas NH_4^+, NO_2^-, and PO_4^{3-} remained comparatively stable and varied between 0.05–1.35 (0.74±0.34 μM), 0.67–1.09 (0.87±0.14 μM), and 0.96–2.22 (1.74± 0.46 μM), respectively. It is observed that elevated ambient NH_4^+ concentrations may have a crippling inhibitory effect on NO_3 uptake by phytoplankton, however this is particularly not applicable in the SO, where dissolved iron concentrations are considered limiting to phytoplankton growth (Cochlan, 2008). Moreover, the observed NH_4^+ concentration was not high enough to exert any such impact on NO_3^- uptake. Both NO_3^- ($R^2 = 0.82$, $p < 0.001$) and SiO_4^{4-} ($R^2 = 0.63$, $p < 0.001$) depicted significant negative linear relationship with SST indicating lesser nutrient availability in the warmer northern part of the SO. Similar relationship between NO_3^- concentrations and SST was reported by Savoye et al. (2004). Analysis of nutrient ratios (N:P, N:Si, Si:P) indicated potential N-limited (N:P < 10) conditions (Levasseur and Therriault, 1987) at the STF and SAF. Our data suggests that SiO_4^{4-} was highly limited (5 μM) for the growth of diatoms and/or silicoflagellate (Westwood et al., 2011) in the surface layer of the STF and SAF. Conversely, such stoichiometry was not observed at the PF, indicating favorable milieu for growth of diatoms in this region.

3.2 Light and chlorophyll *a* regime

During the observation period, the daily integrated incident PAR at surface varied between 12.44 and 58.58 (31.13±12.76 $E\cdot m^{-2}\cdot d^{-1}$) with highest intensity at STF attributable to the clear sky condition and latitude effect. Considerably high intensity of PAR was also observed for other locations (Fig. 2(a)), which is comparable with the earlier reports from this region (Jasmine et al., 2009; Tripathy et al., 2014, 2015) and indicates improbability of light-limitation of photosynthesis in this season. Incident daily PAR didn’t show any north-south trend implying its link with the prevailing cloud-cover over the study area during the time of sampling.

Quantitative analysis of phytoplankton biomass indicated that PF1 (0.82 $mg\cdot m^{-3}$) was most productive in terms of Chl *a* followed by SAF (0.71 $mg\cdot m^{-3}$) whereas PF2 was the least productive region. The Chl *a* concentration varied from 0.08 to 0.82 (0.34±0.26 $mg\cdot m^{-3}$) during the observation period. Though macronutrients and light were not limited, low phytoplankton biomass in the PF2 is probably due to grazing pressure exerted by mesozooplankton (Jasmine et al., 2009). Furthermore, the observed high and low Chl *a* at PF1 and PF2 are in accordance with a previous study by Pavithran et al. (2012) which has shown that prevalence of microbial food web at PF1 and conventional food web at PF2 might be responsible for causing the contrasting pattern in Chl *a* distribution.

