

Phytoplanktonic nutrient utilisation and nutrient signature in the Southern Ocean

L. Goeyens^{a,*}, M. Semeneh^a, M.E.M. Baumann^b, M. Elskens^a, D. Shopova^a,
F. Dehairs^a

^a *Vrije Universiteit Brussel, Laboratorium voor Analytische Chemie, Pleinlaan 2, B-1050 Brussels, Belgium*

^b *Alfred Wegener Institut für Polar- und Meeresforschung, Postfach 120161, D-27515 Bremerhaven, Germany*

Received 15 August 1995; accepted 15 October 1996

Abstract

The separation in Southern Ocean provinces of silicate excess at nitrate exhaustion and of nitrate excess at silicate exhaustion was already introduced by Kamykowski and Zentara (Kamykowski, D., Zentara, S.J., 1985. Nitrate and silicic acid in the world ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 26, 47–59; and Kamykowski, D., Zentara, S.J., 1989. Circumpolar plant nutrient covariation in the Southern Ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 58, 101–111) and our investigations of the silicate to nitrate uptake ratios confirm the earlier distinction. Oligotrophic antarctic waters mainly exhibit proportionally higher silicate removal what induces a potential for nitrate excess. The nitrogen uptake regime of such areas is characterised by low absolute as well as specific nitrate uptake rates throughout. Maximal values did not exceed $0.15 \mu\text{M d}^{-1}$ and 0.005 h^{-1} , respectively. Corresponding *f*-ratios ranged from 0.39 to 0.86. This scenario contrasts strikingly to the more fertile ice edge areas. They showed a drastic but short vernal increase in nitrate uptake. Absolute uptake rates reached a maximum value of $2.18 \mu\text{M d}^{-1}$ whereas the maximal specific uptake rate was 0.063 h^{-1} . In addition to an optimal physical environment for bloom development, accumulation of ammonium stimulated nitrate uptake in a direct or indirect way. Since ammonium build-up in surface waters traces enhanced remineralisation, release of other essential compounds during degradation of organic matter might have been the main trigger. This peak nitrate utilisation during early spring led to the observed potential for silicate excess. With increasing seasonal maturity the nitrate uptake became inhibited by the presence of enhanced ammonium availability (up to 8% of the inorganic nitrogen pool), however, and after a short period of intensive nitrate consumption the uptake rates drop to very low levels, which are comparable to the ones observed in the area of nitrate excess at silicate exhaustion.

Résumé

La distinction entre différents domaines de l'Océan Austral, basée sur l'étude des rapports élémentaires nitrate: silicate, introduite par Kamykowski et Zentara (Kamykowski, D., Zentara, S.J., 1985. Nitrate and silicic acid in the world ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 26, 47–59; et Kamykowski, D., Zentara, S.J., 1989. Circumpolar plant nutrient covariation in the Southern Ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 58, 101–111), se révèle en bonne conformité avec nos calculs concernant les rapports d'assimilation de ces nutriments. Les eaux oligotrophes antarctiques présentent en général une consommation prononcée en silicates par rapport aux nitrates ce qui induit un potentiel pour un

* Corresponding author. Tel.: +32-3-629-3263; Fax: +32-2-629-3274; E-mail: Leo.Goeyens@ihe.be

excès relatif en nitrates. Le régime d'assimilation de l'azote dans ces zones est caractérisé par de faibles taux d'absorption des nitrates: les valeurs maximales des vitesses absolues et spécifiques ne dépassant guère 0.15 μM par jour et 0.005 par heure. Les valeurs du rapport f varient entre 0.39 et 0.86. Cette situation est fortement différente de celle observée dans les zones fertiles en bordure des glaces. Au début du printemps, ces dernières sont caractérisées par une augmentation significative, quoique de courte durée, des taux d'absorption des nitrates. Les vitesses absolues maximales sont de l'ordre de 2.18 μM par jour et les vitesses spécifiques correspondantes de 0.063 par heure. Pendant cette période, en plus de conditions physiques optimales pour le développement du bloom, nous observons une convergence entre l'accumulation d'ammonium et l'accroissement des taux d'absorption des nitrates. Puisque la production d'ammonium dans les eaux de surface reflète l'activité hétérotrophique, il est possible que des composés libérés par la dégradation de la matière organique stimulent l'utilisation des nitrates par le phytoplancton. La consommation prononcée en nitrates, qui en résulte, conduit d'autre part à un excès relatif en silicates. Au cours de l'évolution saisonnière, les taux d'absorption de nitrate diminuent toutefois progressivement en relation avec une augmentation de la disponibilité en ammonium (jusqu'à 8% du pool d'azote inorganique). Après une courte période d'utilisation intensive, les taux d'absorption de nitrates tendent alors vers des valeurs comparables à celles observées dans les zones oligotrophes. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Southern Ocean; silicate excess area; nitrate excess area; nitrate uptake rate; f -ratio

1. Introduction

1.1. Historical milestones

Pleading for more intimate co-operation between specialists of different marine sciences, Sverdrup (1955) stressed that nutrient renewal in the ocean's upper layer occurs by physical processes such as upwelling, turbulent diffusion and convection, and that productivity is intrinsically linked to the rate at which nutrients become available. Hence, he expected high productivity in the Antarctic, although as yet it was not known if these conclusions were valid. Recent research gave rise to a re-examination of this traditional view of antarctic richness.

However, Hart (1934) recognized already the disequilibrium between nutrient abundance and paucity of phytoplankton development in antarctic waters. Even when present-day oceanographic and antarctic investigations have scored significant success, his contention

... this condition indicates control of something other than nitrate and phosphate, but the nature of this control is at present unresolved...

still triggers new research efforts. He identified iron as one of the possible limiting elements but, aware of the complexity of marine systems, he also emphasized that plankton production is always governed by several interdependent factors.

Later studies concluded that the productivity level in antarctic waters can vary by approximately two orders of magnitude, approaching that of oligotrophic regions in the open ocean and displaying the earlier recognized richness in the vicinity of the coasts only. Additionally, the latter studies promoted the new paradigm of the antarctic food web, including the pico-, nano- and microplankton producers and predators as well as bacterial secondary producers (El-Sayed, 1987).

1.2. Recent developments

The persistence of excess nutrients at the surface of the Southern Ocean connotes regulation of autotrophic processes by something other than nutrient availability. The chlorophyll and productivity levels are markedly lower than expected if all inorganic nitrogen had been assimilated; the autotrophic development is seemingly suppressed.

According to the definition introduced by Eppley and Peterson (1979), new production is quantitatively equivalent to the organic material exported from the production system of the euphotic layer without its running down. This definition of new production is also termed net community production (Minas et al., 1986). Since new production and/or net community production are fuelled by nutrients in the euphotic layer, the rate of new production (mainly nitrate based production) is highly relevant to the

condition of nutrient excess observed in antarctic waters. Cullen (1991) published a comprehensive discussion of the different hypotheses invoking impaired nitrogen uptake, including low temperature effects (Neori and Holm-Hansen, 1982; Jacques, 1983), shift-up of nitrate assimilation (Dugdale and Wilkerson, 1991) and minor nutrient limitation (Martin and Fitzwater, 1988; Martin, 1990; de Baar, 1994).

The observation of intensive new production and concomitantly decreased ambient nitrate in the wake of the retreating pack ice led to the introduction of nitrate depletions as a convenient tool for estimating the integrated nitrate uptake since the onset of the growth season (Le Corre and Minas, 1983; Jennings et al., 1984). Elevated nitrate depletions mainly characterise the stabilised marginal ice zone (MIZ) and coastal and continental shelf zone (CCSZ) environments, whereas open ocean zones (OOZ) exhibit significantly less phytoplankton development and limited nutrient removal (Tréguer and Jacques, 1992). Furthermore, elaborated pattern analyses of the nitrate vs. silicate regressions (Kamykowski and Zentara, 1985, 1989) reveal that waters south of the Subtropical Convergence generally show a potential for nitrate excess at silicate depletion, whereas the opposite holds for waters south of the Antarctic Divergence. Nitrate excess exhibits a declining gradient from the Polar Front towards higher latitudes, which is continued by areas of silicate excess in the Weddell and Ross Seas.

1.3. Objectives

This paper aims at a better understanding of the nutrient status and corresponding nutrient uptake regime in both the areas of silicate excess at nitrate depletion and of nitrate excess at silicate depletion. We emphasize the role of ammonium, irrespective of influence and weight of numerous other regulating parameters.

2. Methods

Results were obtained during five different cruises: EPOS LEG 2 (20 November 88 to 7 January 89),

ANTARKTIS IX/2 (14 November to 30 December 1990) and ANTARKTIS X/7 (3 December 1992 to 22 January 1993) aboard RV *Polarstern*, MARINE SCIENCE VOYAGE 6 (3 January to 20 March 1991) aboard RV *Aurora Australis* and ANTARES 2 (26 January to 23 March 1994) aboard RV *Marion-Dufresne*.

