



HAL
open science

THE SILICA CYCLE IN THE ANTARCTIC OCEAN - IS THE WEDDELL SEA ATYPICAL

Aude Leynaert, David L. Nelson, Bernard Queguiner, Paul Tréguer

► **To cite this version:**

Aude Leynaert, David L. Nelson, Bernard Queguiner, Paul Tréguer. THE SILICA CYCLE IN THE ANTARCTIC OCEAN - IS THE WEDDELL SEA ATYPICAL. Marine Ecology Progress Series, 1993, 96 (1), pp.1-15. hal-00456581

HAL Id: hal-00456581

<https://hal.univ-brest.fr/hal-00456581v1>

Submitted on 10 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

The silica cycle in the Antarctic Ocean: is the Weddell Sea atypical?

Aude Leynaert¹, David M. Nelson², Bernard Quéguiner¹, Paul Tréguer¹

¹URA CNRS 1513, Institut d'Etudes Marines, BP 452, F-29275 Brest Cedex, France

²College of Oceanography, Oregon State University, Corvallis, Oregon 97331-5503, USA

ABSTRACT: The lowest biogenic silica production rates in the Southern Ocean (average of 2.59 mmol Si m⁻² d⁻¹) have been recorded in an area of heavy ice cover along a transect through the Weddell Sea from Joinville Island to Cap Norvegia (November–December 1990). The associated biomass was also very low (concentrations $\leq 0.6 \mu\text{mol l}^{-1}$ for biogenic silica and $\leq 0.8 \mu\text{g l}^{-1}$ for chlorophyll *a*). Based upon these direct measurements of biogenic silica production rates and other data available from the marginal ice zone and open ocean areas, we estimated the annual production of biogenic silica in the northern Weddell Sea to be 810 to 870 mmol m⁻² yr⁻¹. This leads to a revised estimate of the total annual biogenic silica production in the Southern Ocean of between 11 and 32 Tmol Si yr⁻¹. Comparing our annual production estimate to previous estimates of vertical flux of opal in the Weddell Sea, we conclude that no more than 1 % of the silica produced annually by phytoplankton in the upper water column reaches a depth of 800 m. This is consistent with the general distribution of high accumulation rates of opal in Southern Ocean sediments which evidence an unexplained gap in the Weddell Sea. Thus, regarding the cycling of biogenic silica in the Southern Ocean, the Weddell Sea appears to be atypical.

INTRODUCTION

The major role of the Southern Ocean in the global production of biogenic silica (BSi) has been emphasized by many studies (review in Tréguer & van Bennekom 1991). Recently Tréguer & van Bennekom (1991) gave an estimate of 50 Tmol Si yr⁻¹ for the total annual production of BSi in the Southern Ocean, but large uncertainties remain mostly because of imprecisions in the estimates for several of the major subsystems that have been identified in this area (Tréguer & Jacques 1992).

Much attention has been given to the silica cycle of the seasonal ice zone (SIZ) especially in the Weddell Sea. BSi standing stocks in that system have been reported for winter (Cota et al. 1992), spring (Nelson et al. 1987, Leynaert et al. 1991, Quéguiner et al. 1991, Tréguer et al. 1991), and late summer (Nelson et al. 1989). Direct measurements of BSi production rates in the Weddell Sea have been reported only for spring (Quéguiner et al. 1991, Tréguer et al. 1991). However 2 indirect estimates of seasonal BSi production have

been calculated. By assuming interannual differences in winter nutrient distribution to be minimal, Jennings et al. (1984) estimated the average net production rate to be about 12 mmol Si m⁻² d⁻¹ for a 60 to 90 d period, from the depletion of silicic acid in the surface layer of the eastern Weddell Sea (along the Greenwich meridian) from winter to spring. Tréguer & van Bennekom (1991) estimated the mean silica production rate in summer (November–April) to be about 7 mmol Si m⁻² d⁻¹ in the South Scotia area and at the Weddell-Scotia Confluence, based upon ¹⁴C production rates and BSi/POC (particulate organic carbon) ratios.