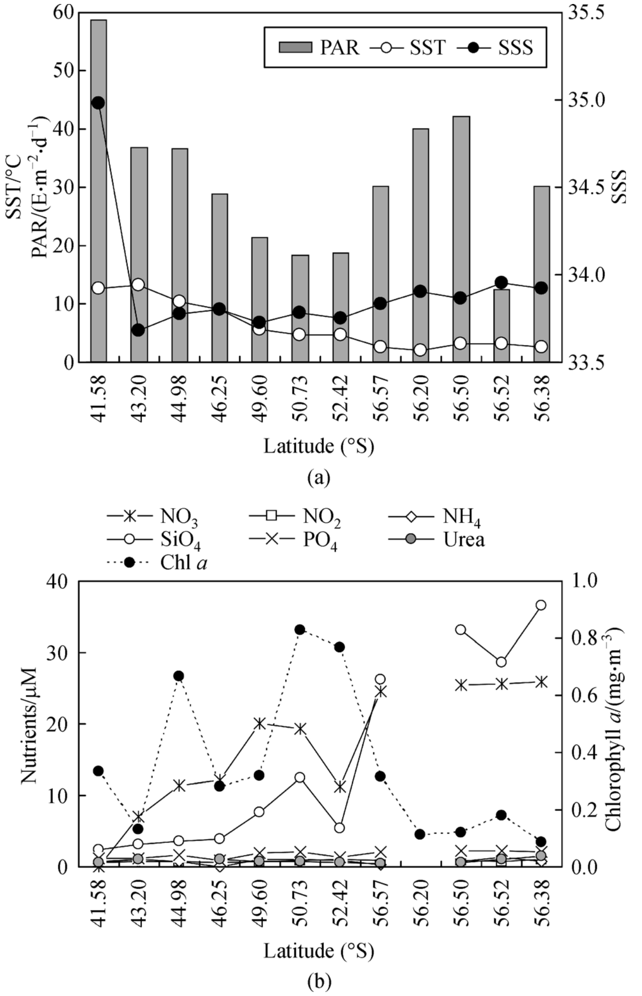


Fig. 2 Variation of (a) SST, SSS and PAR, (b) nutrients and chlorophyll *a* concentrations in the Indian sector of Southern Ocean.

3.3 Nitrogen uptake rates

$Na^{15}NO_3$ uptake rate or new production (NP) increased with latitude (from 0.08 at STF to 0.15 mmol $N\cdot m^{-3}\cdot d^{-1}$ at PF2), with an average value of 0.12±0.02 mmol $N\cdot m^{-3}\cdot d^{-1}$, whereas no systematic spatial variation from north to south was discerned for $^{15}NH_4Cl$ (0.07±0.01 mmol $N\cdot m^{-3}\cdot d^{-1}$) and $CO(^{15}NH_2)_2$ (0.03±0.01 mmol $N\cdot m^{-3}\cdot d^{-1}$) uptake rates, which showed somewhat undulating pattern in the studied locations (Fig. 3(a)). Unlike phytoplankton biomass, spatial variation in nitrogen uptake regime was small. NP was higher in PF region than the subtropics. $Na^{15}NO_3$ uptake rate was higher than $^{15}NH_4Cl$ and $CO(^{15}NH_2)_2$ uptake rates, except at the STF where it was slightly less than the $^{15}NH_4Cl$ uptake rate, while $^{15}NH_4Cl$ uptake rate was always higher than $CO(^{15}NH_2)_2$ uptake rate (Fig. 3(a)) at all the stations (latitude-wise uptake rates data are shown in Table 1) indicating the predominance of NP in this region (Joubert et al., 2011). From STF to PF the contribution (%) of NP and RP varied from 44.27–59.13 (53.12±5.03) and 40.87–55.73 (46.88±5.03), respectively signifying nearly similar contributions to the total productivity, which is analogous to earlier studies (Gandhi et al., 2012; Prakash et al., 2015).

Total N-uptake rates ranged from 0.18 to 0.28 and averaged around 0.22 (±0.04) mmol $N\cdot m^{-3}\cdot d^{-1}$ ($n = 12$), where the numbers in parenthesis represents spatial variability. Minimal total N-uptake rate was observed at the STF (0.18 mmol $N\cdot m^{-3}\cdot d^{-1}$) and increased southward similar to the pattern of $Na^{15}NO_3$ uptake rate, whereas maximum uptake rate (0.28 $mmol\cdot m^{-3}\cdot d^{-1}$) was noticed at PF2. The graph between $Na^{15}NO_3$ uptake and total N-uptake (Fig. 3(b)) reveals a significant correlation ($R^2 = 0.83, p < 0.001$). From the slope computed from regression analysis it can be inferred that the maximum value of *f*-ratio for the study area was ~0.61 in austral summer, which is comparable to an earlier reported estimate (~0.63) by Prakash et al. (2015). This indicates that the region is capable of exporting up to 61% of the total production to below the euphotic zone if the environmental conditions are conducive. However, an earlier study (Gandhi et al., 2012) has shown higher (78%) export production potential of this region.

The mean specific uptake rates for $Na^{15}NO_3$, $^{15}NH_4Cl$ and $CO(^{15}NH_2)_2$ were 0.009, 0.005, and 0.002 h^{-1}, respectively, which was much higher than the values reported by Mengesha et al. (1998) during the ANTARES

