

Nutrient depletions in the Ross Sea and their relation with pigment stocks

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Abstract

The present article depicts a first attempt to relate the governing nutrient uptake regime and phytopigment signature of the Ross Sea. Based on nutrient and phytopigment data obtained during two cruises in the Ross Sea, two distinct groups were recognised. The first one was characterised by moderate nutrient (nitrate and silicic acid) depletions in combination with relatively high diatom and *Phaeocystis* abundance. The second group showed very low nutrient depletions and very poor diatom abundance. Average depth specific nitrate depletions were 8.1 and 1.1 μM and average silicic acid depletions were 21.5 and 1.3 μM , respectively. The nutrient consumption patterns did not match the conditions of silicic acid excess (SEA) or nitrate excess areas (NEA), a clear trend being probably obscured by very poor seasonal maturity of several sampling stations.

The contrast between both groups is largely explained by small differences in nitrogen uptake regime of the major phytoplankters. During early season, the diatoms meet the majority of their nitrogen requirements by nitrate uptake, with few exceptions where ammonium is the most important nitrogenous substrate. On average, their nitrate uptake capacity is lower than that of *Phaeocystis* (average specific nitrate uptake rates were 0.021 and 0.036 day^{-1} for diatoms and *Phaeocystis*, respectively). The latter phytoplankton always shows predominance of nitrate uptake. Both groups are subject to inhibition of nitrate uptake when ammonium availability increases, and it is likely that the diatoms are more sensitive to the inhibitory effect of ammonium. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Earlier investigations on nutrient distributions in the World Ocean stress the occurrence of (1) a decreasing gradient of nitrate excess at silicic acid depletion from the Polar Front towards higher lati-

tudes and (2) an area of potential silicic acid excess at nitrate depletion in the Weddell and Ross Seas (Kamykowsky and Zentara, 1985, 1989). Moreover, the Southern Ocean is exceptional within the oceanic realm due to its imposing biogeochemistry, more particularly a plenteous and likely superfluous nutrient supply. The persistence of excess nutrients in the surface layer of the Southern Ocean presumably connotes regulation of nutrient uptake (autotrophic

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processes) by something other than the nutrient availability (Fanning, 1992; Goeyens et al., 1998).

Despite the ubiquitous nutrient abundance in antarctic waters, the intensity of primary production exhibits pronounced spatial variability (cf. a comprehensive comparison by Mathot et al., 1992). Often intensive autotrophic production and concomitantly elevated nutrient removal occur in the immediate vicinity of ice edges (Sullivan et al., 1988). This is not a general rule, however, and sometimes very poor build-up of phytoplankton biomass was observed in the wake of retreating ice (Bathmann et al., 1997; Quéguiner et al., 1997).

Nitrate depletions, defined as the differences between the concentration in the remnant winter water and the in situ concentration (Jennings et al., 1984), are highest in typical marginal ice zone (MIZ) and coastal and continental shelf zone (CCSZ) environments. In contrast, herewith, nitrate removal in the permanently open ocean zone (POOZ) is mostly low, an expression of functional oligotrophy in the ice free antarctic waters (Jones et al., 1990; Tréguer and Jacques, 1992). Intensive vertical mixing within the shelf break area dramatically obscures the temperature minimum, however, and the determination of nutrient depletions is generally not possible during summer.

Furthermore, the nitrate depletions and the corresponding silicic acid depletions are generally disproportionate when compared to their respective availabilities. Even when the general scenario in the Southern Ocean is one of limited nutrient uptake, depletion ratios differ markedly from the ratios of the winter water concentrations, which are available for phytoplankton development at the onset of vernal ice melting. These differences led to the distinction between nitrate excess areas (NEA) and silicic acid excess areas (SEA). The former group exhibits a relatively constant evolution with poor nitrate removal and prevailing absence of dense phytoplankton blooms throughout the season. On average, the nitrate contribution to the total nitrogen requirement of the phytoplankton amounts to 60%. The SEA ecosystems are characterised by elevated nitrate uptake rates during early spring followed by a dramatic decrease in nitrate consumption long before exhaustion of the nitrate pool. Moreover, the contribution of nitrate is highly variable, with maximal values of

~ 100% during early spring and lowest contributions of < 25% during summer (Goeyens et al., 1998). Fertile MIZ and CCSZ waters often demonstrate SEA characteristics.

Satellite imagery revealed that densest phytoplankton blooms in the Ross Sea occur where large offshore polynyas develop during spring (Comiso et al., 1993; Arrigo and McClain, 1994). Moreover, field studies confirm that the Ross Sea exhibits most consistently the largest surface accumulations of phytoplankton biomass in the Southern Ocean (DiTullio and Smith, 1996). In the Ross Sea, pronounced horizontal gradients in phytoplankton distribution are observed, with either diatoms or the colonial prymnesiophyte *Phaeocystis antarctica* dominating the autotrophic assemblages (Leventer and Dunbar, 1996; Smith et al., 1996; Goffart et al., 2000).