Indirect methods cannot give more than approximate values for 2 reasons. First, large spatial and temporal variations have been shown for BSi/POC ratios in the Weddell Sea (range: 0.01 to 1.00 by moles; Tréguer et al. 1990, 1991, Leynaert et al. 1991, with the maximum values corresponding to phytoplankton blooms dominated by highly silicified diatoms). Second, the exact duration of the different phases of the phytoplankton growth is not easy to determine and this could lead to substantial errors in seasonal production

estimates. Thus, improved estimates of the annual BSi production for the Weddell Sea, the Southern Ocean or the world ocean require data based on direct measurements in the identifiable major subsystems, made during different seasons, and an improved understanding of how BSi production is related quantitatively to primary productivity, phytoplankton species composition and food-web dynamics.

The aims of this paper are: (1) to report standing stocks and production rates of biogenic silica and organic carbon in the Weddell Sea (along a transect from Joinville Island to Cap Norvegia; Fig. 1) for a pre-spring situation (i.e. in waters with significant ice cover during a period of ice retreat); (2) to explain the large seasonal variations of BSi/POC ratios reported both for standing stocks and for production rates, in relation to phytoplankton growth, species composition and activity of the second trophic level; (3) to derive a new estimate of the annual biogenic silica production in the Weddell Sea; and (4) to propose a new silica budget for the Southern Ocean based on our Weddell Sea data and estimates from other Antarctic and subantarctic systems.

METHODS

All data were collected during the ANT IX-2 cruise aboard RV 'Polarstern' between 22 November and 20 December 1990. One transect (Fig. 1) was conducted across the Weddell Sea, from Joinville Island (63° 12' S, 53° 41' W) to Cap Norvegia (71° 06' S, 11° 23' W). Eleven stations were sampled for biogeochemical measurements, of which only the first and the last were in open water. At each station, vertical profiles of temperature and salinity were obtained using a Neil Brown Mark IIIB CTD. Seawater samples were

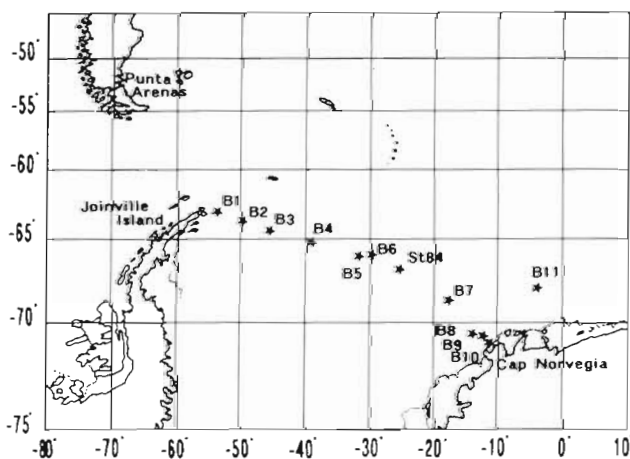


Fig. 1. Position of the biological stations during ANT IX/2 cruise (Nov–Dec 1990)

collected in rosette-mounted, 12 l Niskin bottles from 11 depths between the surface and 400 m to determine nutrient concentrations (silicate, nitrate, nitrite, ammonium, phosphate), chlorophyll *a* (chl *a*), POC, particulate organic nitrogen (PON), and BSi. For production experiments sampling depths were determined with reference to vertical irradiance profiles (respectively 100, 25, 10, 3, 1 and 0.1% of surface incident light measured as photosynthetically available radiation (PAR) at wavelengths from 400 to 700 nm using a LICOR 92SB quantameter).

Nutrient analyses were performed immediately after collection, using the Alpkem RFA-300 continuous flow analysis system (Alpkem Corp. 1986). For chl *a* determinations 500 ml were filtered onto Whatman GF/F filters, and immediately frozen on board at –20°C. Further analyses were performed at the Institut d'Etudes Marines (Brest, France), using a fluorometric method (Neveux 1976). At each station, Lugol's-preserved samples were obtained from surface water for phytoplankton species identification and counting (Utermöhl 1931).