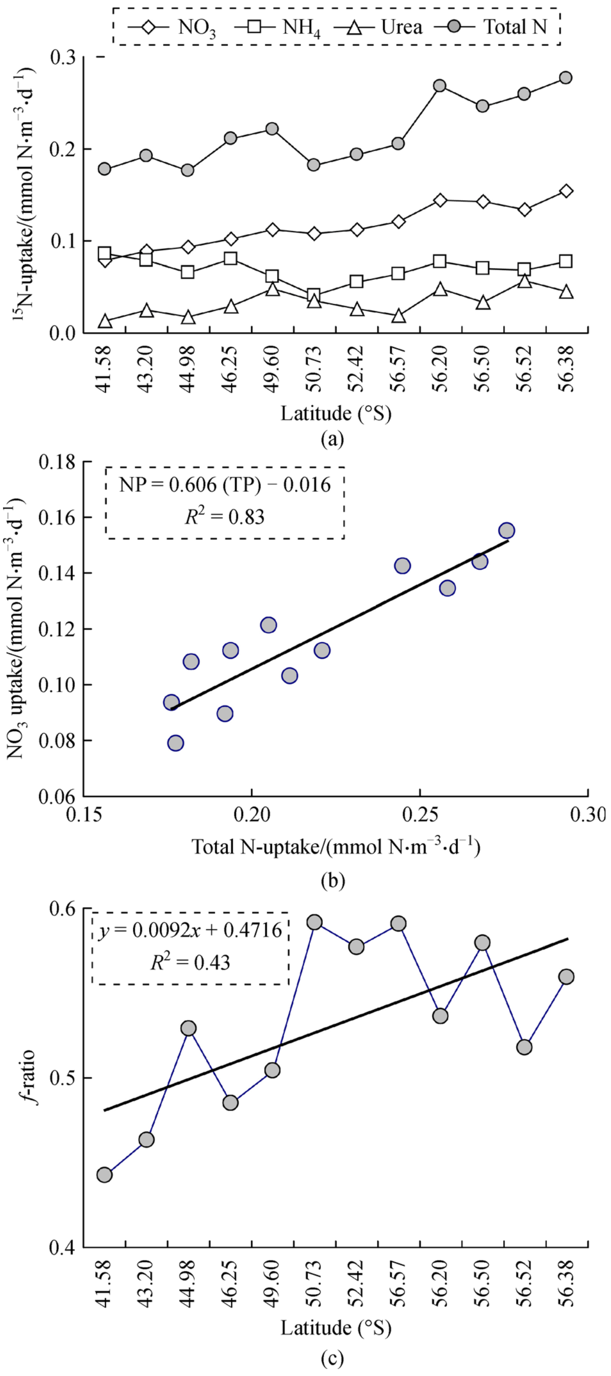


Fig. 3 (a) Latitudinal variation in nitrate, ammonium, urea and total N-uptake rates, (b) relationship between nitrate uptake and total N-uptake (NP and TP symbolize new and total production, respectively), (c) *f*-ratios in the study area.

II cruise along 62°E transect. They observed low mean specific Na^{15}NO$_3$ and ^{15}NH$_4$Cl uptake rates (0.001 and 0.002 h^{-1}, respectively; CO(^{15}NH$_2$)$_2$ uptake was not reported) and suggested that lower Na^{15}NO$_3$ uptake rates were indicative of prevailing regenerated production in summer and reported high specific Na^{15}NO$_3$ uptake rates (indicative of predominant new production) during spring. Nonetheless, our observations were comparable to the specific Na^{15}NO$_3$ (0.005 h^{-1}) and CO(^{15}NH$_2$)$_2$ (0.001 h^{-1}) uptake rates reported by Prakash et al. (2015). The discrepancies between the observed values and reported values (previous studies) could be due to the fact that, we report only surface layer observations whereas the earlier studies have taken depth profiles into consideration.

3.4 Variation in *f*-ratio

The *f*-ratio varied from 0.44 to 0.59 (Table 1) and averaged 0.53±0.05. At SAF the *f*-ratio slightly decreased, but subsequently increased southward till PF2. Overall, the *f*-ratio increased with latitude (i.e. with decreasing temperature and increasing NO$_3^-$ concentration) (Fig. 3(c)). The observed average *f*-ratio (0.53) was consistent with the previous reports from the Indian sector (Gandhi et al., 2012; Prakash et al., 2015), the Pacific (Savoye et al., 2004), and the Atlantic (Joubert et al., 2011), and highlights the potential ability of SO in significant export production (Olson, 1980) and global carbon cycle. Compared to the subtropics, most of the PF stations showed higher *f*-ratios (~0.6); however these values are significantly lower than those reported by Collos and Slawyk (1986) for the Indian sector along 66.5°E, and higher than those reported by Mengesha et al. (1998) during austral summer. Relatively, higher *f*-ratios in PF region could be due to the supply of micro/limiting-nutrients by melting of sea ice during spring season (Sambrotto and Mace, 2000); whereas, low or unavailability of NO$_3^-$ could be the reason for the relatively higher regenerated production and hence slightly low *f*-ratios at STF (Savoye et al., 2004; Joubert et al., 2011). Additionally, the reason for comparatively low *f*-ratio at STF could be silicate-limitation, which plays an important role in controlling Na^{15}NO$_3$ uptake rates in diatoms (Sambrotto and Mace, 2000).