The current paper aims at a better understanding of the nutrient depletion patterns in the Ross Sea during the growth season. Two aspects received our special attention: the distributions and ratios of the dominant phytopigments, which characterise the differences in phytoplankton assemblage (diatom vs. *Phaeocystis* predominance), and the corresponding nitrogen uptake regime in the different communities.

2. Methods

Samples were collected during two Italian Antarctic expeditions: cruise A (sampling between January 01 and 05, 1990) on board RV *Cariboo* and cruise B (sampling between November 14 and December 15, 1994) on board RV *Italica*. Cruise A covered the margin area of the continental Ross Shelf east of Cape Adare and a transect through the Ross Sea at a latitude of ~ 75°S. During cruise B, sampling was carried out at 27 stations located from 76°S to 71°S along 175°E, following the northward ice retreat.

During cruise A, nutrient concentrations were determined by means of a Technicon II Autoanalyzer (Hansen and Grasshoff, 1983), while during cruise B, an Alpkem autoanalyzer was adopted according to "Alpkem Flow Solution Methodologies" (ALPKEM, 1992a,b,c). Ammonium was always determined with a Technicon autoanalyzer, according to the indophenol blue method adapted for segmented flow analyz-

ers by Tréguer and Le Corre (1975). Hypochlorite solution was used as chlorine donor; freshly prepared Millipore Milli Q water served as the blank solution. Original data on nutrient concentrations are reported by Catalano et al. (1991, 1997).

The nitrate and silicic acid uptake regimes are characterised by the respective nutrient depletions. Le Corre and Minas (1983), Jennings et al. (1984), Goeyens et al. (1995), Rubin et al. (1998) and Hoppema et al. (2000) have previously used depletion calculations in antarctic research. Calculated nutrient depletions represent seasonally integrated nutrient removal in the surface layer down to the depth, where the in situ nitrate and silicic acid concentrations equal the winter values NiWi and SiWi, respectively. Nitrate depletion (NiDe) values are believed to be associated with “new” production, sensu Dugdale and Goering (1967). The silicic acid depletion (SiDe), on the other hand, depicts diatom production. Hence, diatom abundance and productivity are very relevant parameters shaping the nutrient distributions and more particularly the nutrient depletion ratios in the surface layer.

As pointed out by the above cited authors, there are some implicit assumptions in using this methodology. Nutrient depletion values can be biased by either physical reintroduction or biological processes such as nitrification (Bianchi et al., 1997), and should therefore be considered as minimal values. Moreover, it must be stressed that NiDe does not reflect total dissolved nitrogen uptake since concomitant uptake of other nitrogenous nutrients such as dinitrogen, ammonium and dissolved organic nitrogen is not negligible (Bronk et al., 1994). Most important is the assumption that vertical and lateral mixing in both the temperature minimum and surface layer are small. This condition is fulfilled; the evidence herefor is that the observed temperature in the remnant winter water is approximately equal to the temperature in the winter surface water (near the freezing point: all values are $\leq -1.70^\circ\text{C}$). Additionally, fluxes due to vertical gradients in the surface layer should be small. Taking into consideration a coefficient of diffusion of $8 \text{ m}^2 \text{ day}^{-1}$ (Gordon et al., 1984), the maximal contributions from vertical fluxes could amount to 1% and 13% for nitrate and silicic acid depletions, respectively. These values are in good agreement with earlier determined deviations

(Goeyens et al., 1991, 1995). Finally, possible nutrient changes due to the addition of melt water from the sea ice should be accounted for by normalization to a constant salinity; a detailed procedure for calculating the depletions is given by Hoppema et al. (2000). In the current investigation, no corrections for possible dilution by melting ice were introduced, since there is no evidence for enhanced effects when considering average nutrient concentrations and salinities of sea ice and a “conservative” nutrient to salinity relation in the surface water (Goeyens et al., 1995). This study is largely founded on comparisons with earlier studies; hence, the authors are confident that the general pattern is well described by the data given and that the closeness of agreement between the given and correct values (or the accuracy of the data) is comprised within the maximal deviation of 15%.

Pigment concentrations were obtained with HPLC techniques; pigment stocks represent the integrated concentrations of chlorophyll *a* (Chl *a*), fucoxanthin (Fuco) and 19'-hexanoyl-oxyfucoxanthin (HF), respectively down to the temperature minimum layer. The integration is also based on six to eight samplings at discrete depths in the water column, confined between surface and temperature minimum layers. Particulate matter for pigment analysis was separated by low vacuum filtration of 1 l of sea water onto Whatman GF/F filters. Afterwards, the filters were immediately frozen at -25°C until analysis on board. Frozen filters were extracted in 100% methanol, using grinding and refiltration to remove cellular debris. Phytoplankton pigments were separated and quantified by HPLC, following the procedure of Williams and Claustre (1991). Chl *a* is used as the universal index of phytoplankton biomass. Fuco and HF are used as chemotaxonomic tools to identify diatoms (Jeffrey, 1980; Claustre et al., 1994) and prymnesiophytes (Gieskes and Kraay, 1986; DiTullio and Smith, 1995), respectively. The HF stock is assumed to be indicative of the presence of *Phaeocystis*. This assumption is based on the reported predominance of *Phaeocystis* and minor contribution of other prymnesiophytes in the Ross Sea (Palmisano et al., 1986; DiTullio and Smith, 1995; Goffart et al., 2000).