POC and PON concentrations were measured by filtering 2.5 l through 25 mm precombusted Whatman GF/F filters. Each filter was dried at 60°C for 12 h and stored at –20°C in glass vials. They were analysed using the combustion method of Strickland & Parsons (1972) with a modified Carlo Erba analyser, model N1500 (blank = 0.1 $\mu\text{mol l}^{-1}$ for C and <0.02 $\mu\text{mol l}^{-1}$ for N). BSi was collected by filtering 2.5 l of seawater through a 47 mm Nuclepore membrane (0.4 μm pore size); each filter was dried at 60°C for 12 h and stored in a polystyrene petri dish. BSi was determined using the NaOH digestion method (Paasche 1973) as modified by Nelson et al. (1989).

Production experiments were carried out under natural daylight conditions using a transparent Plexiglas incubator maintained at sea-surface temperature ($\pm 1^\circ\text{C}$) by a continuous flow of surface seawater. *In situ* light conditions were simulated by using neutral density nickel screens (100, 25, 10, 3, 1 and 0.1% of surface light). For carbon production experiments, 300 ml seawater collected in polycarbonate bottles was inoculated with 20 μCi (740 kBq) of $\text{NaH}^{14}\text{CO}_3$. After 24 h incubation, samples were filtered onto Whatman GF/F filters which were placed into scintillation vials. After addition of ACF Amersham scintillation cocktail, counting was done on board using a Packard 1600 TR scintillation counter.

For silica production experiments, 1.0 l of seawater from each depth was drawn into a polycarbonate incubation bottle covered with neutral density screen to simulate the irradiance at the depth from which it had been collected. Samples from most stations were enriched with 13 ml of ^{30}Si tracer solution (93.5%, 1.5 mM). For Stns B4, B5 & B6, ^{29}Si (95.6%, 1.45 mM)

Table 1. Bottom and photic depth (0.1 % of surface irradiance), hydrological parameters, and nutrient concentrations in surface waters for biological stations studied during the ANT IX/2 cruise

Stn	Bottom (m)	Ice cover (0–10)	Photic depth (m)	Temperature (°C)	Salinity (PSU)	PO ₄ (μM)	Si(OH) ₄ (μM)	NO ₃ (μM)	NH ₄ (μM)
B1	405	0	123	-1.48	34.40	2.05	72.4	29.5	0.28
B2	2900	7	97	-1.79	34.36	2.10	81.5	31.3	0.06
B3	4454	7	77	-1.79	34.38	2.06	80.2	29.6	0.15
B4	4776	7	87	-1.71	34.35	2.01	77.8	28.8	0.14
B5	4786	7	98	-1.65	34.37	2.03	73.1	27.6	0.14
B6	4857	7	82	-1.81	34.36	1.85	73.2	28.1	0.18
B8	1222	9	130	-1.81	34.32	1.12	61.1	30.0	0.09
B9	369	6	150	-1.76	34.33	2.08	61.2	30.2	0.19
B10	480	<1	158	-1.88	34.30	2.08	62.5	30.5	0.15
B11	4247	0	52	-1.60	34.15	1.98	72.3	28.7	0.15

was used. After the 24 h incubation period, each sample was filtered through a 0.4 μm Nuclepore filter, dried at 60 °C and stored in a polystyrene petri dish. The silicon isotope analysis was performed on a mass spectrometer (Nuclide Corp. Model 3-60) as described by Nelson & Brzezinski (1990). The analytical uncertainty (ΔV) of the specific uptake rate (V) is estimated as:

