PERGAMON

Deep-Sea Research II 49 (2002) 787–804

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

New and regenerated production and ammonium regeneration in the western Bransfield Strait region (Antarctica) during phytoplankton bloom conditions in summer

Antonio Bode[a,*], Carmen G. Castro[b], M. Dolores Doval[b], Manuel Varela[a]

[a] *Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Apdo 130, E-15080 A Coruña, Spain*
[b] *Instituto de Investigaciones Marinas, CSIC, Eduardo Cabello, 6, E-36208 Vigo, Spain*

Received 26 March 1999; received in revised form 3 December 1999; accepted 16 May 2000

Abstract

Nitrate and ammonium uptake and ammonium regeneration rates were measured with ^{15}N incubations during the austral summer period of 1995–1996 in the Bransfield Strait region (Antarctica). The objective was to quantify new and regenerated production in three zones that included stations with high phytoplankton biomass dominated by large and chain-forming diatoms (Strait of Gerlache) or colonies of *Phaeocystis* (Bellingshausen Sea), and stations with low phytoplankton biomass and high abundance of Cryptophyceae and other flagellates (western Bransfield Strait). All zones were characterized by high nitrate ($>10\,mmol\,N\,m^{-3}$) and low ammonium (generally $<1\,mmol\,N\,m^{-3}$) concentrations. Phytoplankton production in the high-biomass zones was sustained mainly by ammonium, and ammonium regeneration was enough to supply microplankton demands at daily scales. The average values of *f* ratio for Bellingshausen Sea and Gerlache Strait stations were 0.39 and 0.42, respectively. Despite the high biomass observed, chlorophyll-specific inorganic nitrogen uptake was low in these areas when compared with stations in the western Bransfield Strait, where a new bloom (based on nitrate) was developing (mean *f* ratio of 0.64). Dominance of flagellates and small diatoms, accumulations of nitrite, and ammonium regeneration rates exceeding upate rates in the western Bransfield Strait suggest that the bloom was a secondary succession stage. The variability in phytoplankton composition and nitrogen dynamics can be interpreted as a consequence of the diversity of environments in this region, but also as the result of the different temporal stages of seasonal succession of microplankton. Our results show that instead of a gradual change from nitrate-based to ammonium-based production as the summer season progressed, secondary blooms using nitrate as the primary nitrogen source may develop in areas like the western Bransfield Strait during mid summer. Rapid nitrogen uptake and growth efficiencies during active phytoplankton growth periods in these areas may produce large differences between short-term and seasonal estimations of nitrate consumption during the ice-free season.

1. Introduction

Among the various subregions of the Southern Ocean (Tréguer and Jacques, 1992), the waters surrounding the Antarctic Peninsula exhibit a large range of environmental variability, and although their phytoplankton blooms have been studied by different research programmes (El Sayed and Weber, 1982; Holm-Hansen and Mitchell, 1991; Karl et al., 1991, 1996), there are still large uncertainties in the magnitude and fate

*Corresponding author. Tel.: +34-981-205362; fax: +34-981-229077.
E-mail address: antonio.bode@co.ieo.es (A. Bode).

0967-0645/01/$ - see front matter
PII: S0967-0645(01)00124-2

of their biological productivity (Karl et al., 1996). Nitrogen dynamics has been studied often in this area because of its implications in the recycling versus export of organic matter, following the concepts of new and regenerated production (Eppley and Peterson, 1979). A number of studies employed incubations of plankton with ^{15}N tracers to measure short-term uptake rates (Olson, 1980; Glibert et al., 1982a; Rönner et al., 1983; Koike et al., 1986; Goeyens et al., 1991a; Owens et al., 1991; Bury et al., 1995; Waldron et al., 1995). The prevailing conclusion of these studies was that utilization of new nitrogen (nitrate) decreases during the summer season in favour of the use of ammonium (regenerated nitrogen) as the source of inorganic nitrogen for phytoplankton growth. There are reports of such shifts in the f ratio within a period of several weeks after ice melting (Goeyens et al., 1991a), and low values have been generally reported for late summer (Koike et al., 1986; Owens et al., 1991). In addition, size-fractionation studies supported the progressive increase in ammonium utilization by nanophytoplankton, as the succession progressed from diatoms and large cells toward small flagellates (Owens et al., 1991; Bury et al., 1995).

Since the periods of high production and bloom development are irregularly distributed, average f values computed from available data for the west of the Antarctic Peninsula are low, implying an important role of nitrogen recycling in sustaining phytoplankton populations. Some studies estimate that significant amounts of ammonium could be regenerated by the existing plankton, particularly, microbial organisms (Koike et al., 1986), but only few studies report measurements of nitrogen remineralization rates (Glibert, 1982; Goeyens et al., 1991b). This dependence on regenerated nutrients would also imply that export rates of organic matter should be low, however, sedimentation rates measured below the euphotic layer are similar to those obtained in productive coastal systems (Karl et al., 1991). Jacques (1991) concluded that the relationships between new, regenerated, total and export production in the Southern Ocean were different from those found in other areas.

In the context of the FRUELA programme, aimed at the quantification of the carbon cycle during the season of occurrence of phytoplankton blooms in the western Bransfield Strait region, this study examines the use and regeneration of inorganic nitrogen in the area with the aim of ascertaining whether there is a trend toward decreasing f ratios as phytoplankton sucession progresses. Nitrate and ammonium uptake (new and regenerated production), and ammonium regeneration rates were quantified and compared with parallel estimations of nutrient deficit from mass balance calculations (Castro et al., 2002) and carbon production (Morán and Estrada, 2002; Varela et al., 2002). The implications of such rates versus other processes like particle sedimentation (Anadón et al., 2002) and heterotrophic activity of bacteria (Pedrós-Alió et al., 2002) and microflagellates (Vaqué et al., 2002) are also analysed.

2. Methods

Sixteen stations were studied in an area that included the western sector of the Bransfield Strait, the southern sector of the Bellingshausen Sea and the Gerlache Strait (Fig. 1) between December 1995 and January 1996 (FRUELA 95 cruise). Water samples were collected using Niskin bottles in a CTD-rossette system. Temperature, salinity and in situ fluorescence profiles were recorded by a CTD MarkIIIC probe. Dissolved inorganic nutrients (nitrate, nitrite and ammonium), chlorophyll-*a*, and particulate nitrogen were analysed at 5–9 depth levels within the euphotic layer. Dissolved inorganic nitrogen forms (nitrate, nitrite and ammonium) were determined by the methods of Hansen and Grasshoff (1983) and Mouriño and Fraga (1985) using an autoanalyzer Technicon AAII system (Castro et al., 2002). Chlorophyll-*a* was measured in acetonic extracts of particles retained by Whatman GF/F filters. These extracts were used to calibrate the CTD fluorescence sensor. Irradiance profiles were measured at noon at each station using an LiCOR irradiance sensor, and total daily irradiance was recorded on board (Figueroa, 2002). Phytoplankton species composition was analyzed in Lugol's preserved samples

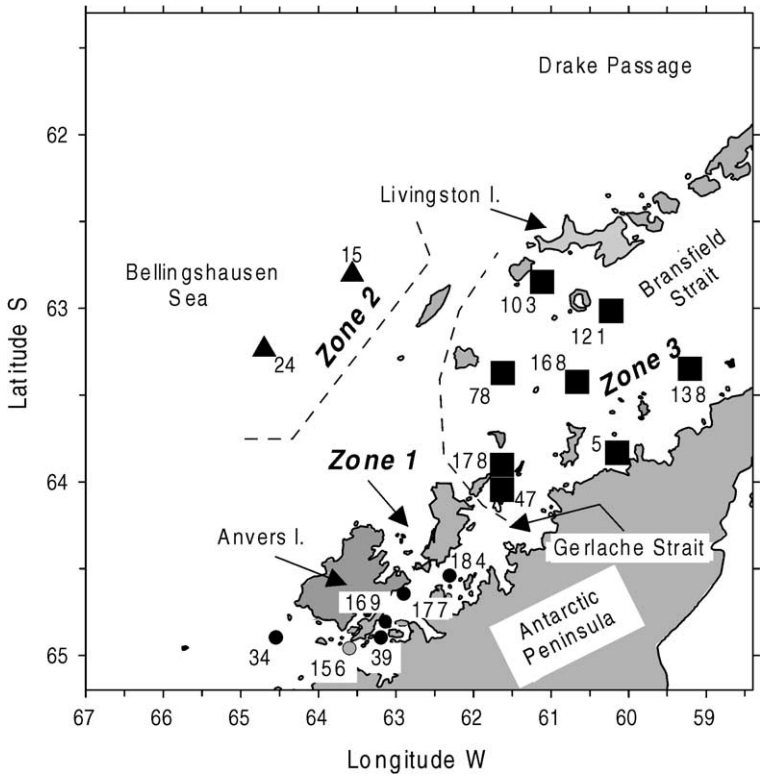

Fig. 1. Map of study area with sampling stations coded according to the zones considered (see text).

with an inverted microscope. Phytoplankton composition and biomass were used to define three distinct zones in the study area. These zones roughly correspond to those defined in Varela et al. (2002) although these authors also study results from additional stations in the same cruise and data from another cruise in January 1996.