Nutrient concentrations, particulate matter concentrations and general physico-chemical parameters are available in three cruise reports (EPOS LEG 2, 1991; Goeyens et al., 1991; Fiala, 1995) and several unpublished workbooks distributed on computer disks.

We describe the nutrient signature of the upper layer in terms of nutrient stocks and availabilities. Nutrient stocks are defined as depth integrated amounts in the upper layer, the section of the water column confined between the surface and temperature minimum layers. Similarly, particulate matter stocks are defined as depth integrated amounts of particulate nitrogen (PN) and chlorophyll. Availabilities of nitrogenous nutrients are defined as their percentage in the total dissolved inorganic nitrogen pool.

The nutrient uptake regime in the surface layer is determined by nutrient depletions, which represent an estimate of seasonally integrated nutrient removal in the upper layer down to the remnant winter layer or temperature minimum layer (Jennings et al., 1984), and by absolute and specific nitrogen uptake rates obtained from ^{15}N incubation experiments. In accordance with Dugdale and Wilkerson (1986) and Collos (1987), specific nitrogen uptake rates (ν , in h^{-1}) are defined as nutrient taken up per unit of particulate nitrogen and per unit of time, whereas absolute uptake rates (ρ , in $\mu\text{mol l}^{-1} \text{h}^{-1}$) are the product of specific uptake rates and PN concentration:

$$\rho_{\text{N}} (\mu\text{mol l}^{-1} \text{h}^{-1}) = \nu_{\text{N}} (\text{h}^{-1}) \times \text{PN} (\mu\text{M}).$$

Three assumptions are implicit in the use of nutrient depletions: (1) vertical homogeneity characterizes the ice covered winter water, (2) lateral and vertical mixing remain negligible and (3) melting of nutrient-poor pack ice does not obscure the signal of nutrient utilisation. A detailed discussion of the hypotheses is given by Goeyens et al. (1995). Addition-

ally, nitrate uptake rates were evaluated by an inverse technique (Shopova et al., 1995). For this purpose we applied a vertical advection–diffusion model; the equation of conservation of nitrate is:

$$\partial_t[\text{NO}_3] = \partial_z(K\delta_z[\text{NO}_3]) - w\partial_z[\text{NO}_3] + J = 0,$$

with $[\text{NO}_3] = [\text{NO}_3](z,t)$ the ambient nitrate concentration, $K(z,t)$ the vertical mixing coefficient, $w(z,t)$ the vertical velocity and $J(z,t)$ the apparent production/consumption rate. Uptake equals consumption in the model. In order to avoid biasing effects of horizontal advection we contrived two ‘average’ stations, the first one representing the MIZ (EPOS LEG 2 stations 157, 158, 164 and 172) and the second one representing the CCSZ (MARINE SCIENCE VOYAGE 6 stations 16, 29, 32 and 48), respectively. The average calculated nitrate uptake rates amount to $0.04 \mu\text{M d}^{-1}$ and to $0.03 \mu\text{M d}^{-1}$, what is in good agreement with the experimental values of 0.06 and $0.04 \mu\text{M d}^{-1}$, obtained from the incubation experiments. Averaging the stations inherently signifies that they are homogeneous (no horizontal advection taking place). The similarity of theoretical and empirical results gives evidence for negligible advection and strengthens the use of nutrient depletions as estimates of time integrated uptake.

Furthermore, reference is made to f -ratios in order to characterise the relative contribution of new nitrogen (mostly nitrate) to primary production (Eppley and Peterson, 1979), and to relative preference indices (RPI), which describe the nitrogen utilisation relative to the nitrogen availability, as defined by McCarthy et al. (1977). Both parameters are common for assessing the interaction between nitrate and ammonium uptake (Dortch, 1990). f -ratios combine preference and inhibition, whereas RPI values must be considered as indicators of preference only. The precision of the RPI is low, however, because of considerable error resulting from the combination of numerous variables.

3. Results

3.1. Nutrient signature

The surface layer of the Southern Ocean is characterised by a ubiquitous abundance of macronutri-

ents, complete exhaustion of nutrient availability being seldom observed. We found variations from 6.6 to $31.8 \mu\text{M}$, 0.66 to $2.17 \mu\text{M}$ and 3.5 to $82.3 \mu\text{M}$ for surface nitrate, phosphate and silicate, respectively. Corresponding stocks (in the upper layer) are slightly less variable; they range from 22.6 to $31.7 \mu\text{M}$, 1.49 to $2.21 \mu\text{M}$ and 24.8 to $83.2 \mu\text{M}$. Summarized descriptive statistics of the nutrient concentrations are given in Table 1. Lowest values correspond to well-sheltered ecosystems in the vicinity of the antarctic continent (MARINE SCIENCE VOYAGE 6, Prydz Bay area), whereas highest values were observed during an early spring transect through the Weddel Sea (ANTARKTIS IX/2). The minimal silicate concentration was measured in waters north of the Polar Front during the ANTARES 2 cruise. Nutrient depletions varied by as much as three orders of magnitude (Table 1). They ranged from 0 to 1574 mmol m^{-2} , from 0 to 86 mmol m^{-2} and from 0 to 1737 mmol m^{-2} for nitrate, phosphate and silicate, respectively. Strikingly high nitrate depletions (NO_3De), occurring mainly in relatively shallow and well-stabilised upper layers of the MIZ and CCSZ, stress the importance of nitrate in shaping the bloom development of the latter environments. Its contribution to primary production as well as its seasonal variability in Southern Ocean MIZ ecosystems was thoroughly investigated in several earlier papers

Table 1
Variability in nutrient signature of Southern Ocean waters

| | <i>n</i> | Mean | Median | Minimum | Maximum |
|----------------------------|----------|------|--------|---------|---------|
| $\text{NO}_3\text{,su}$ | 77 | 25.3 | 26.7 | 6.6 | 31.8 |
| $\text{NO}_3\text{,ul}$ | 66 | 28.0 | 28.1 | 22.6 | 31.7 |
| NO_3De | 66 | 233 | 145 | 0 | 1574 |
| $\text{PO}_4\text{,su}$ | 77 | 1.68 | 1.81 | 0.66 | 2.17 |
| $\text{PO}_4\text{,ul}$ | 66 | 1.89 | 1.90 | 1.49 | 2.21 |
| PO_4De | 66 | 16 | 11 | 0 | 86 |
| Si, su | 77 | 55.3 | 61.1 | 3.5 | 82.3 |
| Si, ul | 66 | 64.4 | 67.8 | 24.8 | 83.2 |
| SiDe | 66 | 406 | 242 | 0 | 1737 |
| $\text{NH}_4\text{Av, su}$ | 77 | 1.32 | 0.84 | 0.15 | 7.55 |
| $\text{NH}_4\text{Av, ul}$ | 61 | 1.71 | 0.97 | 0.15 | 7.32 |

Surface concentrations represent values for the shallowest sampling depth (< 10 m).

Upper layer values are depth weighted averages for the upper water column down to the temperature minimum depth.

Units are μM , mmol m^{-2} and % for surface concentrations, depletions and availabilities, respectively.

(Smith and Nelson, 1990; Cota et al., 1992; Goeyens et al., 1995). Ammonium availability (NH_4Av) shows considerable variability too. On average it represents 1.3% and 1.7% of the dissolved inorganic nitrogen pool in the surface and upper layer, respectively. The values vary between 0.15 and 7.55% in surface water and between 0.15 and 7.32% in the upper layer (Table 1).

Production and/or consumption of nutrients by marine organisms may occur in ratios which differ from the ratios of the ambient concentrations of those nutrients (Fanning, 1992). The author raised already the interesting idea to compare ratios of reaction rates to ratios of upward fluxes of nutrients into the photic layer. In order to unveil the complexity of the Southern Ocean's nutrient uptake regime we compared nitrate and silicate depletions with their availability in the temperature minimum layer. The former parameters depict new production sensu Dugdale and Goering (1967) and diatom production, respectively. The fractions of nitrate and silicate available for phytoplankton nutrition at the onset of the growth season is reflected by the nitrate to silicate ratios in the remnant winter water (temperature minimum layer). They show a relatively constant pattern, whereas the depletion ratios are considerably more variable (Table 2). The mean winter nitrate over winter silicate ratio amounts to $0.46 \text{ mol mol}^{-1}$, ranging from 0.36 to $1.03 \text{ mol mol}^{-1}$. The mean depletion ratio, on the contrary, is $0.78 \text{ mol mol}^{-1}$, with a minimum of $0.11 \text{ mol mol}^{-1}$ and a maximum of $4.05 \text{ mol mol}^{-1}$.