$$V = \frac{{}^{30}A_f - {}^{30}A_n}{t({}^{30}A_i - {}^{30}A_n)} \quad \frac{\Delta V}{V} = \frac{\Delta({}^{30}A_f + \Delta{}^{30}A_n)}{({}^{30}A_f - {}^{30}A_n)} + \frac{\Delta t}{t} + \frac{\Delta({}^{30}A_i)}{{}^{30}A_i} \quad (1)$$

where ${}^{30}A_f$ = atom % ${}^{30}\text{Si}$ of the final particulate silicon; ${}^{30}A_n$ = atom % ${}^{30}\text{Si}$ of natural silicon; ${}^{30}A_i$ = initial atom % ${}^{30}\text{Si}$ of the total (ambient plus labeled) silicic acid pool; t = duration of the incubation (h).

Repetitive analysis of isotopic standards on our instruments indicates that the mass spectrometry determination of ${}^{30}A_f$ and ${}^{30}A_n$ is accurate to within ± 0.03 atom %. Time was always measured to within 1 %. The accuracy of the calculated ${}^{30}A_i$ depends on that of the measured volume, concentration and isotopic composition of the tracer solution, the volume of the sample and the ambient silicate concentration (Nelson & Goering 1977). For these samples the accumulated uncertainty in ${}^{30}A_i$ is $\leq 4\%$. Eq. 1 shows that the uncertainty in V is $\leq 11\%$ when $({}^{30}A_f - {}^{30}A_n)$ is ≥ 1.0 atom %.

RESULTS

Ice coverage, hydrographic and chemical conditions

For most stations, ice coverage ranged between 6 and 9/10 (Table 1). There was open water at Stn B1 situated at the western end of the transect near Joinville Island (Antarctic Peninsula), Stn B10 at the

eastern end of the transect, close to Cap Norvegia and Stn B11, north from Stn B10. Stns B1 & B10 are coastal stations (bottom depths are 405 and 480 m respectively). Stn B11 is a typical oceanic station (bottom depth 4247 m), situated in the seasonal ice zone.

Distributions of temperature, salinity and silicic acid in the upper 500 m are presented in Fig. 2a to c. We found:

(a) The Winter Water (Carmack & Foster 1975) in the surface layer throughout the whole area (WW: -1.84 °C, 34.4 PSU), with silicic acid, nitrate and phosphate concentrations ranging from 61 to 80, 27.6 to 31.3, and 1.85 to 2.12 μM respectively (Table 1). The general domed structure of the isolines shown in Fig. 2 can be explained by the anticyclonic circulation of the Weddell gyre (Fahrbach et al. 1991), which is associated with an upwelling trend in the central zone (Stns B5 & B6). There was no homogeneous mixed layer from Stns B2 to B9; this differs from the mid-winter situation (e.g. Muench 1990). As the winter water is progressively subjected to seasonal warming its characteristics change slightly; by late November it had become warmer (from -1.8 to -1.6 °C) and fresher (from 34.4 to 34.3 PSU) due to ice and snow melting. However, at the western and eastern boundaries of the transect intense vertical mixing caused nearly vertical isolines of temperature and nutrients (Fig. 2a, c).

(b) The Warm Deep Water (Foster & Carmack 1976) is characterized by a salinity maximum of 34.7 PSU and a temperature maximum of 0.8 °C (at 150 m depth) in the eastern part of the transect and 0.4 °C in the west (G. Rohardt unpubl.), evidencing the inflow of the Weddell gyre in the east and the outflow in the west. In that water mass, nutrient concentrations were higher, reaching 110 μM for Si(OH)₄, 33.8 μM for NO₃ and 2.34 μM for PO₄ (at 150 m depth).