Nitrate and ammonium uptake, and ammonium regeneration were determined by means of incubations of 1 l water samples from irradiance levels corresponding to 100%, 10% and 1% of surface irradiance at all stations except for stations 168, 169 and 177, where only samples from 100% and 10% levels were incubated, and stations 178 and 184, where only surface samples were considered. Water for the incubations was collected between 03:00 and 06:00 h (GMT), i.e. near the end of the brief dark period. Additions of 0.1 μmol ^{15}N as nitrate or ammonium were made to duplicate bottles immediately after sampling. These additions produced average increments of only 0.8% ($\pm$0.1% standard error, s.e.) of initial concentration in the case of nitrate and 27.4 ($\pm$7.9% s.e.) in the case of ammonium. Dissolved inorganic nitrogen concentration was measured at the beginning of the incubation (in parallel inoculated bottles) and also at the end of the incubation (in the case of ammonium incubations). Particulate nitrogen concentrations, along with ^{15}N abundance in particles (in nitrate and ammonium incubations) and in the dissolved phase (in ammonium incubations), were analyzed at the end of incubations, using Whatman GF/F filters and an isotope-ratio mass spectrometer (Integra-N, Europa Scientific). Mean ($\pm$s.e.) differences in ^{15}N abundance between two replicates were $1.8\pm0.3\%$ for particulate material ($n = 220$), and $2.5\pm0.5\%$ for dissolved ammonium ($n = 70$). All

samples were incubated on board for up to 3 h using an indoor system with chambers refrigerated at the temperature of sampling depth ($\pm 0.5^{\circ}$C) and illuminated with halogen lamps (maximum photosynthetically active irradiance: 102.8 μmol photons $m^{-2} s^{-1}$). Irradiance levels of 10% and 1% of maximum irradiance were simulated by neutral density screens. At stations 156, 168, 169, 178 and 184, parallel samples were incubated in situ for 24 h using a mooring system, and on board for up to 6 h, to measure uptake and regeneration rates in light and dark conditions at 3 h intervals. Uptake and regeneration rates were computed using the models of Glibert et al. (1982b), taking into account isotope dilution during the incubations with ammonium.

Water-column integrated uptake rates were computed for each station using values of chlorophyll-specific hourly rates averaged within zones, and the vertical profiles of chlorophyll concentration derived from fluorescence. This procedure was adopted because of the lack of uptake measurements at some depths. Values of nitrogen uptake and regeneration rates were interpolated between the sampling depths in intervals of 1 m. Vertical integrations were made either in the euphotic layer, where irradiance was higher than 1% of surface irradiance, and in the upper mixed layer, estimated as the depth where the difference in σ_t values between 5 m intervals was higher than 0.05 (Mitchell and Holm-Hansen, 1991). In the first step, all values were computed using the rates measured on board. For comparative purposes with in situ measurements, uptake and regeneration rates were scaled using a surface irradiance (I_0) value of 21.46 mol photons $m^{-2} d^{-1}$ for all stations, equivalent to the median value received during the cruise, using the irradiance profile and the dependence of uptake from irradiance measured at each station. Finally, measured rates were reported as daily rates after correcting for differences between light and dark periods according to the results of the time series incubations. Relative uptake of nitrate was expressed as f ratio (Eppley and Peterson, 1979) computed from daily rates. In addition, daily nitrate uptake values in the upper mixed layer computed from ^{15}N incubations were compared with values estimated from the nitrate deficit in that layer. The latter was calculated as the difference between winter nitrate concentration (pre-bloom conditions) and average nutrient concentration in the upper mixed layer, following Le Corre and Minas (1983). A phytoplankton growing period of 30 days was considered. Winter nitrate concentration was estimated from the remnant of Antarctic Surface Water as described in Castro et al. (2002).

3. Results

3.1. Environmental and phytoplankton characteristics

Stations were arranged in three distinct zones characterized by a differential phytoplankton composition, though flagellates were the most abundant cells in all zones (Table 1). These zones corresponded to areas with contrasting hydrographic and chemical characteristics (Garcia et al., 2002; Gomis et al., 2002; Castro et al., 2002). Zone 1 was localized mainly near Anvers Island and Gerlache Strait (Stations 34, 39, 156, 169, 177 and 184; Fig. 1). In this zone, large diatoms (e.g., *Eucampia antarctica*) or chain forming diatoms (e.g., *Chaetoceros socialis*) were present in significant numbers. Zone 2 was restricted to Stations 15 and 24 in the Bellingshausen Sea, associated to the Continental Water Boundary frontal region (see Garcia et al., 2002; Gomis et al., 2002). Large colonies of the Prymnesiophyte *Phaeocystis* cf. *antarctica* were characteristic of this region. Stations of zone 3 were located in the western region of the Bransfield Strait (Stations 5, 47, 78, 103, 121, 138, 168 and 178; Fig. 1). Temperature and salinity vertical profiles of zone 1 were quite variable. The lowest temperatures corresponded to station 34, due to the penetration of Antartic Surface Water, whose core completely vanished at approximately station 169 in the Gerlache Strait (Garcia et al., 2002). Most of the stations revealed an upper mixed layer (51 ± 13 m, Table 2) where large fluorescence peaks occurred, mainly near the surface (Fig. 2). Profiles of zone 2 were similar, indicating a depth of ~ 50 m for the upper mixed layer (Table 2). In this case, phytoplankton biomass (indicated by the fluores-

Table 1
Mean abundance (cells ml^{-1}) of the dominant phytoplankton species in the main zones[a]

Zone 1				Zone 2				Zone 3			
Species	Mean	s.e.	*n*	Species	Mean	s.e.	*n*	Species	Mean	s.e.	*n*
Dinoflagellates											
Small dinoflagellates	35.5	4.6	26	*Amphidinium sphenoides*	6.2	3.9	3	Small dinoflagellates	114.1	14.9	38
Other dinoflagellates	4.8	0.6	26	*Gyrodinium glaucum*	5.3	1.3	4	Other dinoflagellates	3.6	0.6	38
				Small dinoflagellates	66.0	18.0	6				
				Other dinoflagellates	6.2	1.3	6				
Diatoms											
Chaetoceros socialis	19.0	3.7	17	*Chaetoceros socialis*	11.3	1.6	6	*Pseudo-nitzschia heimii*	9.2	0.9	38
Eucampia antarctica	19.8	4.9	25	*Corethron cryophilum*	14.0	5.8	6	Other diatoms	4.6	0.5	38
Thalassiosira gravida	19.5	3.3	24	*Thalassiosira gravida*	24.2	9.9	6				
Small diatoms	537.6	303.2	9	Other diatoms	80.5	16.7	6				
Other diatoms	61.7	7.0	26								
Flagellates											
Pyramimonas sp.	167.1	87.0	23	*Phaeocystis* cf. *antarctica*	3583.3	750.3	6	*Pyramimonas* sp.	6.9	1.8	16
Cryptomonas sp.	187.9	116.1	21	*Cryptomonas* sp.	11.3	5.4	4	*Dynobryon belgica*	2.1	0.4	12
Phaeocystis cf. *antarctica*	1470.6	468.0	26	*Distephanus speculum*	5.6	1.2	5	*Cryptomonas* sp.	2151.9	423.4	38
Monads 8–10 μm	107.3	26.1	26	Monads 8–10 μm	75.0	8.9	6	*Phaeocystis* cf. *antactica*	629.5	134.6	26
Monads 5–8 μm	428.1	110.6	26	Monads 5–8 μm	612.2	174.0	6	Monads 8–10 μm	179.2	17.8	38
Monads 3–5 μm	2955.9	343.1	26	Monads 3–5 μm	9718.0	2241.0	6	Monads 5–8 μm	355.8	39.1	38
								Monads 3–5 μm	3544.6	310.6	38

[a] s.e.: standard error of the mean, *n*: number of samples.

Table 2
Mean (and standard error, s.e.) stocks (mmol N m^{-2}) and fluxes (mmol N m^{-2} d^{-1}) of nitrogen integrated in the upper mixing layer in the zones considered in this study[a]

	Zone 1		Zone 2		Zone 3	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Particulate nitrogen	151.6	26.6	204.8	24.7	135.2	22.3
Nitrate	1362.8	391.1	928.5	235.3	1264.0	323.4
Ammonium	31.1	6.3	27.8	3.8	18.4	4.5
Nitrate deficit	3.0	0.7	15.0	4.7	5.1	1.6
Nitrate uptake	9.0	2.7	17.0	2.5	13.0	3.1
Ammonium uptake	24.1	17.0	40.9	10.2	7.8	2.6
Ammonium regeneration	28.6	19.9	44.9	12.6	15.3	5.1
Chlorophyll-*a*	221.8	88.8	665.6	251.8	42.2	10.1
f ratio	0.42	0.08	0.31	0.08	0.64	0.03
Mixing layer depth	50.8	12.9	45.5	3.5	46.9	11.3

[a] The depth of the mixing layer (m) and integrated chlorophyll (mg m^{-2}) are also indicated. Number of stations averaged for zones 1, 2 and 3 are, respectively, 6, 2 and 8. Nitrate concentrations also include nitrite. Nitrate deficit indicated the difference between average nitrate concentration in the upper mixing layer and nitrate concentration in winter water, considering a phytoplankton growing period of 30 d (see Section 2).

cence profiles) appeared quite uniformly distributed by the surface layer. Integrated chlorophyll in the euphotic zone was only 38% of integrated biomass in the upper mixed layer. Stations of zone 3 displayed differences in the temperature profiles in the upper mixed layer, but all had similar fluorescence profiles characterized by relatively low fluorescence values and small (or almost nonexis-