On a plot of specific silicate depletion vs. specific nitrate depletion (the depletions normalised to their

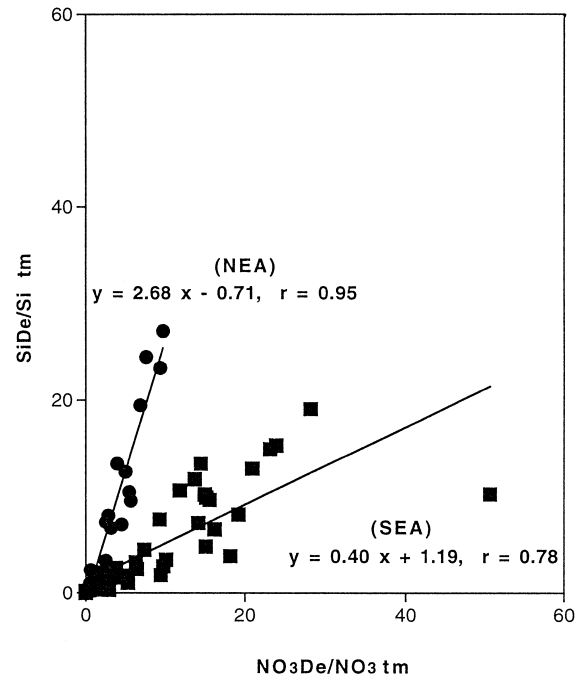


Fig. 1. Specific silicate depletion vs. specific nitrate depletion; the NEA groups all stations with a specific silicate depletion to specific nitrate depletion ratio > 1 , the SEA groups all stations with a specific silicate depletion to specific nitrate depletion ratio < 1 .

corresponding winter concentrations) all data fall apart in two groups (Fig. 1). The first one gathers all stations with normalised silicate depletions exceeding normalised nitrate depletions. Rearrangement of the equation shows that silicate to nitrate depletion ratios which exceed ratios of the winter concentrations correspond with ratios of ambient concentrations which are inferior to the ratios of the winter concentrations:

$$\frac{\text{SiDe}}{\text{NO}_3\text{De}} > \frac{\text{Si, wi}}{\text{NO}_3, \text{wi}} \rightarrow \frac{\text{Si, su}}{\text{NO}_3, \text{su}} < \frac{\text{Si, wi}}{\text{NO}_3, \text{wi}}$$

The significance of this dissimilarity is that silicate is removed from the water at a proportionally higher rate than nitrate. Such a process generates nitrate excess at silicate exhaustion, when persisting for a sufficiently long period. In the second group, on the other hand, we find all stations with proportionally higher specific nitrate depletion, meaning

Table 2

Variability in nutrient concentration ratio for the temperature minimum and upper layers and in depletion ratio

| | <i>n</i> | Mean | Median | Minimum | Maximum |
|--|----------|------|--------|---------|---------|
| $\frac{\text{NO}_3, \text{wi}}{\text{Si, wi}}$ | 65 | 0.46 | 0.42 | 0.36 | 1.03 |
| $\frac{\text{NO}_3, \text{ul}}{\text{Si, ul}}$ | 65 | 0.46 | 0.41 | 0.33 | 1.14 |
| $\frac{\text{NO}_3\text{De}}{\text{SiDe}}$ | 59 | 0.78 | 0.61 | 0.11 | 4.05 |

Units are in mol mol^{-1} .

that those waters carry a potential for silicate excess at nitrate exhaustion:

$$\frac{\text{SiDe}}{\text{NO}_3\text{De}} < \frac{\text{Si, wi}}{\text{NO}_3, \text{wi}} \rightarrow \frac{\text{Si, su}}{\text{NO}_3, \text{su}} > \frac{\text{Si, wi}}{\text{NO}_3, \text{wi}}$$

The distinction between these two groups agrees well with the earlier separation introduced by Kamykowski and Zentara (1985, 1989). It inspired us to develop the concept of separation between two groups, which we denominated as nitrate excess area (NEA) and silicate excess area (SEA), respectively.

3.2. The corresponding nitrogen uptake regime

Differences in SEA values for $\rho\text{-NO}_3$ are more pronounced than the faint variability of NEA values (Table 3). The maximal value observed in the SEA amounts to $2.18 \mu\text{M d}^{-1}$, what is approximately 3 orders of magnitude higher than the observed minimal value and also > 1 order of magnitude higher than the NEA maximal value of $0.15 \mu\text{M d}^{-1}$. Minimal values of both groups are very similar ($\sim 0.007 \mu\text{M d}^{-1}$). Elevated absolute nitrate uptake rates indicate either high specific uptake rates or high biomasses or both (Dugdale and Goering, 1967). Inspection of $\nu\text{-NO}_3$ reveals highest values to occur in the SEA also (Table 3), with a maximum of 0.0625 h^{-1} , exceeding by 1 order of magnitude the observed maximum of the NEA (0.0046 h^{-1}). The ammonium uptake rates fluctuate less. The mean SEA value amounts to $0.07 \mu\text{M d}^{-1}$, ranging from 0.003 to $0.18 \mu\text{M d}^{-1}$. Those values are but slightly

higher than the ones observed in the NEA: the mean ammonium uptake rate is $0.02 \mu\text{M d}^{-1}$, the minimal and maximal uptake rates amount to 0.004 and $0.07 \mu\text{M d}^{-1}$, respectively. Additionally, it is obvious that biomass parameters as PN and chlorophyll a concentrations reach highest values in the SEA (Table 3). Maximal PN and chlorophyll stocks of the SEA are $3.52 \mu\text{M}$ and $2.6 \mu\text{g l}^{-1}$, whereas the maximal values observed in the NEA amount to $1.31 \mu\text{M}$ and $0.9 \mu\text{g l}^{-1}$, respectively.

Seasonal patterns of the nutrient status and productivity regime in the MIZ were given by Cota et al. (1992) and Goeyens et al. (1995). In an attempt to estimate the degree of seasonal progress we introduce the seasonal maturity, a 'subjective' parameter based on the observed NO_3De in the water and on the corresponding nitrate uptake rate. Assuming that the nitrate uptake rate remains constant with time, the NO_3De to $\rho\text{-NO}_3$ ratio can provide an estimate of how long nitrate uptake lasted in that particular water mass. There is abundant evidence for decreasing nitrate uptake rates with seasonal progress, however, and estimates of the ongoing season's duration by NO_3De to $\rho\text{-NO}_3$ ratios are only realistic when the uptake rate remains constant or nearly constant. Referring to the observed seasonal evolution in typical MIZ ecosystems (Goeyens et al., 1995), we assume drastic increase of the nitrate uptake rate during early spring followed by progressive decline till the end of spring to correspond with maximal NO_3De occurring during late spring and minimal values during winter time (Fig. 2). With this statement in mind and the additional hypothesis that a similar scenario holds for the whole seasonally ice covered Southern Ocean we found that a stretched out S-shape curve fits best with the variation of NO_3De to $\rho\text{-NO}_3$ ratios. During the first 50 days we observed a general agreement between NO_3De to $\rho\text{-NO}_3$ ratios and the actual season's duration. The discrepancy increases dramatically after $\rho\text{-NO}_3$ reaches its peak value and becomes asymptotic from the moment on $\rho\text{-NO}_3$ is minimal and NO_3De is maximal. The asymptotic maximum occurs after approximately 117 days. In order to equate the relation between 'erroneous' NO_3De to $\rho\text{-NO}_3$ ratios and 'factual' durations of the growth season we utilised a sigmoid regression of the available data (Fig. 2). Here must be added a word of caution, however.

Table 3

Variability in absolute uptake rate, specific uptake rate, PN concentration and chlorophyll a concentration in both NEA and SEA

| | | <i>n</i> | Mean | Median | Minimum | Maximum |
|-----|--------------------|----------|--------|--------|---------|---------|
| NEA | $\rho\text{-NO}_3$ | 17 | 0.034 | 0.029 | 0.008 | 0.146 |
| SEA | $\rho\text{-NO}_3$ | 44 | 0.282 | 0.108 | 0.007 | 2.179 |
| NEA | $\rho\text{-NH}_4$ | 17 | 0.024 | 0.019 | 0.004 | 0.066 |
| SEA | $\rho\text{-NH}_4$ | 44 | 0.073 | 0.075 | 0.003 | 0.184 |
| NEA | $\nu\text{-NO}_3$ | 17 | 0.0017 | 0.0016 | 0.0003 | 0.0046 |
| SEA | $\nu\text{-NO}_3$ | 44 | 0.0057 | 0.0029 | 0.0002 | 0.0625 |
| NEA | PN | 17 | 0.75 | 0.78 | 0.14 | 1.31 |
| SEA | PN | 44 | 1.37 | 1.11 | 0.06 | 3.52 |
| NEA | chlor a | 17 | 0.21 | 0.19 | < 0.01 | 0.95 |
| SEA | chlor a | 44 | 0.60 | 0.29 | 0.02 | 2.58 |

Units are in $\mu\text{M d}^{-1}$, h^{-1} , μM and $\mu\text{g l}^{-1}$ respectively.