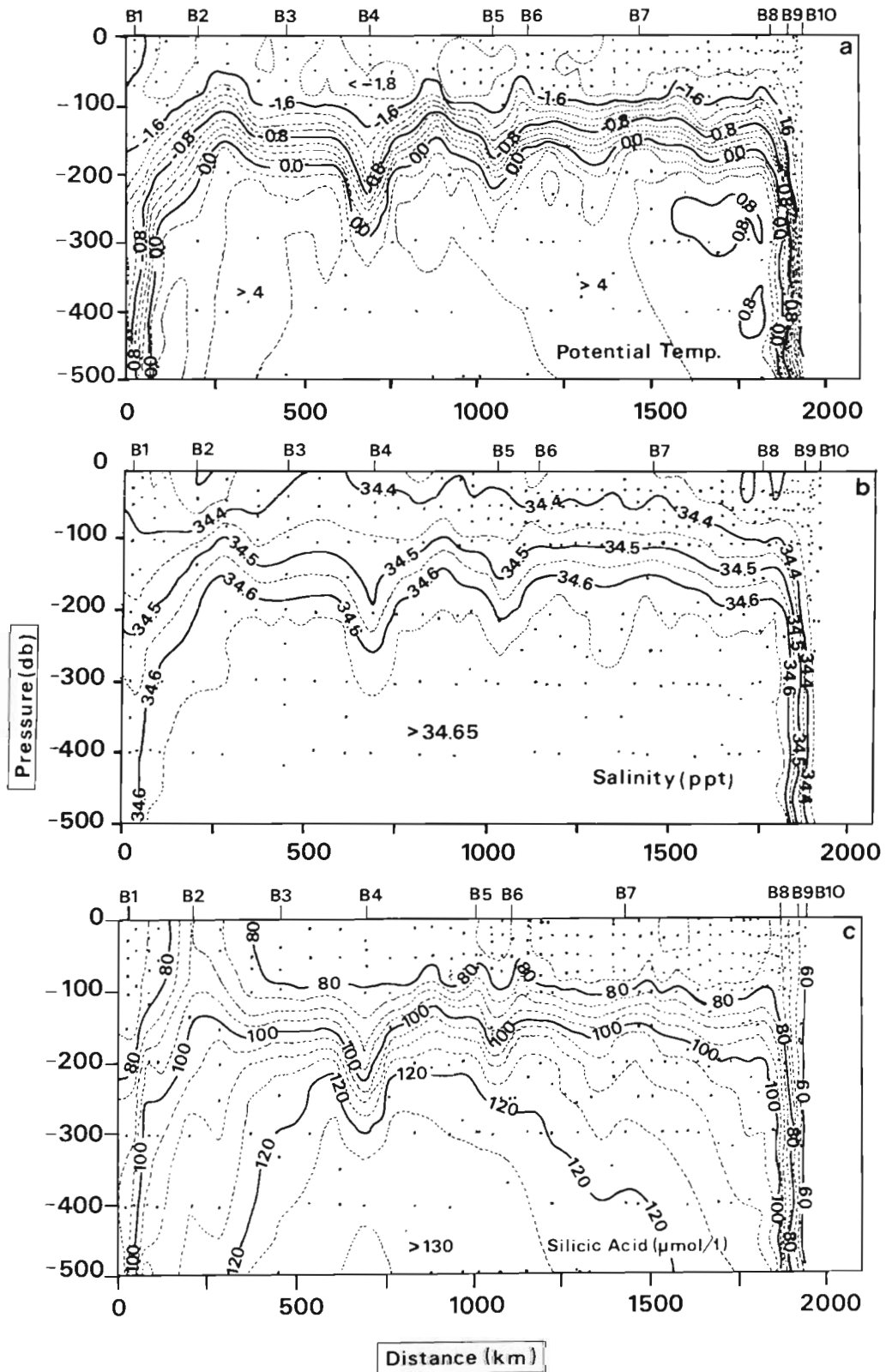


Fig. 2. (a) Potential temperature, (b) salinity and (c) silicic acid concentrations in the upper 500 m during the investigation period along the northeastern to southwestern transect across the Weddell Sea

Biomass distribution (chl *a*, BSi, POC, PON)