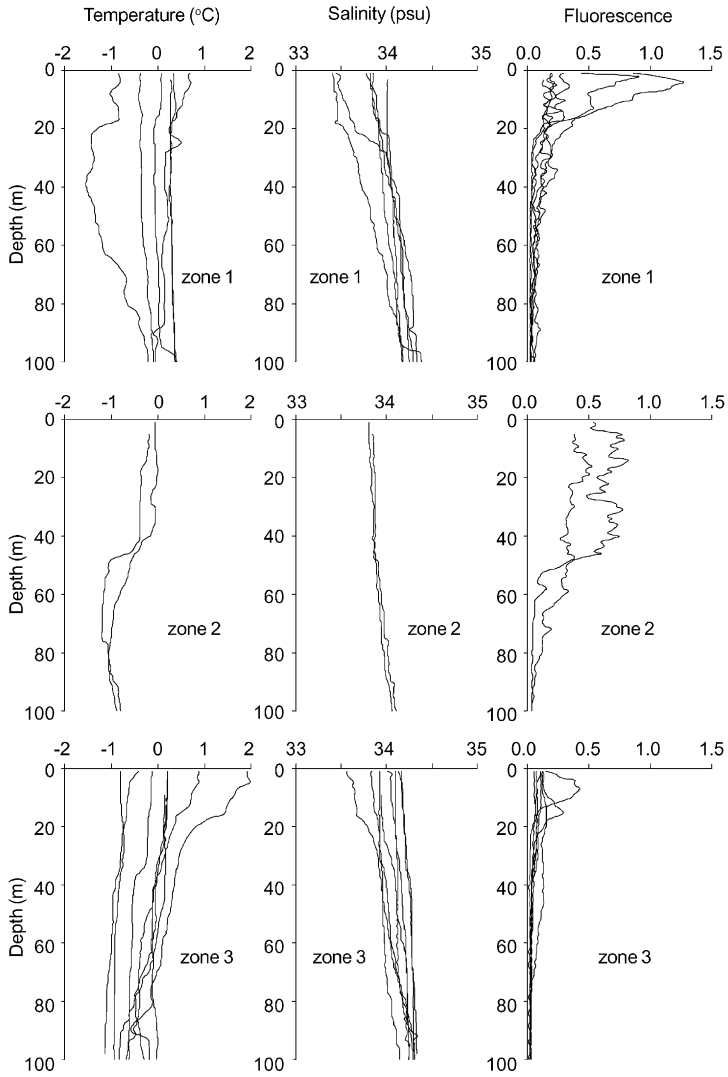

Fig. 2. Vertical profiles of temperature (°C), salinity (psu) and in situ fluorescence (relative units) in the sampling stations grouped by zones (see text).

tent) subsurface peaks restricted in general to the upper 20 m (Fig. 2).

Oxidized forms (nitrate and nitrite) were the dominant forms of inorganic nitrogen in all stations (Fig. 3). Surface values of nitrate were always higher than 10 mmol N m^{-3} and increased to near 30 mmol N m^{-3} towards the bottom of the euphotic zone. Marked slopes in the profiles of this nutrient were observed in some cases when large peaks of phytoplankton biomass occurred near the surface (e.g., zone 1). Nitrite concentrations (not shown) were always less than 1% of total oxidized nitrogen, and did not display noticeable maxima in the upper mixed layer. However, average nitrite concentration in zone 1 was 0.08 ($\pm$0.01 s.e.) mmol N m^{-3} ($n = 20$), while that of zone 3 (0.12 $\pm$ 0.01, $n = 35$) was significantly higher (Mann–Whitney test, $p < 0.001$). Ammonium concentration was generally < 0.2 μmol N l^{-1} near the surface, but vertical profiles were more variable

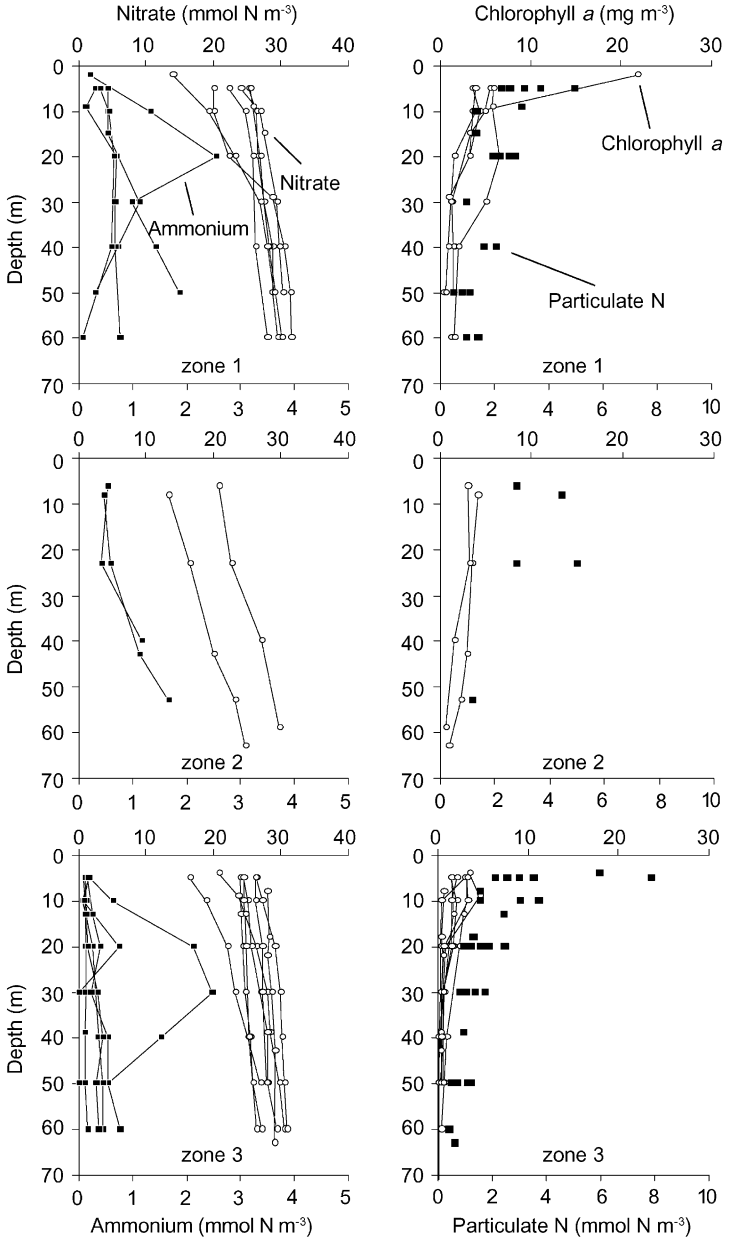

Fig. 3. Vertical profiles of dissolved nitrate (plus nitrite) and ammonium concentrations (mmol N m^{-3}), chlorophyll-*a* (mg m^{-3}) and particulate nitrogen (mmol N m^{-3}) in the sampling stations grouped by zones (see text).

than those of nitrate (Fig. 3). Subsurface peaks occurred between 20 and 40 m in some stations of zones 1 and 3, while concentration increased with depth in the stations of zone 2.

Chlorophyll-*a* profiles in Fig. 3 mirrored those of in situ fluorescence (Fig. 2), but the concentrations of particulate nitrogen suggested the existence of non-phytoplanktonic organic material

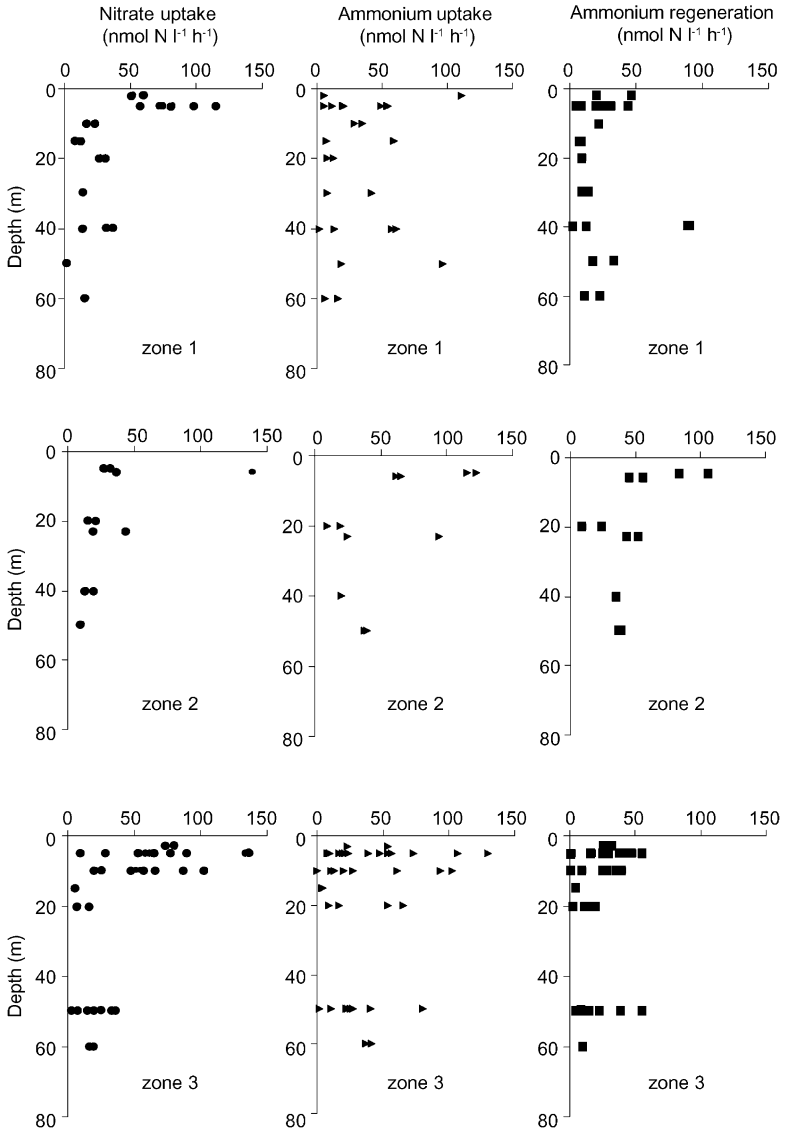

Fig. 4. Measured rates of nitrate uptake, ammonium uptake and ammonium regeneration (nmol $N\,l^{-1}\,h^{-1}$) under constant irradiance on board. Measurements were grouped by zones (see text).