Samples for productivity incubations were obtained from depths corresponding to 100%, 50%,

20%, 10%, 5%, 1% and exceptionally 0.1% of PAR with a CTD rosette fitted with 24 Niskin bottles of 12 l. Nitrogen uptake rates were determined with tracer experiments according to Dugdale and Goering (1967), using the stable isotope ^{15}N and following the JGOFS protocols and the analytical procedures described by Owens (1988) and Owens and Rees (1989). From each depth, two subsamples were transferred into 1 l polycarbonate bottles covered with perforated nickel screens to mimic the in situ irradiance conditions. The samples were spiked respectively with $\text{Na}^{15}\text{NO}_3$ (99.9% ^{15}N) and $^{15}\text{NH}_4\text{Cl}$ (70.4% ^{15}N), placed in on-deck incubators and maintained at sea-surface temperature with running seawater. After 24 h of incubation, the samples were filtered on precombusted Whatman GF/F filters (25 mm diameter), rinsed with filtered seawater and stored frozen until isotope analysis with a continuous flow nitrogen analyzer-mass spectrometer (ANCA 20-20 MS, Europa Scientific). Original data on nitrogen uptake are reported in Lipizer and Catalano (1999). Specific uptake rates (ν , in day^{-1}) are defined as the nutrient removed per unit of particulate nitrogen (PN) and per unit of time; absolute uptake rates or transport rates (ρ , in nM day^{-1}) are the products of specific uptake rates and PN concentrations (Wilkerson and Dugdale, 1992). The relative importance of new vs. total production was expressed as the f -ratio (Eppley and Peterson, 1979).

3. Results and discussion

A compilation of all NiDe and SiDe values of both cruises A and B emphasizes predominantly poor nutrient consumption with few enhanced values

only (Table 1). Both the average and median nutrient depletions are very low, their corresponding interquartile ranges vary from 7 to 70 mmol m^{-2} and from 5 to 72 mmol m^{-2} for NiDe and SiDe, respectively. Only a small number of higher values — all referring to cruise A — corresponds to the ones typically observed in productive antarctic waters (Jennings et al., 1984; Karl et al., 1991; Goeyens et al., 1995). Additionally, ammonium concentrations as well as pigment stocks are low. Ammonium stocks never exceed 50 mmol m^{-2} , with corresponding ambient concentrations of $< 0.5 \mu\text{M}$ throughout. Chl a concentrations $\geq 1 \mu\text{g l}^{-1}$, worthy of the term phytoplankton bloom (Sakshaug and Holm-Hansen, 1984), were rarely observed. These parameters corroborate prevalence of early season conditions during the sampling periods.

However, the NiDe and SiDe patterns do not match the pronounced distinction between NEA and SEA conditions. Generally, the specific depletion ratios (defined as the quotients of the depletion to winter concentration ratios) largely exceed 1 in NEA surface waters, whereas the opposite holds for the SEA. Our observations in the Ross Sea fit an intermediate situation with all ratios amounting to approximately 1 (the 95% confidence interval ranges from 0.87 to 1.12, Fig. 1A). Few stations adhere conceptually to the NEA conditions with ratios slightly > 1 , whereas most of the stations adhere to the SEA conditions with ratios slightly < 1 . On average, NEA and SEA specific depletion ratios from the current investigation amount to 1.24 and to 0.76 (Fig. 1B,C). These values are significantly different from the earlier determined specific depletion ratios of 2.68 (NEA) and 0.40 (SEA), respectively. The latter values are derived from a comparative

Table 1
Nutrient and pigment status of the Ross Sea during cruises A and B

	NiDe (mmol m^{-2})	SiDe (mmol m^{-2})	Ammonium (mmol m^{-2})	Chl a ($\mu\text{g m}^{-2}$)	Fuco ($\mu\text{g m}^{-2}$)	HF ($\mu\text{g m}^{-2}$)
Average	61	127	7.5	42 448	19 261	20 351
Median	16	13	4.9	28 446	5 868	6 603
Minimum	1	0	0.1	3 480	865	694
Maximum	484	1362	49.2	159 553	179 016	105 118
First quartile	7	5	2.6	11 201	2 483	3 574
Third quartile	70	72	10.5	61 648	15 420	31 916