Comparisons of *f*-ratios from the present and previous studies (Fig. 4) were conducted to identify any temporal and/or seasonal variation in different zones. Results indicated that the observed values are well within the reporting range and consistent with the values recorded by Gandhi et al. (2012) and Prakash et al. (2015); however, were higher than the values observed during late summer, which was attributed to declining phytoplankton community and inhibitory effect of NH$_4^+$ on NO$_3^-$ uptake by phytoplankton (Mengesha et al., 1998). Overall, we observed comparatively higher NH$_4^+$ concentrations, but did not notice any decline in Na^{15}NO$_3$ uptake (*f*-ratio). Higher *f*-ratio (0.75±0.08) was reported by Mengesha et al. (1998) during the spring when influx of melt water-induced trace nutrients (i.e., Fe, Cu etc.) are found in the SO (Sambrotto and Mace, 2000). Conversely, drastically lower *f*-ratios (0.09±0.04) have been reported from the vicinity of Prince Edward Islands (Thomalla et al., 2011), and Crozet Islands (Sanders et al., 2007), and the observed

Table 1 Latitude-wise distribution in sea surface temperature (SST) and salinity (SSS), photosynthetically active radiation (PAR), nitrate (NO_3), chlorophyll *a* (Chl *a*), N-uptake rates (ρ) and *f*-ratio in surface waters of different sampling locations in the Indian sector of Southern Ocean

stn. no	Date of sampling	Lat. (°S)	Long. (°E)	SST/(°C)	SSS	PAR/($E\cdot m^{-2}\cdot d^{-1}$)	NO_3/(μM)	Chl *a*/($mg\cdot m^{-3}$)	ρNO_3	ρNH_4	ρNH_2	Total N-uptake rates	*f*-ratio
									/($mmol\ N\cdot m^{-3}\cdot d^{-1}$)				
1	30-01-2013	41.35	57.45	12.5	34.98	58.58	0	0.33	0.079	0.086	0.014	0.178	0.44
2	20-02-2013	43.12	57.27	13.2	33.68	36.76	7.04	0.13	0.089	0.079	0.025	0.193	0.46
3	31-01-2013	44.59	57.32	10.3	33.77	36.56	11.40	0.66	0.093	0.065	0.018	0.176	0.53
4	19-02-2013	46.15	57.20	8.9	33.80	28.72	12.20	0.28	0.103	0.080	0.029	0.212	0.48
5	02-02-2013	49.36	57.31	5.5	33.72	21.27	20.02	0.31	0.112	0.061	0.049	0.222	0.50
6	15-02-2013	50.44	50.29	4.5	33.78	18.31	19.30	0.82	0.108	0.040	0.034	0.182	0.59
7	14-02-2013	52.25	48.08	4.5	33.75	18.59	11.25	0.76	0.112	0.055	0.027	0.194	0.58
8	05-02-2013	56.34	57.39	2.5	33.83	30.19	24.61	0.31	0.121	0.065	0.019	0.205	0.59
9	08-02-2013	56.12	55.55	2.0	33.90	40.01	*	0.11	0.144	0.077	0.048	0.269	0.54
10	09-02-2013	56.30	52.31	3.0	33.86	42.15	25.51	0.12	0.142	0.070	0.033	0.245	0.58
11	11-02-2013	56.31	49.42	3.0	33.95	12.44	25.67	0.18	0.134	0.068	0.056	0.259	0.52
12	12-02-2013	56.23	48.00	2.5	33.92	30.02	25.86	0.08	0.155	0.077	0.045	0.277	0.56

*No data.