near the surface of zones 2 and 3. The depth of the euphotic layer ranged from 16 to 38 m, and the range of the upper mixed layer was between 16 and 100 m. No significant differences resulted between values averaged by zones due to large variances (Kruskall–Wallis test, $p > 0.05$, $n = 16$).

3.2. Nitrogen uptake and regeneration rates

Nitrate uptake rates measured on board were generally higher in surface than in deep-water samples (Fig. 4). Maximum values did not exceed 150 nmol $N\,l^{-1}\,h^{-1}$ for zones 1 and 2 but reached

ca. 280 nmol N l^{-1} h^{-1} in some stations of zone 3, the highest values for this rate. Ammonium uptake was more variable with depth than nitrate, with high values in intermediate or deep-water samples (Fig. 5). The measured values were in the range of 0.4–130 nmol N l^{-1} h^{-1}. Ammonium regeneration was in general lower than 100 nmol N l^{-1} h^{-1}, and peak values in the water column occurred near the surface in all zones as well as in some deep-water samples (e.g., zone 3). No significant differences were found between ammonium transport rates measured with trace (i.e. $<10\%$ of initial ammonium concentration) or non-trace additions (Mann–Whitney test, $p > 0.05$, $n = 59$).

All measurements of ammonium uptake and regeneration made at stations of zone 2 employed trace additions (i.e. additions of ^{15}N that increased the ambient concentration of ammonium by less than 10%), while those made at stations of zone 3 employed non-trace additions. However, half of the ammonium uptake and regeneration rates determined at stations of zone 1 were made with trace additions, which allowed for the study of possible effects of the addition of excess ammonium during the measurements. The differences in average values of both uptake and regeneration rates measured with trace and non-trace additions of ammonium (Fig. 5) were statistically non-significant (Mann–Whitney test, $p > 0.05$, $n = 16$), either in absolute value or when normalized to particulate nitrogen or chlorophyll-*a*, suggesting that the ammonium additions employed did not affect the measured process rates.

The values of chlorophyll-normalized nitrogen uptake and regeneration rates averaged according to the irradiance level (Fig. 6) resulted in non-significant differences within zones for nitrate uptake, but significant differences resulted in ammonium uptake rates corresponding to samples from the 1% irradiance level of zone 3 (ANOVA and Student—Neuman–Keuls 'a posteriori' test, $p < 0.05$). This indicates that, due to the relatively high variance of the results obtained for each irradiance level, the apparent differences in mean values for the three irradiance levels are not large enough to produce significant differences when taken into account to compare water column rates within zones. As a consequence, we used the average value of chlorophyll-specific uptake rates within zones (except for ammonium uptake in zone 3) in the computation of depth-integrated rates.

Nitrate uptake rates resulted significantly higher in light than in dark periods (Mann–Whitney test, $p < 0.01$, $n = 22$; Fig. 7A). On an average, uptake rates measured during light periods nearly doubled those measured during dark periods. However, large variances produced non-significant differences for ammonium uptake or regeneration rates between light and dark periods (Fig. 7A). Daily nitrogen transport rates computed from 3 h incubations on board were equivalent to those measured in 24 h incubations (Mann–Whitney test, $p > 0.05$, $n = 7$; Fig. 7B).

Daily nitrate uptake was similar in all zones (Kruskal–Wallis test, $p > 0.05$; Fig. 8A). Average values were ca. 10 mmol N m^{-2} d^{-1} in the euphotic layer and ca. 20 mmol N m^{-2} d^{-1} in the upper mixed layer. High values (up to 26 mmol N m^{-2} d^{-1}) were computed for some stations of zone 3 with high abundance of *Cryptomonas* (Stations 47, 78, 121 and 178). Large apparent differences appeared in ammonium uptake and regeneration rates between zones, but again due to large variance these differences were non-significant (Kruskal–Wallis test, $p > 0.05$, Fig. 8B and C). Average ammonium uptake and regeneration rates were approximately balanced within zones (Mann–Whitney test, $p > 0.05$). However, mean f ratio values for both the upper mixed and the euphotic layer at stations of zone 3 were significantly higher than those at zones 1 and 2 (ANOVA and Student–Neuman–Keuls a posteriori test, $p < 0.05$; Fig. 8D).

Daily primary production estimated from ^{15}N uptake (nitrate plus ammonium) was significantly correlated with carbon uptake ($r = 0.89$, $n = 11$, $p < 0.001$), measured in parallel samples inoculated with ^{14}C bicarbonate and incubated in situ or on board for 24 h, as described in Varela et al. (2002). The mean molar C : N uptake ratio computed from these values was 9.2 (± 1.2 s.e.).

3.3. Nitrogen budgets for the upper mixed layer

Average stocks of particulate *N* and chlorophyll were significantly higher in zone 2 compared with

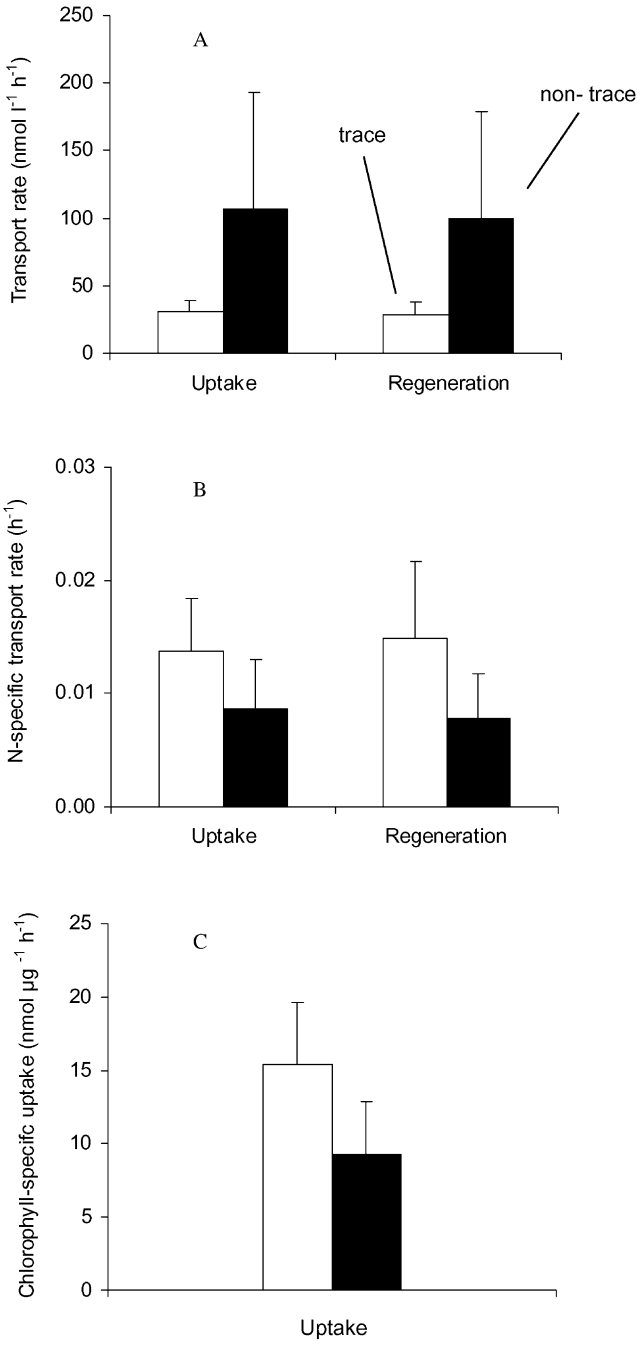

Fig. 5. Mean (+standard error) values of ammonium uptake and regeneration rates measured with trace (white bars) or non-trace ^{15}N-additions (black bars) at stations of zone 2 ($n = 8$). (A) Absolute transport rates (nmol N l^{-1} h^{-1}). (B) N-specific transport rates (h^{-1}). (C) Chlorophyll-specific ammonium uptake (nmol N (µg chl *a* h)$^{-1}$). None of the pairs of trace vs. non-trace means were significantly different (Mann–Whitney test, $p > 0.05$, $n = 16$).