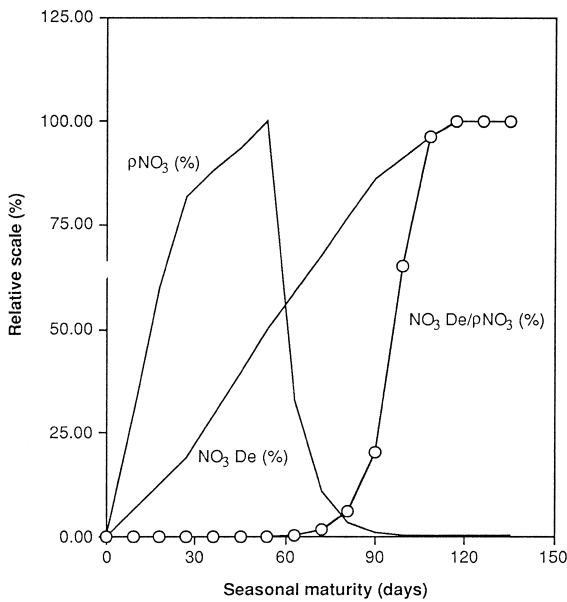


Fig. 2. Ratios of nitrate depletion (NO_3De) to absolute nitrate uptake rate ($\rho\text{-NO}_3$) as 'subjective' parameters of seasonal maturity.

Several factors, other than the nitrate uptake regime, determine the state of seasonal progress in the Southern Ocean (as well as in the World Ocean) and considering nitrate uptake as the only determining parameter, irrespective of other important physical biological and chemical effects, signifies anyhow a serious simplification. Therefore, we prefer to use the NO_3De to $\rho\text{-NO}_3$ ratio merely as an index of the seasonal state, which we have denoted as maturity on a scale of 0 to 100% (± 117 days), rather than to relate the ratio to a duration expressed in days. Not its real value is important for the following discussion; the percentage of maturity was introduced as a useful tool describing seasonal progress in a qualitative way only.

Seasonal variabilities of $\rho\text{-NO}_3$, $\nu\text{-NO}_3$ and PN concentration are shown in Fig. 3a, b and c, respectively. Both the absolute and specific uptake rates exhibit similar patterns with little seasonal variation in the NEA in contrast to enhanced variation in the SEA. The distinct pattern in the SEA is mainly evidenced by significantly increased values at the beginning of the productivity season, an observation that has already been described (Smith and Nelson, 1990; Cota et al., 1992; Goeyens et al., 1995). The

PN values are somewhat scattered, on the contrary, with high values occurring during the earliest phase as well as at greater seasonal maturity.

4. Discussion

Obviously, we face a twofold track in the course of Southern Ocean waters. On one hand, a total lack of increased ecosystem's capacity to ingest nitrate into its structure depicts the NEA. All NEA stations being situated in the vicinity of the northernmost boundary of the winter ice extension fit well with the definition and functional characteristics of the Ooz (Tréguer and Jacques, 1992). Biomass build-up and primary production of typical Ooz ecosystems were found to be close to those of oligotrophic waters. Especially the Indian Ocean sector, which was extensively sampled during the last decades, showed poor chlorophyll contents and low carbon assimilation rates (Jacques and Minas, 1981; Jacques, 1989). Observed biomass accumulations and primary production levels in the Scotia Sea were somewhat higher, as illustrated by the comprehensive comparison of literature data by Mathot et al. (1992). On the other hand, the SEA clearly shows enhanced but short-lived capacity to remove nitrate. The latter environment, profiting by a physical trigger like upper layer stabilisation in combination with nutrient abundance (Table 1), exhibits a potential of dense phytoplankton development, generating considerable nitrate depletion but never or seldom complete exhaustion of the nitrate pool. The SEA groups typical MIZ and CCSZ stations. It is well-known that oceanographic processes at the ice edge stimulate primary production: satellite observations provided clear evidence for a girdle of enhanced phytoplankton standing crops along the ice edges (Sullivan et al., 1988). Differences in primary production between the MIZ and Ooz can easily exceed two orders of magnitude (Smith and Nelson, 1986).

A key parameter shaping the difference between NEA and SEA is the contrasting nitrate uptake regime of both ecosystems (Fig. 3a). Observed low and seasonally constant absolute nitrate uptake rates in the NEA (mean value = $0.03 \mu\text{M d}^{-1}$, Table 3) could never induce complete exhaustion of the available nitrate pool. At a constant uptake rate of 0.03

$\mu\text{M d}^{-1}$ and with complete absence of any refilling by physical processes as diffusion and advection or by biochemical processes as nitrification, complete removal of available nitrate would not happen before approximately 3 years. This unrealistic view stresses how limited nitrate uptake in NEA waters is. On the other hand, the observed nitrate uptake rates in the SEA were remarkably higher at least during the start of the productive season but did not lead to exhaustion of the nitrate pool either. The maximal absolute uptake rate ($2.2 \mu\text{M d}^{-1}$, Table 3) could easily reduce the ambient nitrate stock to undetectable levels within a period of less than 1 month, but this scenario did not occur. Long before complete exhaustion of available nitrate uptake rates had decreased to low values, comparable to the ones of the NEA. The similarity of the minimal nitrate uptake

rates in both systems strengthens the importance of highly increased nitrate uptake rates, observed during the early growth phase, for the configuration of silicate excess at nitrate depletion. The absence of such a vernal increase in the nitrate uptake capacity of NEA ecosystems, on the contrary, induces a potential for nitrate excess at silicate depletion.

The separation between both groups is paralleled by the variability in specific nitrate uptake rate (Table 3, Fig. 3b). Dugdale and Wilkerson (1991) recognized low specific nitrate uptake rates as a common feature of HNLC provinces such as the equatorial Pacific, the sub-arctic Pacific and most notably the Southern Ocean. The 'traditional' values of specific nitrogen uptake rates (Dugdale and Goering, 1967) are essentially normalized to the PN trapped on glass fiber filters, which can include non-phyto-

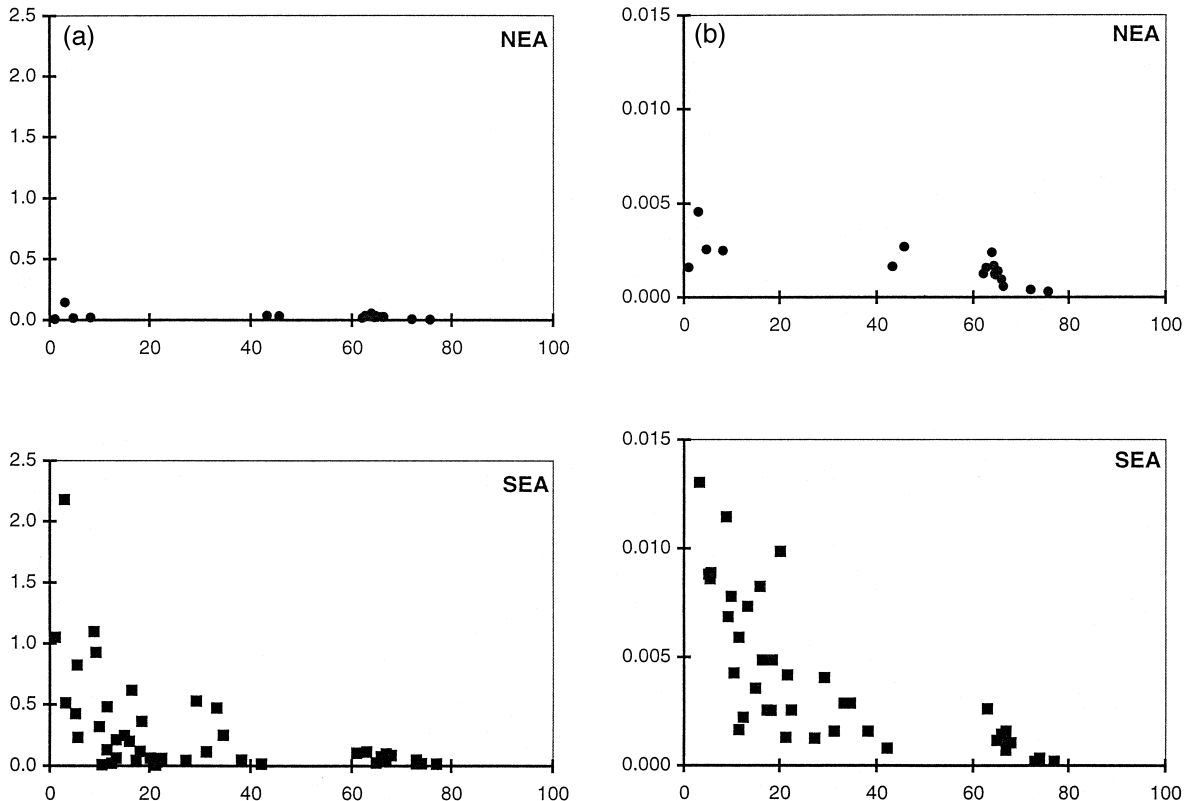


Fig. 3. (a) Absolute nitrate uptake rate (ρNO_3 , $\mu\text{M d}^{-1}$) vs. seasonal maturity (%) in NEA (upper graph) and SEA (lower graph) waters respectively. (b) Specific nitrate uptake rate ($v\text{-NO}_3$, h^{-1}) vs. seasonal maturity (%) in NEA (upper graph) and SEA (lower graph) waters respectively. (c) Particulate nitrogen concentration (PN, μM) vs. seasonal maturity (%) in NEA (upper graph) and SEA (lower graph) waters, respectively.