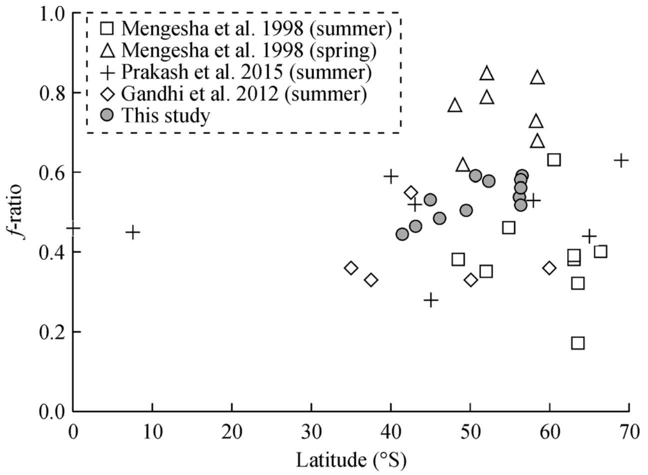
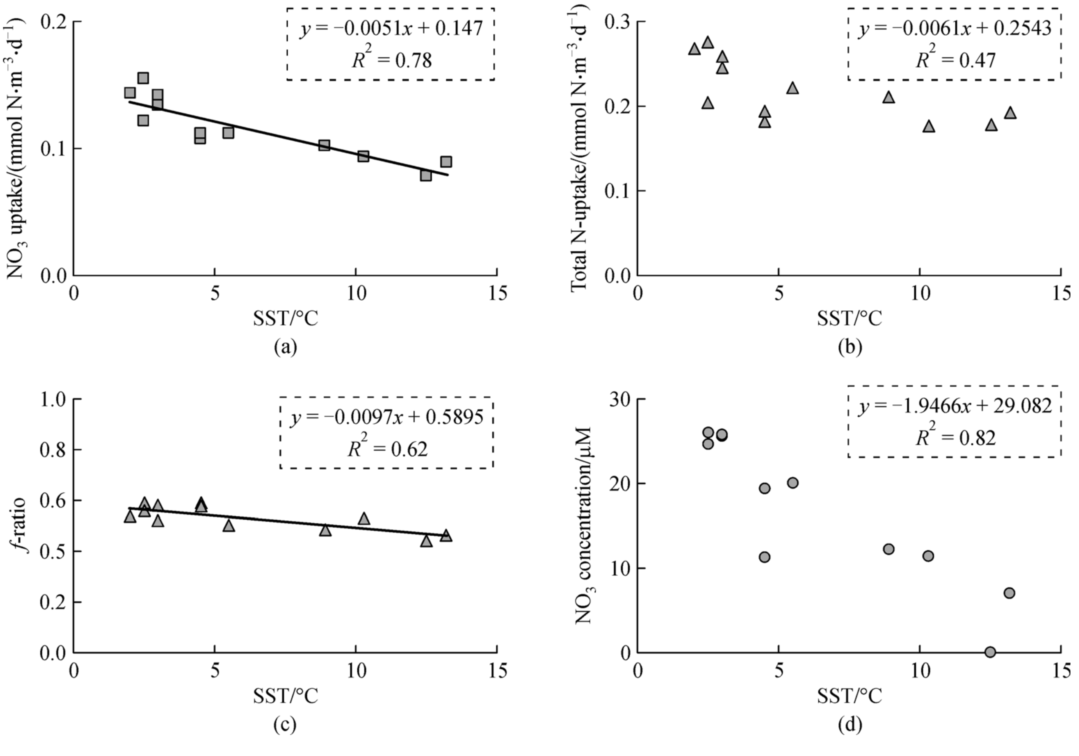


Fig. 4 Comparative account of average *f*-ratios observed during the present study and earlier studies in the Indian sector of Southern Ocean.

variability could be due to geographical differences (Lucas et al., 2007). Moreover, the comparison of *f*-ratios indicates its significant spatial and temporal variations during different seasons, attributable to the underlying dominant factors governing growth and maintenance of phytoplankton, thereby their uptake rate (Mengesha et al., 1998). Considering this variability, more *in situ* measurements on larger spatiotemporal scales are required to understand biogeochemistry of this region. From this study it can be inferred that the average *f*-ratio (0.53) implies potentially near equal contributions by $Na^{15}NO_3$ (NP) and $^{15}NH_4Cl$/$CO(^{15}NH_2)_2$ (RP) to the total productivity, and that a large portion of it may be exported out of the surface layer (Olson, 1980; Joubert et al., 2011) in the study area. Olson (1980) observed average *f*-ratio in the Scotia Sea (0.54) in spring and Ross Sea (0.40) in summer. In this study, the enrichment (% increase) of NH_4^+ and $CO(NH_2)_2$, varied from 7.3% to 30.76% (13.96±6.3%) and 6.94% to 20.22% (13.17±4.37%), respectively. According to Reay et al. (2001) the increase in NH_4^+ concentration beyond 10% increment will lead to underestimation of *f*-ratio. Thus, the observed mean *f*-ratio might be slightly underestimated, as the mean % increase of tracers for NH_4^+ and $CO(NH_2)_2$ was < 15%.