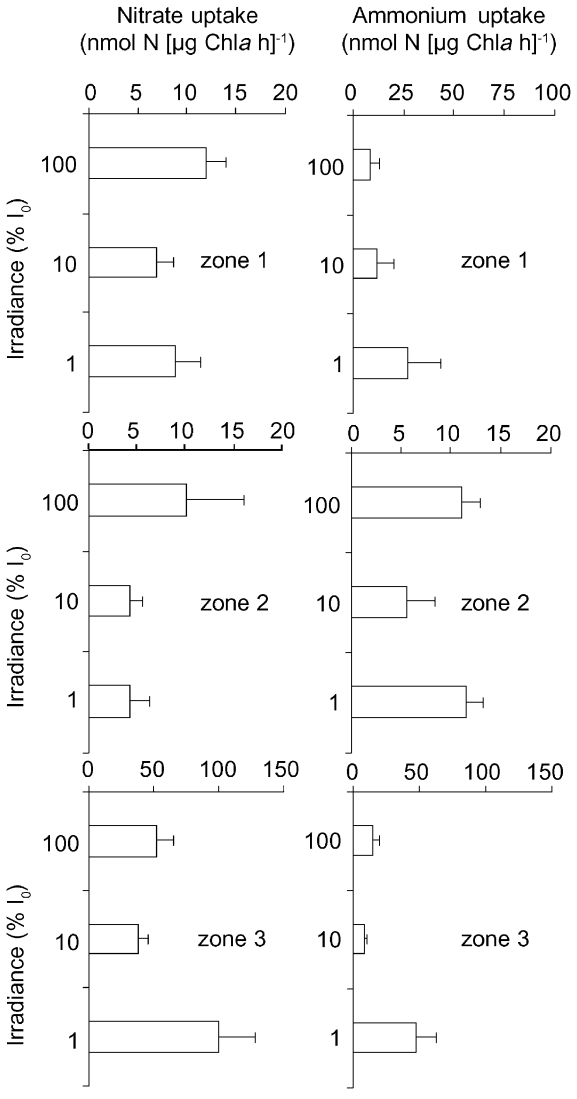

Fig. 6. Mean (+standard error) values of chlorophyll-specific nitrate and ammonium uptake (nmol N (µg chl *a* h)$^{-1}$) measured at the simulated irradiance levels on board (percent of maximum irradiance I_0). Measurements were grouped by zones (see text).

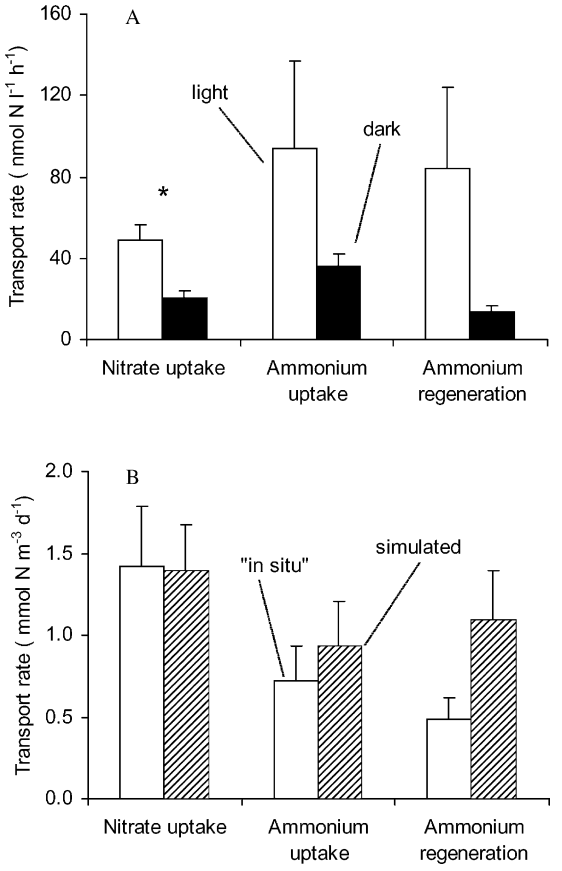

Fig. 7. (A) Comparison of mean (+standard error) values of absolute nitrate and ammonium uptake, and ammonium regeneration rates (nmol N l^{-1} h^{-1}) during short-term light (open bars) and dark incubations (black bars) on board. Asterisks indicate significant mean values (Mann–Whitney test, $p<0.05$, $n=7$). (B) Comparison of mean (+standard error) values of daily nitrate and ammonium uptake, and ammonium regeneration rates (nmol N m^{-3} d^{-1}) measured in 24 h moored bottles (white bars) and calculated from short-term incubations on board (black bars). None of the paired means were significantly different (Mann–Whitney test, $p>0.05$, $n=7$).

the other zones (Kruskal–Wallis test, $p<0.05$, $n=16$, Table 2). Despite these differences, uptake rates of ammonium were high (24.1–40.9 mmol N m^{-2} d^{-1}) in zones 1 and 2 and low (7.8 mmol N m^{-2} d^{-1}) in zone 3. Inorganic nitrogen stocks were similar in all zones, but mean nitrate (plus nitrite) concentration was lower in zone 2 compared with mean values in the other zones. Nitrate uptake rates computed from ^{15}N incubations at stations of zone 2 agree with nitrate deficit estimated from differences between measured nitrate concentrations and nitrate concentrations in winter (Castro et al., 2002). However, average nitrate deficit estimated for zones 1 and 3 was up to 3 times lower than daily nitrate uptake computed from ^{15}N incubations (Table 2).

According to values given in Table 2, nitrate stocks would allow the maintenance of the

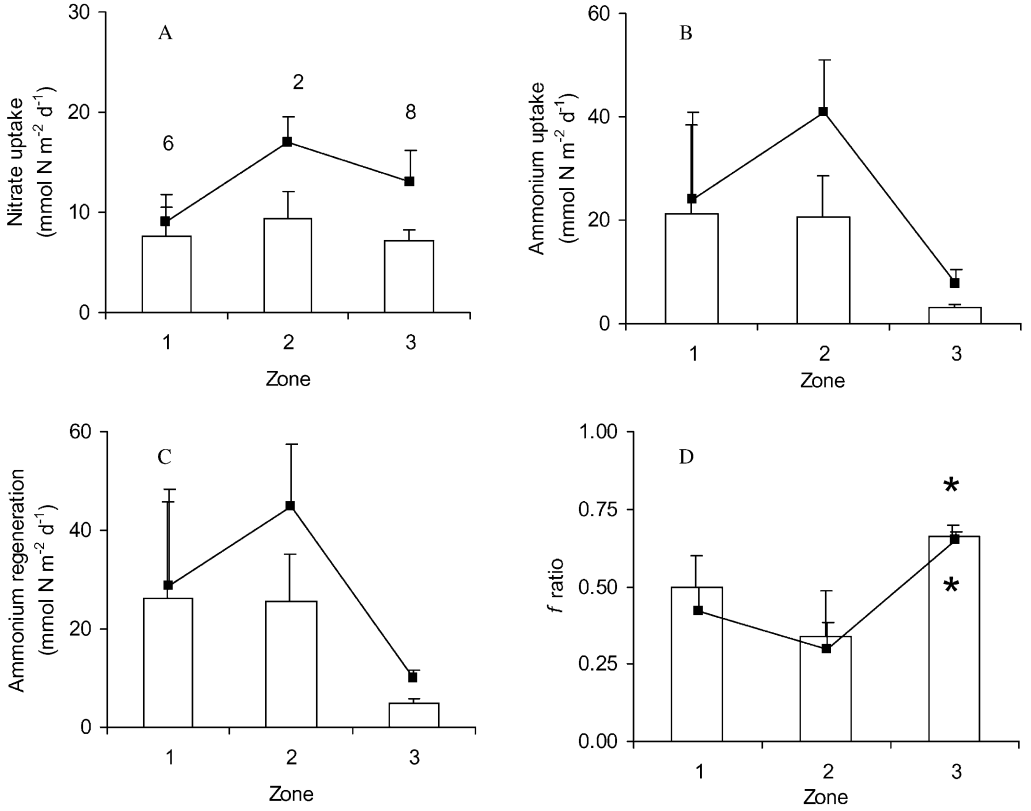

Fig. 8. Mean (+standard error) daily water-column integrated rates of nitrate uptake (A), ammonium uptake (B), ammonium regeneration (C) and f ratio (D) in the selected zones. Rate values (mmol N m^{-2} d^{-1}) were integrated either in the euphotic layer (white bars) and in the upper mixing layer (black squares and lines). Values of the f ratio were computed from water-column integrated rates. Asterisks indicate significant mean values ($p<0.05$). Number of stations averaged are indicated above bars in the upper left panel.

estimated rates for 151, 54 and 97 days in zones 1, 2 and 3, respectively, if the nitrate uptake rates were kept constant and water-column nitrification and external inputs were neglected. Furthermore, ammonium regeneration can supply a large portion of nitrogen requirements in all zones, since average ammonium uptake was approximately equivalent to regeneration in zones 1 and 2, and half of regeneration values in zone 3.

The differences in chlorophyll-normalized uptake rates between zones indicate that phytoplankton in zone 3 was on average more efficient in taking up inorganic nitrogen (Table 3). On the other hand, rates normalized to particulate N show similar average efficiencies in all zones for nitrate uptake but lower values in zone 3 for ammonium uptake. Using the estimated total N uptake we computed turnover rates of particulate N stocks, as the reciprocal of the particulate nitrogen-normalized total N uptake, that ranged from 3.6 days in zone 2 to 6.7 days in zone 3.