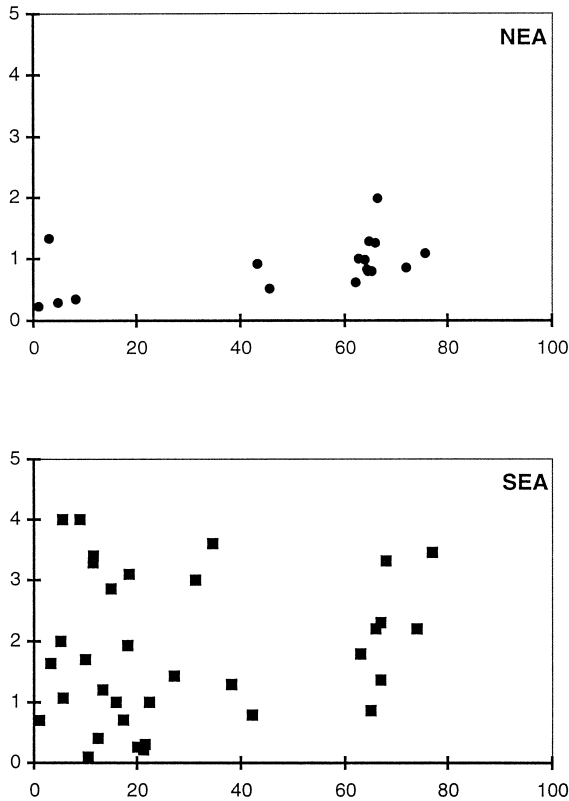


Fig. 3 (continued).

planktonic and detrital PN. On many occasions, phytoplankton made up a minor fraction of the planktonic biomass only (Fiala et al., 1998) and when this occurred PN-specific uptake rates underestimated true phytoplankton-specific nutrient uptake. Main question for this study is therefore: is there a significant difference between the highest and lowest observed values? In an attempt to evade artefacts due to the presence of non-phytoplanktonic nitrogen we compared PN-specific uptake rates with chlorophyll-specific uptake rates and with uptake rates normalized to phytoplankton particulate nitrogen (PPN). Chlorophyll-specific uptake rates are the quotients of absolute uptake rates and the corresponding chlorophyll concentration, units are $\mu\text{mol } \mu\text{g}^{-1} \text{d}^{-1}$. PPN-specific uptake rates are the product of chlorophyll-specific uptake rates and chlor to PPN ratios; units are d^{-1} . PPN values are estimates of the phytoplanktonic nitrogen biomass, obtained from cell counts and cell volume determinations, using a conversion factor of six for the POC to PN ratio

(Semeneh, unpublished results). The three expressions show a consistent pattern with slightly less pronounced extremes for chlorophyll-specific uptake rates in the SEA though (Fig. 4a and b). Hence, we feel confident that the separation between highest and lowest uptake rates as observed in the SEA reflects significantly different situations. Moreover, a regression analysis of $\rho\text{-NO}_3$ vs. $\nu\text{-NO}_3$ and PN reveals that the variability in absolute uptake rate must be seen as a result of variable specific uptake rates rather than variable biomasses. Notwithstanding predominant influence of the specific uptake rate, the results clearly show that biomass and possibly other parameters can not be disregarded for the variability in ρ (Table 4). This holds especially for the SEA data.

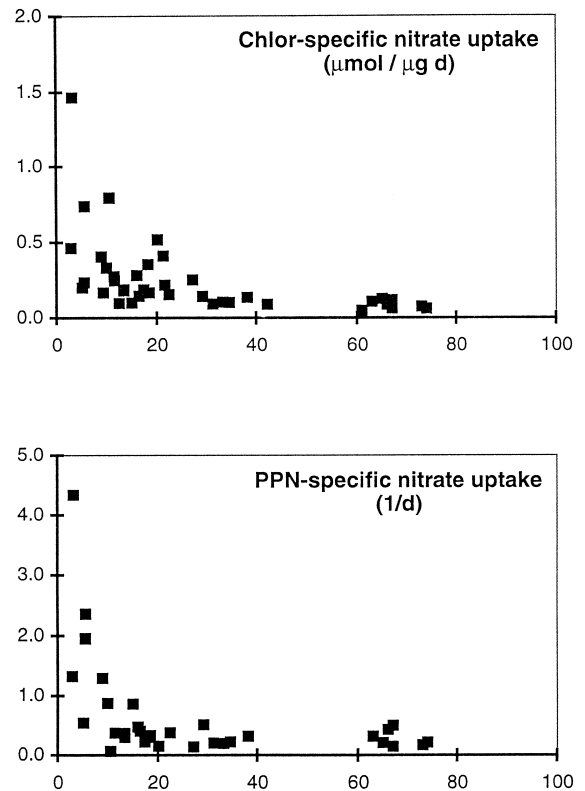


Fig. 4. Chlor-specific nitrate uptake ($\mu\text{mol } \mu\text{g}^{-1} \text{d}^{-1}$, upper graph) and PPN-specific nitrate uptake (d^{-1} , lower graph) vs. seasonal maturity in SEA waters.

Table 4

Regression analyses of ρ -NO₃ vs. ν -NO₃ and PN values; units are in $\mu\text{M d}^{-1}$, h^{-1} and μM , respectively

| | | <i>n</i> | Slope | Intercept | <i>R</i> ² | <i>p</i> | <i>F</i> |
|-----|--|----------|-------|-----------|-----------------------|----------|----------|
| NEA | ρ -NO ₃ vs. ν -NO ₃ | 17 | 24.95 | -0.01 | 0.66 | 0.0001 | 25.52 |
| NEA | ρ -NO ₃ vs. PN | 17 | 0.03 | 0.01 | 0.16 | 0.1129 | 2.84 |
| SEA | ρ -NO ₃ vs. ν -NO ₃ | 44 | 79.02 | -0.06 | 0.56 | 0.0001 | 47.49 |
| SEA | ρ -NO ₃ vs. PN | 44 | 0.09 | 0.04 | 0.21 | 0.0028 | 10.21 |

Variable nitrate uptake rates (Fig. 3a and b) in combination with relatively constant ammonium uptake rates (Table 3) lead to important differences in the nitrogen uptake regime of the investigated environments. A summary of the leading parameters is given in Table 5. The average *f*-ratio for the NEA amounts to 0.58 ± 0.13 , the corresponding average RPI value is 43 ± 15 and the minimal value is 10. Similar average values are observed for the SEA; they amount to 0.65 ± 0.21 and to 36 ± 32 for *f*-ratio and RPI, respectively. Both parameters indicate predominance of the nitrate contribution to primary production with rather limited occurrence of *f*-ratios < 0.5 and high demand for ammonium. Despite these similar average values, both areas display important nonuniformity, however, which is mirrored by the distinct seasonal patterns. NEA data exhibit a constant evolution, with absence of very high and very low *f*-ratios and consistent preference for ammonium. On the other hand, the SEA data evidence a marked decrease in *f*-ratio at greater seasonal maturity (Fig. 5) and elevated RPI values in agreement with declining *f*-ratios (Fig. 6). The transience of the latter system confirms the earlier described variability in nitrate uptake. Both the *f*-ratio and RPI are

Table 5

Variability in nitrogen uptake regime of NEA ($n = 17$) and SEA ($n = 44$), respectively

| | | Mean | Median | Minimum | Maximum |
|-----|-----------------|------|--------|---------|---------|
| NEA | <i>f</i> -ratio | 0.58 | 0.60 | 0.39 | 0.86 |
| SEA | <i>f</i> -ratio | 0.65 | 0.64 | 0.25 | 0.98 |
| NEA | RPI | 43 | 43 | 10 | 75 |
| SEA | RPI | 36 | 22 | 2 | 139 |