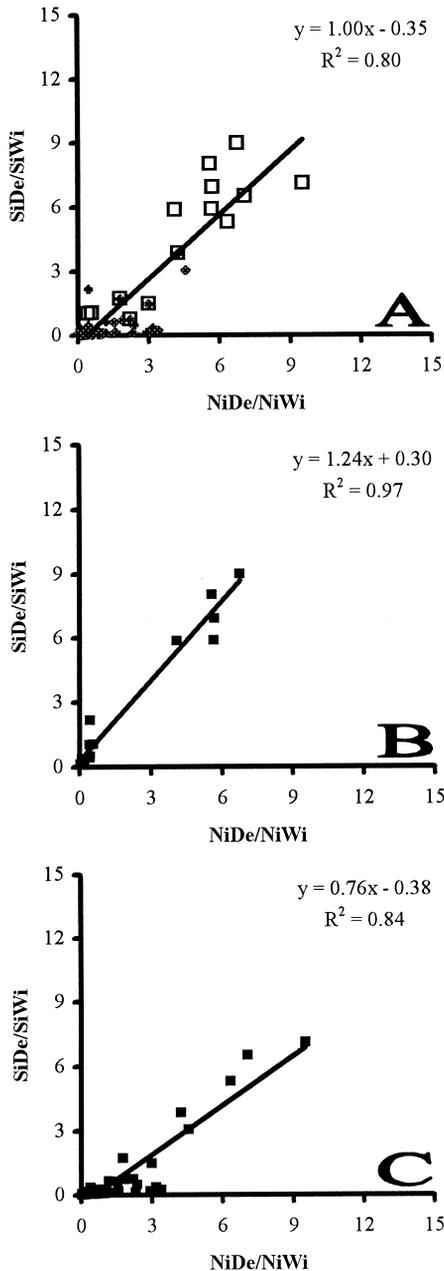


Fig. 1. Specific silicic acid depletion vs. specific nitrate depletion for all available data (A), for the stations adhering to NEA conditions (B) and for the stations adhering to the SEA conditions (C); open squares represent cruise A data (enhanced seasonal maturity) and black diamonds represent cruise B data (poor seasonal maturity), specific nutrient depletions are defined as the ratios of the depletion over the winter concentration.

study based on nutrient uptake data obtained during five different cruises in the Atlantic and Indian sectors of the Southern Ocean (Goeyens et al., 1998). Presumably, “the very early season” conditions observed during cruise B (1994, RV *Italica*) obscure the distinction between NEA and SEA conditions. The observed maximal depletions are a factor of 2 or more less than the maximal values observed in areas of intensive nutrient removal such as the MIZ and CCSZ of the Weddell Sea and Prydz Bay (Goeyens et al., 1998).

Any departure of the SiDe/NiDe ratio from the SiWi/NiWi ratio, meaning that the nutrient removal ratio differs from the nutrient availability ratio, signifies that NiDe and SiDe are disproportionate due to differences in either the Si uptake regime (predominant vs. reduced abundance of diatoms) or the N uptake regime (oxidised vs. reduced nitrogen assimilation). Our data set of all depth specific depletions (the differences between the concentration in the temperature minimum layer and the in situ concentration at a particular sampling depth) emphasizes that the SiDe/NiDe ratios fall apart in two distinct groups (Fig. 2). The first one (group 1) shows largely variable SiDe values and constantly low SiDe/NiDe

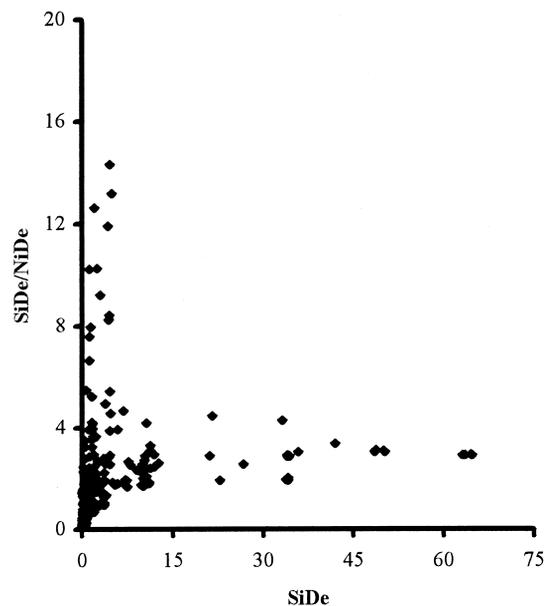


Fig. 2. Depletion ratios vs. silicic acid depletions for all available data.

ratios, indicating a variation of both the SiDe and NiDe values in concert with each other. The second one (group 2), on the contrary, gathers stations with consistently low SiDe values and highly variable SiDe/NiDe ratios.

The contrast between both groups is addressed by the comparison of the nutrient uptake regimes and corresponding pigment contents. Differences are summarised in Table 2. Basically, the NiDe, SiDe, Chl *a* and Fuco stocks of group 1 (constantly low SiDe/NiDe ratios) are significantly higher than those of group 2 (consistently low SiDe values). The HF stocks display a completely different pattern, however, with similarly high values and a well comparable spread in both groups. Maximal HF stocks even occur in group 2. A hasty look at the data learns that denser phytoplankton with relatively high diatom abundances are responsible for considerable nitrate and silicic acid uptake in group 1. On the other hand, group 2 is characterised by dilute phytoplankton assemblages with poor diatom and considerable *Phaeocystis* abundances, which induced rather low silicic acid removal. The occurrence of *Phaeocystis* dominated populations in the Southern Ocean, more particularly in the Ross Sea, has not gone unnoted (El-Sayed et al., 1983; Palmisano et al., 1986; Smith and Sakshaug, 1990; Davidson and Marchant, 1992; Smith et al., 1996; Arrigo et al., 1998; Lancelot et

al., 1998) and their presence and conceivable dominance in the phytoplankton community are likely to affect the nutrient uptake.