4. Discussion

Traditionally, one of the major concerns in the studies of nitrogen uptake in the sea using ^{15}N additions has been the employment of true trace concentrations of the isotope (e.g., Glibert, 1988). The reason is that large additions of inorganic nitrogen may alter actual uptake rates of phytoplankton, particularly in oligotrophic waters when

Table 3
Average values of chlorophyll-normalized (mmol N (mg.chl-a d)$^{-1}$) and particulate nitrogen-normalized (d)$^{-1}$ rates of nitrate and ammonium uptake using mean values integrated in the upper mixing zone for the zones considered in this study (Table 2)[a]

	Zone 1	Zone 2	Zone 3
Chlorophyll normalized rates:			
Nitrate uptake (mmol N (mg chl-a d)$^{-1}$)	0.04	0.03	0.31
Ammonium uptake (mmol N (mg chl-a d)$^{-1}$)	0.11	0.06	0.18
Particulate N-normalized rates:			
Nitrate uptake (d^{-1})	0.06	0.08	0.09
Ammonium uptake (d^{-1})	0.16	0.20	0.06
Total N uptake (d^{-1})	0.22	0.28	0.15
N turnover rate (d)	4.55	3.57	6.67

[a]The average nitrogen turnover rate in particles (d) is also estimated as the reciprocal of the particulate nitrogen-normalized rate of nitrate plus ammonium uptake (total N uptake). Number of stations averaged for zones 1, 2, 3 are, respectively, 6, 2 and 8.

cells are nitrogen limited. High nitrate concentrations in Antarctic surface waters make unnecessary large additions of ^{15}N-labelled nitrate, but ammonium concentrations are generally well below 1 mmol N m^{-3}, and even small additions may cause significant enrichments, as in our study. However, we did not find any significant relationship in ammonium uptake or regeneration rates between true trace and non-trace isotope additions, which suggests that the response of phytoplankton cells was not perturbed during our experiments. Furthermore, while the comparison of uptake rates measured with true trace and non-trace additions of ^{15}N is often used to ascertain the nutritional status of phytoplankton, the non-trace additions employed are often much greater (usually 10 times the ambient concentrations, e.g., Glibert and McCarthy, 1984) than those produced during our experiments.

Another methodological problem is related to the length of the incubations, since the rate at which nitrogen is incorporated into particulate material may be non-linear. This is particularly important in the case of ammonium because of the rapid decrease in the uptake response shortly after the enrichment (Glibert and Goldman, 1981; Wheeler et al., 1982; Harrison, 1983) and the increase in isotope dilution as a consequence of ammonium regeneration in long incubation periods (Glibert et al., 1982b). Most of the studies using ^{15}N incubations near the Antarctic Peninsula employed 24 h incubations to compute daily nitrogen uptake rates and f ratios (Koike et al., 1986; Goeyens et al., 1991a, b; Owens et al., 1991; Bury et al., 1995; Waldron et al., 1995). These studies report net uptake rates but generally neither gross nitrogen uptake nor regeneration rates in the water column are known. Koike et al. (1986) performed time-course incubations and reported variations in both nitrate and ammonium uptake related to light–dark cycles. While nitrate uptake displays a clear pattern of light dependence in most studies (Koike et al., 1986; Cochlan et al., 1991; this study), ammonium uptake may have a light response similar to that of nitrate (Cochlan et al., 1991), weak light dependence (Koike et al., 1986) or non-significant pattern, as in our study. These variations in nitrate uptake rates during the day–night cycle may underestimate daily f ratios if daily rates are computed only for the light period and dark uptake is neglected. However, daily uptake and regeneration rates computed in our study using short incubations, which take into account both the actual irradiance and variations related to the photoperiod, were similar to those measured in 24 h in situ incubations. We did not measure urea uptake; however, urea uptake is known to be important only in waters under the ice (Bury et al., 1995). Similarly, additional inputs of new or regenerated nitrogen from atmospheric or nearby coastal sources are expected to be small (Karl et al., 1996).

While chlorophyll concentrations found during FRUELA 95 cruise were within the range of values reported during studies of nitrogen dynamics in the area, particulate nitrogen reached values of up to 19 mmol N m^{-3}, which were ca. 2.5 times the maximum concentration known in the region (Owens et al., 1991). Nitrate uptake rates ranged from 0.01 to 1.37 mmol N m^{-3} d^{-1}, which also extend the reported range ca. twofold (Owens et al., 1991; Bury et al., 1995; Waldron et al.,

1995). Ammonium uptake rates were between 0.003 and 0.93 mmol N m^{-3} d^{-1}, similar to the widest range reported for summer cruises (0.01–0.72 mmol N m^{-3} d^{-1}; Owens et al., 1991). However, although uptake rates in most studies with ^{15}N are corrected for isotope dilution due to ammonium regeneration by microheterotrophs during the incubations (Glibert et al., 1982b), few studies report values of ammonium regeneration rates for the study area. Glibert (1982) measured regeneration rates up to 0.13 mmol N–NH_4^+ m^{-3} h^{-1} in the Scotia Sea (equivalent to 3.12 mmol N–NH_4^+ m^{-3} d^{-1} if the rate is maintained for 24 h), and Goeyens et al. (1991b) cited a range from < 0.002 to 0.43 mmol N–NH_4^+ m^{-3} d^{-1} in the nearby Scotia–Weddell Confluence, while our study produced values up to 5.11 mmol N m^{-3} d^{-1}. The range of values of nitrate and ammonium uptake and ammonium regeneration rates obtained during this study suggests that planktonic production during the summer season in the Antarctic Peninsula may be higher than that previously thought.

Recent reviews of Antarctic studies based on the measurement of f ratios (e.g., Smith and Sakshaug, 1990; Karl et al., 1996) have concluded that the source of nitrogen for phytoplankton production gradually changes from a predominantly nitrate nutrition in spring and early summer, to an increase in the use of regenerated nitrogen (predominantly ammonium but also dissolved organic nitrogen). However, the large variability in the values of the f ratio given by the different studies around the Antarctic Peninsula (0.54 in Olson (1980) and Glibert et al. (1982a); 0.37 in El Sayed and Weber (1982); 0.22 in Rönner et al. (1993); 0.07–0.35 in Koike et al. (1986); 0.30–0.78 in Goeyens et al. (1991a); 0.08–0.96 in Owens et al. (1991); 0.11–0.86 in Bury et al. (1995); 0.09–0.87 in Waldron et al. (1995); 0.39–0.86 in Goeyens et al. (1998)) not only reflects the progress from early to late summer, but also the variability due to the high spatial heterogeneity of the area, containing a large number of islands, straits, passages and more or less permanent frontal zones that modify the phytoplankton environment. The variation of f ratio observed during this study (from 0.17 to 1.00 in the upper mixed layer) supports the importance of spatial variability. Undersampling of zones with high f values might explain the reported discrepancy between low f ratios and high export production previously measured with sediment traps in the area (Karl et al., 1991). Results from daily sedimentation rates (Anadón et al., 2002) and carbon uptake rates (Varela et al., 2002) measured at some stations in parallel with our study allow for an independent estimation of short-term f ratios (daily export production relative to daily total production) to compare with our results. Station 184, in the high biomass large-phytoplankton zone 1, showed an f ratio value computed from carbon measurements of 0.15 that is equivalent to the value of 0.16 computed from ^{15}N incubations at the same station. In contrast, the average f ratio from carbon uptake and sedimentation of stations 168 and 178, in the low-chlorophyll zone 3, was ca. 0.30, while our average value for this zone was 0.65. These differences may be explained in part by the size-composition of the phytoplanktonic community, as there were large, fast-sinking diatoms in zone 1 and small, slow-sinking flagellates in zone 3. In addition, the release of recent photosynthates would increase the amount of export production at daily time scales. This is supported by the accumulation of dissolved organic carbon in the study area found during FRUELA cruises (Doval et al., 2002), although the values of the ratio dissolved-to-particulate carbon production measured in surface waters by Morán and Estrada (2002) resulted low while accounting for the difference at some stations.

Nitrogen dynamics and microplankton composition in the zones investigated during FRUELA 95 cruise can be interpreted in terms of the spatial variability introduced by the diverse environments provided by water circulation and coastal features (islands, passages, straits, among others) and the influence of the retreating ice. However, the observed variability also can be linked to the seasonal succession of microplanktonic communities. For instance, the biomass and productivity gradient observed from the rich zones 1 and 2 to the low-biomass zone 3 may reflect the progress from a primary bloom of large phytoplanktonic particles (zone 1, Gerlache Strait), which reaches a

final stage at the shelf-break (zone 2, Bellingshausen Sea), to an emerging secondary bloom of small phytoplankters during mid summer (zone 3, western Bransfield Strait). Varela et al. (2002) have shown that phytoplankton composition in the studied area changed between early (FRUELA 95) and mid-summer (FRUELA 96) cruises, particularly in the Bellingshausen Sea and western Bransfield Strait zones. The most noticeable changes were the dissapearance of most *Phaoecystis* colonies from the Bellingshausen Sea and the replacement of *Cryptomonas* by increasing numbers of diatoms and isolated *Phaeocystis* cells in the western Bransfield Strait.