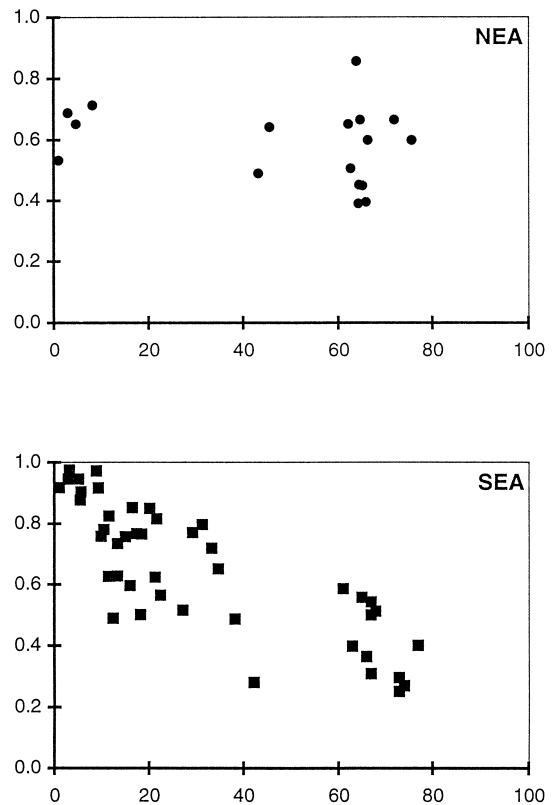


Fig. 5. Comparison of the seasonal variability in *f*-ratio for both the NEA (upper graph) and SEA (lower graph).

unbiased by possible contamination with non-phytoplanktonic PN, since the latter factor is cancelled out in the formulas. Decreasing *f*-ratios primarily reflect the decrease in nitrate uptake at relatively constant ammonium uptake (Fig. 7).

Winter plankton in the Antarctic Ocean consist of dilute regenerating communities (Garrison et al., 1993), with phytoplankton meeting their nitrogen requirements mainly by uptake of ammonium (mean *f*-ratio = 0.4, Cota et al., 1992). Diatoms represent a significant, though not predominant, fraction of the autotrophs. Such communities are likely the rule in the antarctic pelagial and superimposed blooms, utilising elevated amounts of nitrate, occur at the event scale (Smetacek et al., 1990). The NEA configuration matches fairly well with these regenerating characteristics. Maximal biomass accumulations (PN stocks) and corresponding nitrate uptake rates do not exceed $1 \mu\text{g l}^{-1}$ and $0.15 \mu\text{M d}^{-1}$, respectively.

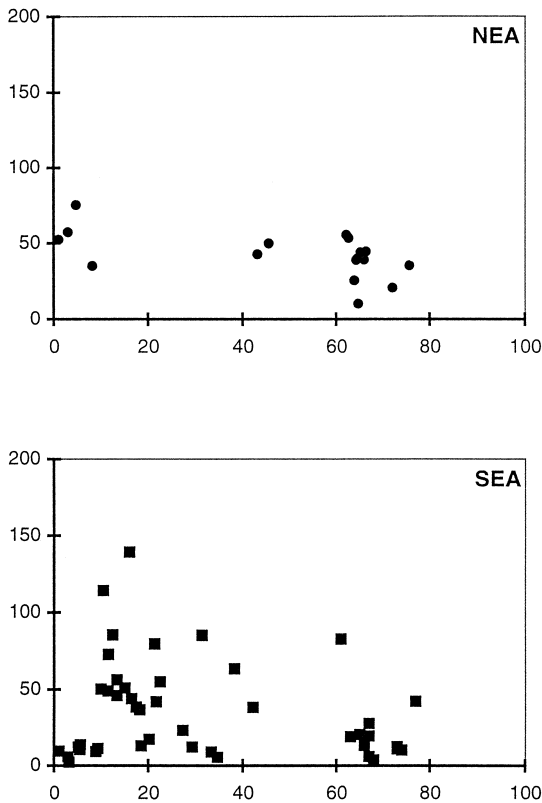


Fig. 6. Comparison of the seasonal variability in relative preference index (RPI) for both the NEA (upper graph) and SEA (lower graph).

The nitrogen uptake regime proves remarkably constant, with f -ratios indicating that both nutrients are removed at similarly low uptake rates throughout with a trend for slightly decreased f -ratios during the second phase of the productive season (Fig. 5). Moreover, ammonium is consistently the preferred nutrient, not one value < 1 being observed. Considering the RPI values as an expression of the ecosystem's demand for ammonium despite the abundance of nitrate, one observes limited variation of the seasonal pattern only. Any trigger for enhanced nitrate uptake (higher f -ratios and/or lower RPI values) and subsequent phytoplankton build-up remains conspicuously absent in this particular environment. Seasonal as well as interannual variation in the NEA will, therefore, be much less than in the case of emerging blooms.

On the other hand, when spring conditions rouse phytoplankton of the SEA to an intensive awakening of life, both a biomass build-up (Fig. 3c) and a parallel increase in PN-specific nitrate uptake rate are observed (Fig. 3b). The rise in nitrate uptake that occurs after winter time is consistent with the observations of Garside (1991) and Dickson and Wheeler (1995) for an upwelling area off the coast of Oregon. Enhanced PN-specific nitrate uptake rates reflect concurrent variations in phytoplanktonic biomass and more specifically in the PPN concentration relative to the total PN concentration. PN to PPN ratios are significantly higher during the earliest phase of the growth season (Semeneh, unpublished results), with maximal ratios being nearly 10. It can not be dismissed, however, that nitrogen uptake rates are also related to the distribution of nitrogenous nutrients,

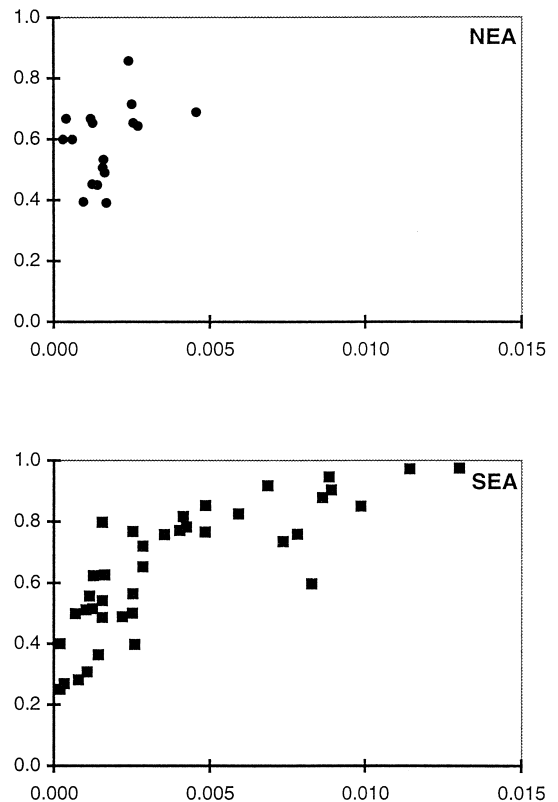


Fig. 7. Relation between f -ratio and specific nitrate uptake rate ($\nu\text{-NO}_3$, h^{-1}) for both the NEA (upper graph) and SEA (lower graph).

invoking physiological regulation of the phytoplankton (Dugdale and Wilkerson, 1991). During the EPOS LEG 2 cruise significant decreases in PN-specific nitrate uptake were not at all accompanied by any substantial increase of non-phytoplanktonic nitrogen (Goeyens et al., 1995).

Two aspects of the seasonal evolution in the SEA deserve our particular attention. The $\nu\text{-NO}_3$ vs. NH_4Av plot (Fig. 8) shows that increased values of NH_4Av bear upon decreased specific uptake rates, with values $\leq 0.002 \text{ h}^{-1}$ occurring mainly at $\text{NH}_4\text{Av} > 2\%$. There is some scatter at low values of NH_4Av , however, and a closer look at the plotted values confirms that a slight increase might occur at the low end side of NH_4Av values (Fig. 8). It is a basic tenet of nitrogen utilisation by phytoplankton that inhibition of nitrate uptake at ammonium con-

centrations $< 1 \mu\text{M}$ is generally lacking or poor (Dortch, 1990) and that ammonium acts as an uncoupler of photosynthesis (Semeneh, unpublished results). The occurrence of stimulation at low concentrations is less known, on the other hand. Earlier investigations in the Scotia and Weddell Seas provided evidence for a potential of enhanced nitrate uptake at low ammonium (Glibert et al., 1982), a phenomenon that was later confirmed by Dortch et al. (1991). Since winter water is generally devoid of high ambient ammonium (Nöthig et al., 1991) and melting of pack ice contributes little to the accumulation of ammonium in the photic zone (Biggs, 1978), antarctic waters generally display poor ammonium availability during early spring. Minor injections of ammonium through heterotrophic activity in the water column or in pack ice might have a stimulatory effect on the nitrate uptake rate. Unfortunately, studies of the stimulatory effect of ammonium were not planned during our field work and firm proof of such a scenario is not available. Moreover, any accumulation of ammonium in the water results from mineralisation of organic substances in excess of autotrophic ammonium removal. The organic substances such as chelates, complexes, colloids and aggregates, carry other vital elements and compounds resulting from numerous metabolic and physico-chemical reactions. Their production and possible accumulation during the mineralisation process in the surface layer might as well stimulate the nitrate uptake process. Earlier experiments provided evidence for increased algal development by release of triggering substances from melting winter ice in the Weddell Sea (Baumann, unpublished results).