Antarctic phytoplankton can either exhibit pronounced seasonal variability in community structure or not. Generally, diatom to non-diatom succession constitutes the most important shift, with bottom-up control as well as top-down control being the steering parameters (Semeneh et al., 1998a,b). This study reveals remarkable differences in *Phaeocystis* and diatom dominance during the earliest stage of the growth season in the Ross Sea, whereby the governing physical conditions are largely determining the phytoplankton distribution (Goffart et al., 2000). The corresponding nitrogen utilisation evidences some small differences between *Phaeocystis* and diatom predominance, the overall trend being highly characteristic for the onset of the phytoplankton development after ice melting though (Cota et al., 1992; Goeyens et al., 1995). A summary of the major nitrogen uptake characteristics measured during cruise B only is given in Table 3.

The absolute nitrate uptake rates range from ~ 1 to ~ 300 nM day⁻¹ and the corresponding specific uptake rates range from ~ 0.001 to ~ 0.12 day⁻¹. The maximal rates are in good agreement with values from earlier investigations during the onset of the productive season (shortly after melting of the

Table 2
Variations in nutrient depletion and pigment stock of groups 1 and 2

	NiDe (μM)	SiDe (μM)	Chl <i>a</i> (ng l ⁻¹)	Fuco (ng l ⁻¹)	HF (ng l ⁻¹)
<i>Group 1</i>					
Average	8.1	21.5	2219	1840	427
Median	4.9	11.3	1877	1200	264
Minimum	0.4	5.0	235	37	44
Maximum	22.1	64.7	6756	6801	2377
First quartile	3.7	10.1	895	491	142
Third quartile	11.9	34.2	3030	3255	495
<i>Group 2</i>					
Average	1.1	1.3	1093	273	679
Median	0.9	0.7	508	136	233
Minimum	0.1	0.1	146	30	26
Maximum	4.5	4.8	4070	1953	3065
First quartile	0.4	0.3	329	65	91
Third quartile	1.6	1.9	1853	296	1294

Table 3

Summary of the depth averaged values characterising the nitrogen uptake regime during cruise B in the Ross Sea

	Average	Median	Minimum	Maximum
Absolute nitrate uptake rate (nM day ⁻¹)	33.84	5.33	1.04	308.08
Specific nitrate uptake rate (day ⁻¹)	0.0243	0.0103	0.0015	0.1169
Absolute ammonium uptake rate (nM day ⁻¹)	12.27	4.03	0.42	112.39
Specific ammonium uptake rate (day ⁻¹)	0.0137	0.0076	0.0008	0.0501
<i>f</i> -Ratio	0.64	0.60	0.25	0.93
Ammonium/nitrate uptake ratio	0.68	0.66	0.08	2.98

winter ice) in the Ross Sea (Nelson and Smith, 1986) and in other regions of the Southern Ocean (Olson, 1980; Nelson et al., 1987; Karl et al., 1991; Kristiansen et al., 1992; Bury et al., 1995). They corroborate typical SEA conditions as proposed by Kamykowsky and Zentara (1985, 1989) and Goeyens et al. (1998). Minute differences with the highest maximal rates observed by other authors in well sheltered and very fertile regions must be explained by limited seasonal maturity and inherently low biomass build-up at the sampling moment.

Additionally, ammonium uptake exhibits less pronounced differences between minimal and maximal uptake rates, a common feature of the nitrogen uptake regime in the World Ocean. The maximal specific uptake rates (~ 0.05 day⁻¹ or ~ 0.002 h⁻¹) compare well to the ones observed during previous early spring studies (Olson, 1980; Nelson et al., 1987; Karl et al., 1991; Kristiansen et al., 1992; Bury et al., 1995).

In order to distinguish the nitrogen uptake by *Phaeocystis* dominated and by diatom dominated assemblages, we arbitrarily defined that 10 stations with minimal Fuco/HF ratios were *Phaeocystis* dominated stations (PDS) and, otherwise, that 10 stations with highest Fuco/HF ratios were diatom dominated stations (DDS). It must be stressed here

that PDS and DDS do not refer to the above-mentioned groups 1 and 2; moreover, these data were collected during cruise B only. The investigated pigment stocks and corresponding nitrogen uptake rates are depth-integrated values for the euphotic layer down to the minimal PAR value. They are snapshots of the ambient conditions at the sampling moment but do not include a seasonal dimension such as the nutrient depletions compared in Table 2. The variability in nitrogen uptake dynamics is summarised in Tables 4 and 5, respectively. The PDS are characterised by increasing nitrate uptake rates, which occur in concert with increasing ammonium uptake rates (Fig. 3A). The maximal observed values amount to > 300 nM day⁻¹ and to > 100 nM day⁻¹ for nitrate and ammonium, respectively, with the highest values meeting HF stocks and overall phytoplankton biomasses (Chl *a*) above the average. However, two stations with highest HF and Chl *a* concentrations exhibit intermediate uptake rates. Estimating their seasonal maturity by taking the ratio of the respective NiDe and ρ -NO₃ values (Goeyens et al., 1998), it cannot be excluded that phytoplankton ingested nitrate at higher uptake rates before being sampled and that seasonal progress proceeded already for a longer time span in those particular water columns. DDS display a less obvious relation of the nitrate vs.