3.5 Effect of temperature on nitrogen uptake and *f*-ratio

Influence of temperature on N composition in phytoplankton cell (Thompson et al., 1992), and N uptake rates (Lomas and Glibert, 1999) is well documented. However, these effects may be subtler than those on growth and photosynthesis. It is likely that they all contribute to species succession and dominance, and thus needs consideration while studying the phytoplankton and N dynamics of the SO (Cochlan, 2008). In this study, $Na^{15}NO_3$ uptake rate (Fig. 5(a)) and total N-uptake rate (Fig. 5(b)) were significantly correlated to SST ($R^2 = 0.78$, $p < 0.001$ and $R^2 = 0.47$, $p < 0.05$, respectively), whereas,



(a) (b) (c) (d)

Fig. 5 Scatter plots between sea surface temperature and (a) nitrate uptake rates, (b) total N-uptake rates, (c) *f*-ratios, (d) ambient nitrate concentrations in the study area.

f-ratio was significantly correlated (Fig. 5(c)) to SST (R^2= 0.62, $p < 0.05$) and to surface NO_3^- (R^2= 0.48, $p < 0.05$) concentration (figure not shown). Furthermore, surface NO_3^- concentration and SST were strongly correlated (R^2= 0.82, $p < 0.001$) (Fig. 5(d)). Such a relationship between *f*-ratio and temperature has been previously reported by Savoye et al. (2004) in the Australian sector during austral spring. Based on a simple ecosystem model Laws et al. (2000) have shown differential responses of autotrophic and heterotrophic (bacteria) organisms to temperature. There are several other likely reasons for its occurrence such as variation in phytoplankton community responses (their physiological characteristics, such as preference for NO_3^- or NH_4^+ could vary considerably even within the groups), correlations of mixed layer-induced light levels with temperature, NH_4^+ inhibition of NO_3^- uptake (Lomas and Glibert, 1999) etc. SST of the SO (south of the PF) ranges from –1.8°C (freezing point of seawater) to 5°C in the summer (e.g., Neori and Holm-Hansen, 1982), but majority of our knowledge on the effects of temperature on phytoplankton N-uptake comes from experiments conducted at temperatures far higher than this range and, thus may not be directly applicable to polar assemblages. However, experiments in the Scotia Sea (Olson, 1980) showed that phytoplankton were not adapted for optimal N-uptake at their *in situ* temperature (0°C), but their uptake rates increased with 5°C –10°C increases in temperature. A study (Priscu et al., 1989) also suggests that at low *in situ* temperatures (e.g., –1.9°C), consumption of N would be limited by transport into the cell, not by intracellular assimilation because of the differential temperature characteristics between N transport and assimilation (Cochlan, 2008). Though we noticed an increasing trend in $Na^{15}NO_3$ and total N-uptake with decreasing SST (minimum SST = 2.0°C) in the study area; there is a possibility that the uptake rates could decline if the temperature approaches freezing point of seawater, which is common in coastal Antarctica except during austral spring and summer.

4 Summary

This study presents further information on *in situ* surface nitrogen uptake rates and *f*-ratio (exportable production) for the Indian sector of the SO during austral summer. Results indicated potentially near equal contributions by new production (53%) and regenerated production (47%) to the total productivity by phytoplankton. Comparison of average *f*-ratio with the previous reports implies that the seasonal variations in the *f*-ratios are much higher than its inter-annual variations, and this region is capable of exporting up to 61% of the total production to the ocean interior if the environmental settings are conducive (i.e., supply of limiting nutrients). Increase in the N-uptake rates (subtropics to polar front region) with decreasing temperature suggest the significant role of SO in draw-down of atmospheric CO_2. Furthermore, the observed moderately high average *f*-ratio (0.53) is indicative of the fact that the SO plays a pivotal role in the global ocean-atmosphere carbon balance despite its overall HNLC status. Considering the significance of *f*-ratio (proxy for the biological pump); further studies, involving extensive *in situ* measurements, on larger spatiotemporal scale is a prerequisite to understand biogeochemistry of this region.

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