Interactions between ammonium and nitrate uptake can be illustrated by the f -ratio (the nitrate to total nitrogen uptake ratio) and the severity of the effect of ammonium is judged from differences between values at ammonium concentrations below and superior to $1 \mu\text{M}$ (Dortch, 1990). Models on external interactions between different nitrogen sources made preferentially use of the relative concentrations of each nutrient though (Harrison et al., 1987; Collos, 1989). Hence, we used the NH_4Av as a better parameter for the description of the regulating effect of ammonium in the ecosystem under study. The average f -ratios amount to 0.73, 0.59 and 0.42 for $\text{NH}_4\text{Av} < 1.54$, for $1.54 \leq \text{NH}_4\text{Av} \leq 1.97$

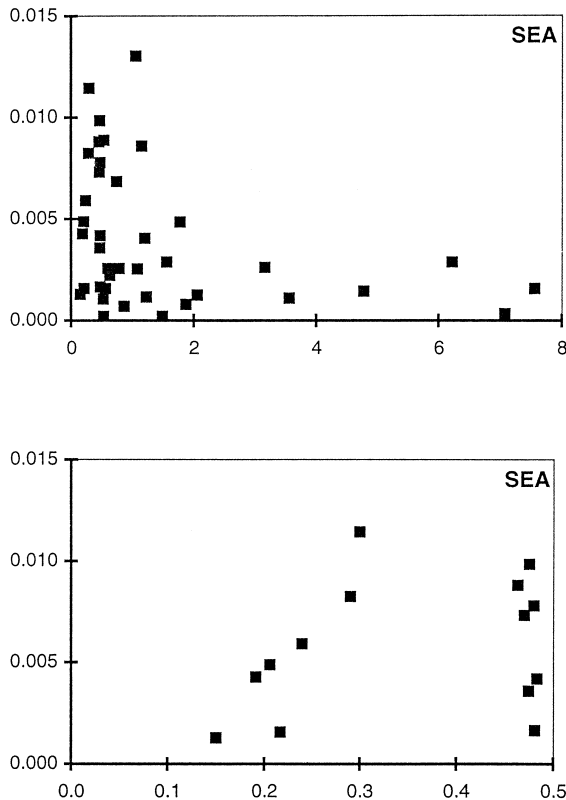


Fig. 8. Observed relation between specific nitrate uptake rate ($\nu\text{-NO}_3$, h^{-1}) and ammonium availability (NH_4Av , %) in the SEA for all available data (upper graph) and for data from the earliest phase of the season only (lower graph, $\text{NH}_4\text{Av} \leq 0.5$).

and for $\text{NH}_4\text{Av} > 1.97$, respectively. The latter values of NH_4Av were found to enclose the range of transition from predominant nitrate uptake ($f\text{-ratio} > 0.5$) to predominant ammonium uptake ($f\text{-ratio} < 0.5$) in typical MIZ systems of the Weddell Sea (Goeyens et al., 1995). The average f -ratios measured in SEA surface waters confirm that these systems pivoted at about the same NH_4Av .

Both the good agreement with earlier data and the significant seasonal decrease in f -ratio (Fig. 5) underpin that ammonium acts as a regulator of the nitrogen uptake regime in SEA waters. However, the variability of the f -ratio reflects the combination of numerous processes, such as species preference and inhibition, involved in the nitrate/ammonium interactions (Dortch, 1990). The hyperbolic trend of the $\nu\text{-NO}_3$ vs. NH_4Av plot (Fig. 8) strongly suggests inhibition of nitrate uptake by increased ammonium availability, as modelled already by Zevenboom and Mur (1981) and Collos (1987). However, even when a Michaelis–Menten relation describes well the nutrient uptake by phytoplankton, the saturation curve is not always linked to one single substrate. Moreover, it might prove much more difficult to apply an inhibition equation, whether it be competitive, non-competitive or uncompetitive, to an ecosystem of different phytoplankton species than to one single species, assuming its K_S and V_{\max} values remain constant. Differences in phytoplankton species (different K_S and V_{\max} values) obscure somehow the effect of ammonium on the nitrate uptake. With the available data it is not possible to infer whether the inhibition is competitive, non-competitive or uncompetitive. However, for antarctic waters characterised by superfluous stocks of nitrate (and other macronutrients), we suspect that the elevated availability of nitrate does not suppress the inhibition by ammonium and that therefore non-competitive or uncompetitive inhibition are more likely. Although our data set supports this conclusion, it still requires additional empirical confirmation.

Decreases in f -ratio were not inherently linked to a shift from diatom to non-diatom predominance. In a typical SEA of the Weddell Sea we observed the substitution of a large diatom bloom by a nearly pure cryptophycean bloom which was accompanied by a drastic decrease in f -ratio. On the contrary, the on shelf zone of Prydz Bay displayed a largely regener-

ation based community (mean f -ratio = 0.3), consisting mainly of diatoms (Semeneh et al., 1998)

5. Conclusion

The Southern Ocean is the world's largest water body with an enormous stock of likely superfluous nutrients. Except for a few very sheltered sites the available nutrients are not completely removed from the water by primary producers. The general scenario is one of limited nutrient uptake and corresponding oligotrophy. However, important differences in nutrient uptake were observed; they underbuild a separation between two major groups, the NEA and SEA, respectively.

The former group exhibits a relatively constant seasonal evolution. Despite nitrate abundance, absolute as well as specific nitrate uptake rates remain low throughout the season and dense bloom development does not occur. Moreover, nitrate and ammonium, contribute in a similarly low way to primary production. Nitrate concentrations remain high since the system is characterised by a reduced capacity to remove the ambient stock and ammonium accumulation as a result of heterotrophic remineralisation is absent. The dilute phytoplankton communities generally evidence a significant presence of diatoms, although they are not always the predominant component. This constant lack of fertility contrasts strikingly with the temporal bloom events in the SEA.

The key process governing the SEA configuration is the enhanced nitrate uptake at the start of the productive season. A combination of several triggering effects resulting in an 'ideal' physical and chemical environment as observed in the antarctic MIZ and CCSZ, stimulates proportionally higher uptake of nitrate and induces the observed potential for silicate excess at nitrate depletion. Possibly, small injections of ammonium or other essential compounds in a sea of nitrate constitute a stimulation of nitrate uptake. The elevated nitrate consumption is quickly terminated, however, and severe exhaustion of the nitrate pool does generally not occur in antarctic waters. Kamykowski and Zentara (1985) argued already that variations in the slopes of nitrate to silicate regressions are sensitive to the dominant nitrogen source. We conclude that the second ni-

trogenous nutrient has a major role in the decrease of specific nitrate uptake rates and consequently in the decrease of f -ratios. Build-up of exceptionally high ammonium stocks through heterotrophic activity inhibits phytoplanktonic nitrate uptake. The fertility of the SEA dwindles rapidly due to a combination of top-down control (grazing pressure reducing the phytoplankton biomass) and bottom-up control (reduced nitrate uptake as a result of higher ammonium availability).

The variable nitrogen uptake regime and its possible implications for the phytoplankton community structure might open new research interests in view of describing and modelling the development of lower trophic levels in antarctic waters. Could differences in fate gear the uptake of 'functional' nutrients as nitrate and 'structural' nutrients as silicate in the SEA?

Acknowledgements

We take the opportunity to thank the captains and crew members of the three research vessels, the chief scientists and all colleagues for their magnificent treatment and assistance during work. The authors are very grateful to Jean-Pierre Clement (VUB) for tireless technical assistance. The present study was funded by the Belgian Scientific Research Programme on the Antarctic. Frank Dehaire is a research associate at the National Fund for Scientific Research. Part of the research was performed while Leo Goeyens hold a position as a visiting scientist at AWI. Mengesha Semeneh was awarded a VUBAROS fellowship by the Vrije Universiteit Brussel. This is AWI publication 1457.