The high biomass of phytoplankton in the western part of the study area (Bellingshausen Sea and Gerlache Strait) was mostly due to diatoms (zone 1) and to colonies of *Phaeocystis antarctica* (zone2). Phytoplankton in zone 1 was characterized not only by high abundance of large diatoms but also by flagellates, some of them, like those of genus *Pyramimonas*, of relatively large size, which resulted in most of the biomass being particles larger than 20 μm. Primary production in this zone ranged between 0.87 and 4.54 g $C\,m^{-2}\,d^{-1}$, displaying the highest values measured during both FRUELA cruises (Varela et al., 2002). Large phytoplankton blooms have been previously reported for the Gerlache Strait during summer, reaching concentrations of up to 700 mg chl-*a* m^{-2} (Holm-Hansen and Mitchell, 1991). Phytoplankton biomass and high primary production rates concentrated in the upper 30 m of this zone (Varela et al., 2002). At the same time, we found that chlorophyll-specific nitrogen uptake rates during light hours were approximately constant through the euphotic layer in this zone, indicating that uptake processes occurred with the same efficiency at all depths and irradiances that were considered, and therefore the existence of healthy and nutrient-adapted phytoplankton cells. However, there are several indications that the bloom observed in this zone was not in its initial stage. First, both the average chlorophyll-normalized and PN-normalized nitrogen uptake rates reached intermediate values compared to those measured in the other zones. Second, the mean *f* ratio of 0.42 indicated that nitrate was not the preferred nitrogen source as in the developing blooms. Third, despite the relatively low ammonium concentrations measured in the upper mixed layer, ammonium regeneration was sufficiently to compensate uptake at daily time-scales. The higher protection from the wind, the frequent presence of melting ice floes, and the absence of strong currents in the Gerlache Strait compared to the Bellingshausen Sea (Gomis et al., 2002) may provide the adequate conditions for the persistence of phytoplankton blooms in this zone during most of summer. This is supported by the finding of high phytoplankton biomass and primary production values during FRUELA 96 cruise, some weeks after our study (Varela et al., 2002). According to our results, the persistence of these blooms largely depends on regenerated nutrients (such as ammonium), that supply on an average near 60% of the microplankton nitrogen requirements.

In zone 2, the *Phaeocystis* bloom was restricted to a frontal area related to the Continental Water Boundary clearly marked during FRUELA 95 cruise (Garcia et al., 2002; Gomis et al., 2002), and were probably the remains of a spring bloom previously developed in the area, since *Phaeocystis* were not observed some weeks later (FRUELA 96 cruise, Varela et al., 2002). Water-column dynamics (Gomis et al., 2002), and nutrient concentrations (Castro et al., 2002) did not support the hypothesis of rapid in situ growth of the observed phytoplankton. In addition, our results show a preference for ammonium in the upper mixed layer in this zone (mean *f* ratio of 0.39 and average nitrogen-specific ammonium uptake rates higher than those of nitrate; Table 3) indicative of the final stages of the bloom (Glibert et al., 1982a; Wheeler et al., 1982). Furthermore, while the average chlorophyll-to-PN ratio for zone 2 was the highest of the study area (3.25 g chl-*a* $(mol\,N)^{-1}$, computed from values of Table 2), reflecting the dominance of phytoplankton in the seston, the sum of nitrate plus ammonium uptake rates normalized to chlorophyll (0.09 mmol N (mg chl-*a* $d)^{-1}$, computed from values of Table 3) was the lowest of this study, suggesting low efficiency of phytoplankton cells in this zone. Average turnover rates of PN and the high values of

ammonium regeneration, which were coincident with relatively high rates of bacterial production (Pedrós-Alió et al., 2002) and enhanced grazing activity of flagellates (Vaqué et al., 2002) also suggest that the *Phaeocystis* bloom was dissapearing. Previous reports related large blooms in the Bellingshausen Sea to ice melting during early summer (eg. Waldron et al., 1995).

In contrast to the other zones, the western Bransfield Strait (zone 3) displayed characteristics indicative of the development of a new secondary bloom, despite low phytoplankton biomass and primary production rates (Varela et al., 2002). Chlorophyll-specific nitrogen uptake reached maximum values in this zone, while average chlorophyll-to-PN ratio was the lowest of all zones studied. Similarly, Varela et al. (2002) noted that chlorophyll-specific carbon production rates were high in this zone. Furthermore, and in contrast to all other zones, nitrate was preferred to ammonium for uptake (mean f ratio of 0.64). The mismatch found between the measurements of nitrate uptake with ^{15}N incubations and the estimations of the average daily nitrate deficit computed from winter nitrate concentrations (Table 2) suggests that the measured rates, would be closer to maximum rates, but at the same time it indicates that they could not be maintained for a long period, as they would not agree with the nitrate deficit observed during the season (Castro et al., 2002).

Other studies have reported the persistence of phytoplankton populations with large abundances of Cryptophyceae near the Bransfield Strait region associated to ice melting (Schloss and Estrada, 1994; Socal et al., 1997). Differences in the characteristics of water bodies in which these populations grow (Schloss and Estrada, 1994), selective grazing by krill (Jacques and Panouse, 1991) or a combination of both (Socal et al., 1997) are some of the factors that presumably originated and maintained the Cryptophyceae in Bransfield Strait waters. However, in our study, there are indications that the developing bloom of small green flagellates, mostly *Cryptomonas* (Rodríguez et al., 2002; Varela et al., 2002) was produced after a previous one. First, regeneration rates largely exceeded uptake, suggesting the degradation of excess organic matter. Doval et al. (2002) found accumulations of dissolved organic carbon in excess to winter concentrations in the Bransfield Strait, which would result both from the transport from the Gerlache Strait by the Bransfield current (Gomis et al., 2002) and also from in situ production by phytoplankton (Morán and Estrada, 2002). Organisms of microbial food webs are known to be the main regenerators of ammonium in these waters (Koike et al., 1986; Tupas et al., 1994), while the contribution from larger heterotrophs, mostly crustacean plankton, would be small (Biggs, 1982; Huntley and Nordhausen, 1995). Heterotrophic bacteria (Pedrós-Alió et al., 2002) displayed low production values in Bransfield Strait during FRUELA 95 cruise, but at the same time Vaqué et al. (2002) showed that heterotrophic nanoplankton daily grazed up to 174% of bacterial carbon production in this zone, providing an indirect evidence of enhanced ammonium regeneration by microheterotrophs. Also, the high nitrite concentrations found in the upper water column of stations of zone 3 compared to the other zones is indicative of the existence of a previous bloom in that area. Dore and Karl (1992) reported the accumulation of nitrite in the Gerlache Strait as a bloom progressed from early to mid summer in 1991.

The prevailing view of nitrogen dynamics in the study area is based on a gradual change of phytoplankton preference from nitrate-based production during early spring to a regenerative system using ammonium as the preferred nitrogen source during late summer (e.g., Karl et al., 1996; Goeyens et al., 1998). This behaviour is expected to occur mainly in open-ocean areas and is coupled to ice retreating. However, the results presented in this study show that the use of inorganic nitrogen is highly variable in the western Bransfield Strait region and nearby areas during summer, not only because a different phytoplankton species composition in the zones were considered but also because of the temporal stage of bloom development in each zone. Based on our results and the change in phytoplankton species composition observed by Varela et al. (2002) during summer, we hypothesize that secondary blooms of green flagellates and small diatoms,

based mainly on nitrate uptake in their initial stages, may occur in Bransfield Strait waters following the dissapearance of a previous bloom. At the same time, ammonium regenerated through the microbial food web could favour the maintenance of blooms of large diatoms and *Phaeocystis* for most of the summer in wind-protected areas like the Gerlache Strait. Nitrogen dynamics in Antarctic waters during the seasonal succesion of phytoplankton is complicated by the high spatial and temporal variability found in coastal and shelf areas as those reported here for the Bransfield Strait region. Future studies must take into account the possible discontinuities in the progression from nitrate-based to regenerative systems.

Acknowledgements

We are grateful to all participants in FRUELA 95 cruise and to the crew of the BIO *Hesperides* for their technical support. Irradiance data were kindly collected and provided by Félix López Figueroa and chlorophyll and primary production data by Emilio Fernández and Pablo Serret. E. Fernández and two anonymous referees provided valuable suggestions in the earlier versions of the manuscript. We acknowledge the continuous support of Ricardo Anadón, as the coordinator of the whole project, and Marta Estrada, as the Chief Scientist of the cruise. This work was funded by the Spanish Antarctic Programme project number ANT94/1010.

References

Anadón, R., Alvarez-Marqués, F., Fernández, E., Varela, M., Zapata, M., Gasol, J.M., Vaqué, D., 2002. Vertical biogenic particle flux during Austral summer in the Antarctic Peninsula area. Deep-Sea Research II 49, 883–901.

Biggs, D.C., 1982. Zooplankton excretion and NH_4^+ cycling in near-surface waters of the Southern Ocean. I. Ross Sea, austral summer 1977–1978. Polar Biology 1, 55–67.

Bury, S.J., Owens, N.J.P., Preston, T., 1995. ^{13}C and ^{15}N uptake by phytoplankton in the marginal ice zone of the Bellingshausen Sea. Deep-Sea Research II 42, 1225–1252.

Castro, C.G., Ríos, A.F., Doval, M.D., Pérez, F.F., 2002. Nutrient utilisation and chlorophyll distribution in the Atlantic sector of the Southern Ocean during Austral summer 1995–96. Deep-Sea Research II 49, 623–641.