Table 4

Summarised nitrogen uptake regime in the *Phaeocystis* dominated samples

	Average	Median	Minimum	Maximum
Absolute nitrate uptake rate (nM day ⁻¹)	87.27	44.37	1.04	308.08
Specific nitrate uptake rate (day ⁻¹)	0.0362	0.0176	0.0033	0.1044
Absolute ammonium uptake rate (nM day ⁻¹)	23.15	6.18	0.42	112.39
Specific ammonium uptake rate (day ⁻¹)	0.0092	0.0059	0.0010	0.0293
<i>f</i> -Ratio	0.73	0.69	0.56	0.93
Ammonium/nitrate uptake ratio	0.42	0.45	0.08	0.77

Table 5
Summarised nitrogen uptake regime in the diatom dominated samples

	Average	Median	Minimum	Maximum
Absolute nitrate uptake rate (nM day^{-1})	10.84	9.04	2.04	34.14
Specific nitrate uptake rate (day^{-1})	0.0211	0.0079	0.0015	0.1169
Absolute ammonium uptake rate (nM day^{-1})	8.50	6.46	1.07	36.10
Specific ammonium uptake rate (day^{-1})	0.0179	0.0153	0.0010	0.0383
<i>f</i> -Ratio	0.52	0.51	0.23	0.81
Ammonium/nitrate uptake ratio	0.86	0.69	0.12	2.98

ammonium uptake; more particularly the maximal uptake rates are nearly one order of magnitude lower than the ones observed for PDS (Table 5, Fig. 3B). Since absolute uptake rates combine specific uptake rates and concentrations of particulate matter, the differences in uptake dynamics emphasize the role of

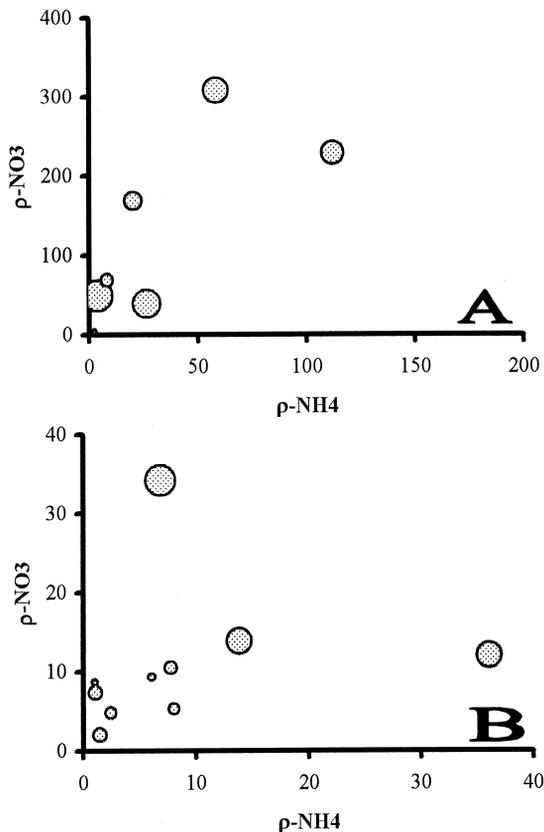


Fig. 3. Variation of the absolute nitrate and absolute ammonium uptake rates (nM day^{-1}) in *Phaeocystis* dominated samples (A) and diatom dominated samples (B); bubble sizes correspond to relative phytoplankton biomasses in the samples.

both the biomasses and uptake capacities (or specific uptake rates). Fig. 4A and B in fact reveals important differences in specific uptake rates (absolute uptake rates normalized to the corresponding biomasses). Particularly in the PDS, the trend is one of enhanced nitrate uptake capacity and reduced ammonium uptake capacity. The interquartiles for nitrate uptake (50% of the data) range from ~ 0.01 to $\sim 0.06 \text{ day}^{-1}$ and from ~ 0.01 to $\sim 0.02 \text{ day}^{-1}$ in the PDS and DDS, respectively, meaning that a majority of the *Phaeocystis* has three times higher nitrate uptake capacity. Seemingly, *Phaeocystis* manifest themselves as the better nitrate removers. On the other hand, the diatoms demonstrate a little lead over *Phaeocystis*, with the ammonium uptake rate's interquartile range being twice the one of the nitrate uptake. This general pattern as it is observed for depth weighted averages of the nitrogen uptake rates is in perfect agreement with the uptake regime in the Chl *a* maximum layer of each station (data not shown).