References

- Biggs, D.C., 1978. Non-biogenic fixed nitrogen in antarctic surface waters. *Nature* 276, 96–97.
- Collos, Y., 1987. Calculations of ^{15}N uptake rates by phytoplankton assimilating one or several nitrogen sources. *Appl. Radiat. Isot.* 38, 275–282.
- Collos, Y., 1989. A linear model of external interactions during uptake of different forms of inorganic nitrogen by microalgae. *J. Plankton Res.* 11, 521–533.
- Cota, G.F., Smith, W.O. Jr., Nelson, D.M., Muench, R.D., Gordon, L.I., 1992. Nutrient and biogenic particle distributions, primary productivity and nitrogen uptake in the Weddell–Scotia Sea marginal ice zone during winter. *J. Mar. Res.* 50, 155–181.
- Cullen, J.J., 1991. Hypotheses to explain high-nutrient conditions in the open sea. *Limnol. Oceanogr.* 36, 1578–1599.
- de Baar, H.J.W., 1994. Von Liebig's law of the minimum and plankton ecology (1899–1991). *Prog. Oceanogr.* 33, 347–386.
- Dickson, M.L., Wheeler, P.A., 1995. Nitrate uptake rates in a coastal upwelling regime: a comparison of PN-specific, absolute, and chl a -specific rates. *Limnol. Oceanogr.* 40, 533–543.
- Dortch, Q., 1990. The interaction between ammonium and nitrate uptake in phytoplankton. *Mar. Ecol. Prog. Ser.* 61, 183–201.
- Dortch, Q., Thompson, P.A., Harrison, P.J., 1991. Short-term interaction between nitrate and ammonium uptake in *Thalassiosira pseudonana*: effect of preconditioning nitrogen source and growth rate. *Mar. Biol.* 110, 183–193.
- Dugdale, R.C., Goering, J.J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* 23, 196–206.
- Dugdale, R.C., Wilkerson, F.P., 1986. The use of ^{15}N to measure nitrogen uptake in eutrophic oceans; experimental considerations. *Limnol. Oceanogr.* 31, 673–680.
- Dugdale, R.C., Wilkerson, F.P., 1991. Low specific nitrate uptake rate: a common feature of high-nutrient, low-chlorophyll marine ecosystems. *Limnol. Oceanogr.* 36, 1678–1688.
- El-Sayed, S.Z., 1987. Biological productivity of antarctic waters: present paradoxes and emerging paradigms. In: El-Sayed, S.Z., Tomo, A.P. (Eds.), *Antarctic Aquatic Biology*. SCAR, Cambridge, pp. 1–21.
- EPOS LEG 2, 1991. EPOS LEG 2 data report, Hydrography, part 1, second edn. NIOZ, Texel.
- Eppley, R.W., Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282, 677–680.
- Fanning, K.A., 1992. Nutrient provinces in the sea: concentration ratios, reaction rate ratios, and ideal covariation. *J. Geophys. Res.* 97, 5693–5712.
- Fiala, M., 1995. Les rapports des campagnes à la mer. ANTARES 2/MD 78 à bord du Marion-Dufresne, 26 Janvier-23 Mars 1994, No. 95-01. IFRTP, Brest-Iroise.
- Fiala, M., Semeneh, M., Oriol, L., 1998. Size fractionated phytoplankton biomass and species composition in the Indian sector of the Southern Ocean during austral summer. *J. Mar. Syst.* 17, 179–194.
- Garrison, D.L., Buck, K.R., Gowing, M.M., 1993. Winter plankton assemblage in the ice edge zone of the Weddell and Scotia Seas: composition, biomass and spatial distributions. *Deep-Sea Res.* 40, 311–338.
- Garside, C., 1991. Shift-up and nitrate kinetics of phytoplankton in upwelling systems. *Limnol. Oceanogr.* 36, 1239–1244.
- Glibert, P.M., Biggs, D.C., McCarthy, J.J., 1982. Utilization of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Res.* 29, 837–850.
- Goeyens, L., Fahrback, E., Behmann, T., Hinrichsen, H.H., Krest, J., Ross, A., Wisotki, A., 1991. Berichte aus dem Fachbereich Physik, Summer Weddell Gyre Study, Data Report No. 1. AWI, Bremerhaven.

- Goeyens, L., Tréguer, P., Baumann, M.E.M., Baeyens, W., Dehairs, F., 1995. The leading role of ammonium in the nitrogen uptake regime of Southern Ocean marginal ice zones. *J. Mar. Syst.* 6, 345–361.
- Hart, T.J., 1934. On the phytoplankton of the southwest Atlantic and Bellingshausen Sea, 1929–31. *Discovery Rep.* 8, 1–268.
- Harrison, W.G., Platt, T., Lewis, M.R., 1987. *f*-ratio and its relationship to ambient nitrate concentration in coastal waters. *J. Plankton Res.* 9, 235–248.
- Jacques, G., 1983. Some ecological aspects of Antarctic phytoplankton. *Polar Biol.* 2, 27–33.
- Jacques, G., 1989. Primary production in the open Antarctic Ocean during the austral summer. A review. *Vie Milieu* 39, 1–17.
- Jacques, G., Minas, M., 1981. Production primaire dans le secteur indien de l' Océan Antarctique en fin d' été. *Oceanol. Acta* 4, 33–41.
- Jennings, J.C. Jr., Gordon, L.I., Nelson, D.M., 1984. Nutrient depletion indicates high primary productivity in the Weddell Sea. *Nature* 309, 51–54.
- Kamykowski, D., Zentara, S.J., 1985. Nitrate and silicic acid in the world ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 26, 47–59.
- Kamykowski, D., Zentara, S.J., 1989. Circumpolar plant nutrient covariation in the Southern Ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 58, 101–111.
- Le Corre, P., Minas, H.J., 1983. Distributions et évolution des éléments nutritifs dans le secteur indien de l' Océan Antarctique en fin de période estivale. *Oceanol. Acta* 6, 365–381.
- Martin, J.H., 1990. Glacial–interglacial CO₂ change: the iron hypothesis. *Paleoceanography* 5, 1–13.
- Martin, J.H., Fitzwater, S.E., 1988. Iron deficiency limits phytoplankton growth in the northeast Pacific subarctic. *Nature* 331, 341–343.
- Mathot, S., Dandois, J.M., Lancelot, C., 1992. Gross and net primary production in the Scotia–Weddell sector of the Southern Ocean during spring 1988. *Polar Biol.* 12, 321–332.
- McCarthy, J.J., Taylor, W.R., Taft, J.L., 1977. Nitrogenous nutrition of the plankton in the Chesapeake Bay: 1. Nutrient availability and phytoplankton preferences. *Limnol. Oceanogr.* 22, 996–1011.
- Minas, H.J., Minas, M., Packard, T.T., 1986. Productivity in upwelling areas deduced from hydrographic and chemical fields. *Limnol. Oceanogr.* 31, 1182–1206.
- Neori, A., Holm-Hansen, O., 1982. Effect of temperature on rates of photosynthesis in Antarctic phytoplankton. *Polar Biol.* 1, 33–38.
- Nöthig, E.M., Bathmann, U., Jennings, J.C. Jr., Fahrback, E., Gradinger, R., Gordon, L.I., Makarov, R., 1991. Regional relationships between biological and hydrographical properties in the Weddell Gyre in late austral winter 1989. *Mar. Chem.* 35, 325–336.
- Semeneh, M., Dehairs, F., Lancelot, C., Baumann, M.E.M., Kopczynska, E., Elskens, M., Goeyens, L., 1998. Nitrogen uptake regime and phytoplankton community structure in the Southern Ocean. *J. Mar. Syst.* 17, 159–177.
- Shopova, D., Dehairs, F., Baeyens, W., 1995. A simple model of biogeochemical element distribution in the oceanic water column. *J. Mar. Syst.* 6, 331–344.
- Smetacek, V., Scharek, R., Nöthig, E.M., 1990. Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. In: Kerry, K.R., Hempel G. (Eds.), *Antarctic Ecosystems, Ecological Change and Conservation*. Springer-Verlag, Berlin, pp. 103–114.
- Smith, W.O. Jr., Nelson, D.M., 1986. Importance of ice edge phytoplankton in the Southern Ocean. *Bioscience* 36, 251–257.
- Smith, W.O. Jr., Nelson, D.M., 1990. Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. *Limnol. Oceanogr.* 35, 809–821.
- Sullivan, C.W., McClain, C.R., Comiso, J.C., Smith, W.O. Jr., 1988. Phytoplankton standing crops within an antarctic ice edge assessed by satellite remote sensing. *J. Geophys. Res.* 93, 12487–12498.
- Sverdrup, H.U., 1955. The place of physical oceanography in oceanographic research. *J. Mar. Res.* 14, 287–294.
- Tréguer, P., Jacques, G., 1992. Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biol.* 12, 149–162.
- Zevenboom, W., Mur, L.R., 1981. Simultaneous short-term uptake of nitrate and ammonium by *Oscillatoria agardhii* grown in nitrate- or light-limited continuous culture. *J. Gen. Microbiol.* 126, 355–363.