Cochlan, W.P., Harrison, P.J., Denman, K.L., 1991. Diel periodicity of nitrogen uptake by marine phytoplankon in nutrient-rich environments. Limnology and Oceanography 36, 1689–1700.

Dore, J.E., Karl, D.M., 1992. RACER: distribution of nitrite in the Gerlache Strait. Antarctic Journal US 27, 164–166.

Doval, M.D., Álvarez-Salgado, X.A., Castro, C.G., Pérez, F.F., 2002. Dissolved organic carbon distributions in the Bransfield and Gerlache Straits, Antarctica. Deep-Sea Reseach II 49, 663–674.

El Sayed, S.Z., Weber, L.H., 1982. Spatial and temporal variations in phytoplankton biomass and primary production in the southwest Atlantic and the Scotia Sea. Polar Biology 1, 83–90.

Eppley, R.W., Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282, 677–680.

Figueroa, F.L., 2002. Bio-optical characteristics of Gerlache and Bransfield Strait waters during an Antarctic summer cruise. Deep-Sea Research II 49, 675–691.

Garcia, M.A., Castro, C.G., Rios, A.F., Doval, M.D., Roson, G., Gomis, D., López, O., 2002. Water masses and distribution of physico-chemical properties in the Western Bransfield Strait and Gerlache Strait during Austral summer 1995/96. Deep-Sea Research II 49, 585–602.

Glibert, P.M., 1982. Regional studies of daily, seasonal and size fraction variability in ammonium remineralization. Marine Biology 70, 209–222.

Glibert, P.M., 1988. Primary productivity and pelagic nitrogen cycling. In: Blackburn, T.H., Sørensen, J. (Eds.), Nitrogen Cycling in Coastal Marine Ecosystems. Wiley, New York, pp. 3–31.

Glibert, P.M., Goldman, J.C., 1981. Rapid ammonium uptake by marine phytoplankton. Marine Biology Letters 2, 25–31.

Glibert, P.M., McCarthy, J.J., 1984. Uptake and assimilation of ammonium and nitrate by phytoplankton: indices of nutritional status for natural assemblages. Journal of Plankton Research 6, 677–697.

Glibert, P.M., Biggs, D.C., McCarthy, J.J., 1982a. Utilization of ammonium and nitrate during austral summer in the Scotia Sea. Deep-Sea Research 29, 837–850.

Glibert, P.M., Lipschultz, F., McCarthy, J.J., Altabet, M., 1982b. Isotope dilution models of uptake and remineralization of ammonium by marine plankton. Limnology and Oceanography 27, 639–650.

Goeyens, L., Sörensson, F., Tréguer, P., Morvan, J., Panouse, M., Dehairs, F., 1991a. Spatiotemporal variability of inorganic nitrogen stocks and uptake fluxes in the Scotia–Weddell confluence area during November and December 1988. Marine Ecology Progress Series 77, 7–19.

Goeyens, L., Tréguer, P., Lancelot, C., Mathot, S., Becquevort, S., Morvan, J., Dehairs, F., Baeyens, W., 1991b. Ammonium regeneration in the Scotia–Weddell confluence area during spring 1988. Marine Ecology Progress Series 78, 241–252.

Goeyens, L., Semeeh, F., Baumann, M.E.M., Elskens, M., Shopova, D., Dehairs, F., 1998. Phytoplanktonic nutrient utilisation and nutrient signature in the Southern Ocean. Journal of Marine Systems 17, 143–157.

Gomis, D., García, M.A., López, O., Pascual, A., 2002. Quasi-geostrophic 3D circulation and mass transport in the western Bransfield Strait during Austral summer 1995/96. Deep-Sea Research II 49, 603–621.

Hansen, H.P., Grasshoff, K., 1983. Automated chemical analysis. In: Grasshoff, K., Ehrhardt, M., Kremling, K. (Eds.), Methods of Seawater Analysis, 2nd Edition.. Chemie, Weinheim, pp. 347–395.

Harrison, W.G., 1983. The time-course of uptake of inorganic and organic nitrogen compounds by phytoplankton from the Eastern Canadian Arctic: comparison of temperate and tropical populations. Limnology and Oceanography 28, 1231–1237.

Holm-Hansen, O., Mitchell, B.G., 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Research 38, 961–980.

Huntley, M.E, Nordhausen, W., 1995. Ammonium cycling by Antarctic zooplankton in winter. Marine Biology 121, 457–467.

Jacques, G., 1991. Is the concept of new production-regenerated production valid for the Southern Ocean? Marine Chemistry 35, 273–286.

Jacques, G., Panouse, M., 1991. Biomass and composition of size fractionated phytoplankton in the Weddell–Scotia Confluence area. Polar Biology 11, 315–328.

Karl, D.M., Tilbrook, B.D., Tien, G., 1991. Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antarctica. Deep-Sea Research 38, 1097–1126.

Karl, D.M., Christian, J.R., Dore, J.E., Letelier, R.M., 1996. Microbial oceanography in the region west of the Antarctic Peninsula: microbial dynamics, nitrogen cycle and carbon flux. In: Ross, R.M., Hofmann, E.E., Quetin, L.B. (Eds.), Foundations for Antarctic Research West of the Antarctic Peninsula. American Geophysical Union, Washington, DC, pp. 303–332.

Koike, I., Holm-Hansen, O., Biggs, D.C., 1986. Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonium cycling. Marine Ecology Progress Series 30, 105–116.

Le Corre, P., Minas, H.J., 1983. Distribution et évolution des éléments nutritifs dans le secteur indien de l'Océan Antarctique en fin de période estivale. Oceanologica Acta 6, 365–381.

Mitchell, B.G., Holm-Hansen, O., 1991. Observations and modeling of the Antarctic phytoplankton crop in relation to mixing depth. Deep-Sea Research II 38, 981–1007.

Morán, X.A.G., Estrada, M., 2002. Phytoplanktonic DOC and POC production in the Bransfield and Gerlache Straits as derived from kinetic experiments of ^{14}C incorporation. Deep-Sea Research II 49, 769–786.

Mouriño, C., Fraga, F., 1985. Determinación de nitratos en agua de mar. Investigación Pesquera 49, 81–96.

Olson, R.J., 1980. Nitrate and ammonium uptake in Antarctic waters. Limnology and Oceanography 25, 1064–1074.

Owens, N.J.P., Priddle, J., Whitehouse, M.J., 1991. Variations in phytoplanktonic nitrogen assimilation around South Georgia and in the Bransfield Strait (Southern Ocean). Marine Chemistry 35, 287–304.

Pedrós-Alió, C., Vaqué, D., Guixa-Boixereu, N., Gasol, J.M., 2002. Prokaryotic plankton biomass and heterotrophic production in western Antarctic waters, during the 1995–96 Austral summer. Deep-Sea Research II 49, 805–825.

Rodríguez, J., Jiménez-Gómez, F., Blanco, J.M., Figueroa, F.L., 2002. Physical gradients and spatial variability of the size, structure and composition of phytoplankton in the Gerlache Strait (Antarctica). Deep-Sea Research II 49, 693–706.

Rönner, U., Sörensson, F., Holm-Hansen, O., 1983. Nitrogen assimilation by phytoplankton in the Scotia Sea. Polar Biology 2, 137–147.

Schloss, I., Estrada, M., 1994. Phytoplankton species composition in the Weddell–Scotia Confluence area during austral spring in relation to hydrography. Polar Biology 14, 77–90.

Smith, W.O., Sakshaug, E., 1990. Polar phytoplankton. In: Smith, W.O. (Ed.), Polar Oceanography. Part B, Chemistry, Biology and Geology. Academic Press, New York, pp. 477–525.

Socal, G., Nöthig, E.M., Bianchi, F., Boldrin, A., Mathot, S., Rabitti, S., 1997. Phytoplankton and particulate matter at the Weddell/Scotia Confluence (47°W) in summer 1989, as a final step of a temporal succession (EPOS project). Polar Biology 18, 1–9.

Tréguer, P., Jacques, G., 1992. Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. Polar Biology 12, 149–162.

Tupas, L.M., Koike, I., Karl, D.M., Holm-Hansen, O., 1994. Nitrogen metabolism by heterotrophic bacterial assemblages in Antarctic coastal waters. Polar Biology 14, 195–204.

Vaqué, D., Guixa-Boixereu, N., Gasol, J.M., Pedrós-Alió, C., 2002. Distribution of microbial biomass and importance of protists in regulating prokaryotic assemblages in three areas close to the Antarctic Peninsula in spring austral summer 1995–96. Deep-Sea Research II 49, 847–867.

Varela, M., Fernández, E., Serret, P., 2002. Size-fractionated phytoplankton biomass and primary production in Gerlache and south Bransfield Straits (Antarctica Peninsula) in Austral summer 1995–1996. Deep-Sea Research II 49, 749–768.

Waldron, H.N., Atwood, C.G., Probyn, T.A., Lucas, M.I., 1995. Nitrogen dynamics in the Bellingshausen Sea during the Austral spring of 1992. Deep-Sea Research II 42, 1253–1276.

Wheeler, P.A., Glibert, P.M., McCarthy, J.J., 1982. Ammonium uptake and incorporation by Chesapeake Bay phytoplankton: short term uptake kinetics. Limnology and Oceanography 27, 1113–1128.