It is commonly accepted that increased ammonium availability inhibits nitrate uptake (Dortch, 1990), and that this regulatory effect of ammonium contributes to the considerable reduction of the nitrate uptake rate long before the nitrate pool of antarctic surface waters is exhausted (Goeyens et al., 1995). This contention is confirmed by the current data set. With the exception of 1 single data point, all nitrate transport rate values remain very low when the ammonium stocks exceed 5 mmol m^{-2} (Fig. 5A). The only elevated uptake rate ($\rho\text{-NO}_3 = 228.6 \text{ nM day}^{-1}$) must be explained by a comparatively denser phytoplankton biomass since the plot with specific nitrate uptake rates vs. ammonium stocks does not reveal any significant "deviation" (Fig. 5B). Our small data set indicates that the

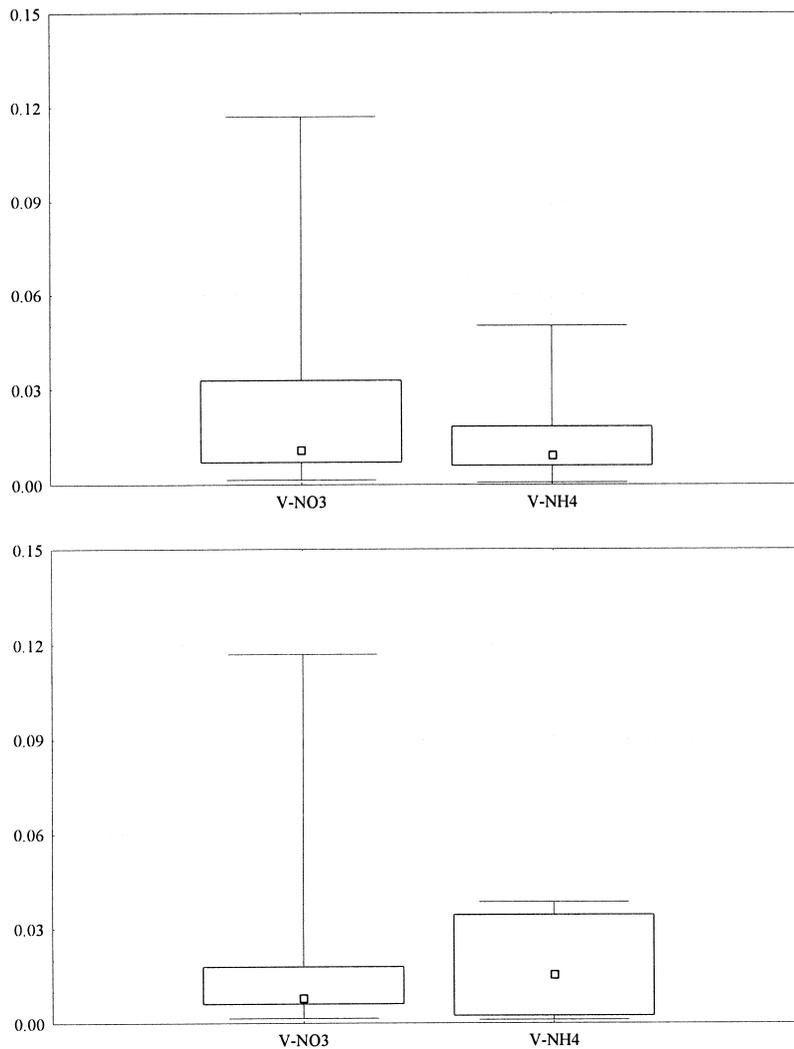


Fig. 4. Box and whisker plots for the non-parametric distributions of specific nitrate and ammonium uptake rates (day^{-1}) in *Phaeocystis* dominated samples (A) and in diatom dominated samples (B).

diatom-dominated populations show generally a lower nitrate uptake capacity. There is only 1 higher value of $\sim 0.10 \text{ day}^{-1}$ corresponding to a negligible ammonium stock; otherwise the uptake rates remain very low ($< 0.03 \text{ day}^{-1}$, Fig. 4). This contrasts with the values obtained for PDS were the average specific nitrate uptake rate at low ammonium is generally higher. It must be stressed here that all stations are characterised by a very low ammonium load, however. The maximal stocks never exceed 30 mmol m^{-2} , meaning that the ambient concentrations in the

water column are generally $< 0.3 \mu\text{M}$. These concentrations are significantly lower than the “elevated” values generally observed in the vicinity of land and in ice edge zones, which can exceptionally exceed $4 \mu\text{M}$ (Koike et al., 1986; Owens et al., 1991).

On the other hand, a compensatory increase of the ammonium uptake at higher ammonium availability does generally not occur. This study confirms that increased ammonium transport rates at higher ammonium availabilities (percentages of ammonium-N in the total inorganic nitrogen pool) do not equal the

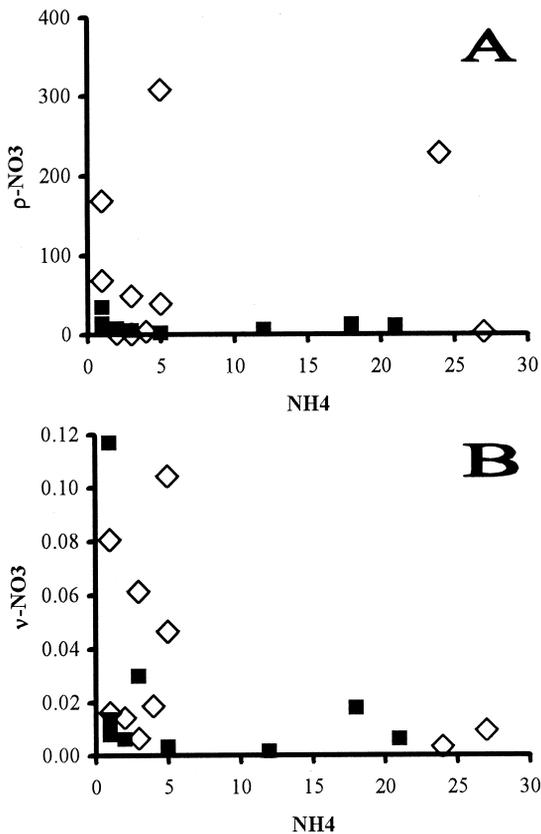


Fig. 5. Illustration of the inhibitory effect of increasing ammonium concentrations (mmol m^{-2}) on the absolute nitrate uptake rate (A) and specific nitrate uptake rate (B); open diamonds represent *Phaeocystis* dominated samples and black squares represent diatom dominated samples.

differences between maximal and minimal nitrate uptake rates (Fig. 6). The highest observed ammonium uptake rate value, which amounts to $> 100 \text{ nM day}^{-1}$, corresponds with an ammonium availability of 1.7% ($> 20 \text{ mmol m}^{-2}$) and with a maximal *Phaeocystis* predominance (Fig. 6A). The average trend in PDS is one of increasing uptake rate for increasing availability and increasing *Phaeocystis* abundance. The DDS display 1 significantly increased ammonium uptake rate at an ammonium availability of 2.2% in addition to consistently low uptake rates throughout (Fig. 6B). The maximal uptake rate does not exceed 40 nM day^{-1} , however, a value that remains a factor of 3 below the maximal PDS uptake rate. These higher ammonium uptake

rates in the PDS must be explained by higher biomasses, since no significant differences in specific uptake rate can underpin a distinction in uptake capacity between PDS and DDS (Fig. 4A and B). On the contrary, even when the ammonium uptake capacity remains low, the diatom-dominated populations are slightly better ammonium utilisers as already shown by Fig. 4B.

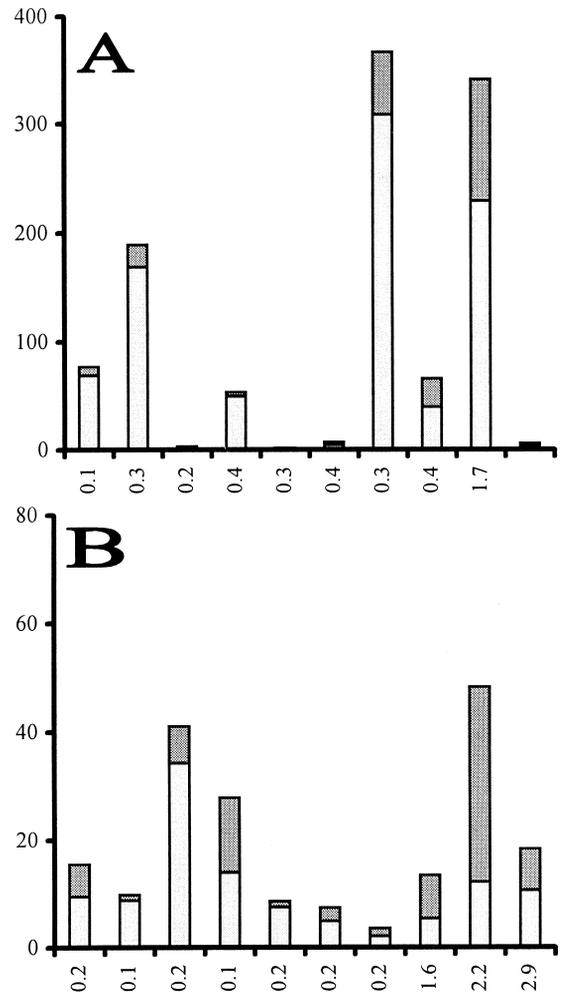


Fig. 6. Variability of nitrate and ammonium contributions to the total absolute uptake rate (nM day^{-1}) as a function of ammonium availabilities (%) in *Phaeocystis* dominated samples (A) and in diatom dominated samples (B); ammonium availabilities are percentages of ammonium-N in the dissolved inorganic nitrogen pool, clear columns represent nitrate uptake and dark columns represent ammonium uptake.

both diatoms and *Phaeocystis* as well as reduced vertical stability and disproportionate nutrient replenishment due to the uncoupling of nitrate and silicic acid regeneration might have caused the highest SiDe/NiDe ratios.

Prominent evidence for potential excess of either nitrate or silicic acid is absent; this must be explained by the very low seasonal maturity, the inherently small ammonium build-up and the low ammonium uptake rates. Therefore, an obvious distinction between NEA and SEA environments is not possible and, hence, the obtained results do not allow a straightforward confirmation of Kamykowsky and Zentara (1985, 1989) original contention.

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