Generally speaking, similar distributions were observed for chl *a*, BSi, POC and PON, although the maxima did not coincide for chl *a*, as compared with the other parameters (Fig. 3). Phytoplankton biomass (as indicated by chl *a* and BSi; see also phytoplankton cell counts, Table 2) was very low and we did not encounter anything that could be characterized as a spring bloom. Stns B1 & B11, which had characteristics significantly different from the others, showed a situation more advanced in the season with higher biomass: BSi concentrations at the surface were $0.47 \mu\text{mol l}^{-1}$ at Stn B1 and $0.58 \mu\text{mol l}^{-1}$ at Stn B11 (not shown in Fig. 3), i.e. 3 to 5 times those at the other stations. In the same way, POC and PON reached their maximum values at the coastal station (B1): 8.40 and $0.80 \mu\text{mol l}^{-1}$ respectively. Chl *a* concentrations were also relatively high, reaching $0.64 \mu\text{g l}^{-1}$ at Stn B1. The general biomass distribution in this portion of the Weddell Sea appears to have been almost symmetrical about the center of the gyre, situated around Stn B5. Concentrations of suspended particulate matter increased from the periphery to the center, where a chl *a* maximum was encountered ($0.76 \mu\text{g l}^{-1}$) together with BSi concentrations higher than in the surrounding waters. Elsewhere, biomass was very low, $<0.2 \mu\text{mol l}^{-1}$ for BSi and $<0.14 \mu\text{g l}^{-1}$ for chl *a*. Surface POC and PON values also increased toward the center, ranging from 3.02 to $5.08 \mu\text{mol l}^{-1}$ for POC and from 0.33 to $0.61 \mu\text{mol l}^{-1}$ for PON (average: 4.43 and $0.49 \mu\text{mol l}^{-1}$ respectively). These concentrations are very similar to those found previously in the Weddell Sea marginal ice zone in winter (Cota et al. 1992). All biomass parameters (chl *a*, BSi, POC and PON) typically decreased with depth within the photic zone, except at the boundaries where vertical mixing resulted in nearly uniform concentrations.

Phytoplankton cell numbers at 10 m depth were in the order of $10^5 \text{ cells l}^{-1}$ (Table 2). The specific diversity (Frontier 1969) was high: $H = 3.25 \pm 0.25$, suggesting a

population in a growing stage. Phytoplankton assemblages in all regions were dominated in number by small autotrophic nanoflagellates (Table 2). Microphytoplankton (20 to $200 \mu\text{m}$) was dominated by small diatoms and *Nitzschia curta* was the most representative species. For example, at Stn B6, the cell densities were 6880, 1200 and $1200 \text{ cells l}^{-1}$ for *N. curta*, *N. longissima* and *N. kerguelensis* respectively. However, a large amount of empty frustules (also dominated by *N. curta*) were observed, suggesting the important influence of biogenic matter released by melting ice and its role in seeding the water column (Lancelot et al. 1991).

Production of organic carbon and biogenic silica

We encountered a pre-spring biological situation confirmed by low rates of primary productivity. The photic layer (depth of 0.1 % of surface irradiance) was very deep and displayed a large range of variations, from 52 to 158 m depth (Table 1). The photoperiod ranged from 20 h for the northern stations to 24 h for the southern ones. Vertical profiles of production rates usually differed for carbon and biogenic silica (Fig. 4). Unlike the rate of photosynthetic carbon production which is strongly light-dependent, as evidenced by the rapid decrease with depth (Figs. 4 & 5a), the rate of BSi production was much more uniform in the water column (Figs. 4 & 5b). As was the case for biomass distributions, higher rates of BSi production were encountered in open waters where they reached 0.09 and $0.05 \mu\text{mol Si l}^{-1} \text{ d}^{-1}$ (Stns B1 & B11). Carbon primary production rates were also relatively high in these waters reaching $0.50 \mu\text{mol C l}^{-1} \text{ d}^{-1}$ at Stn B11 (Fig. 5).

Along the transect, a slight but noticeable increase in carbon and silica production rates was evident toward the center of the transect as shown by Fig. 5a, b. These rates ranged from 0.15 to $0.54 \mu\text{mol C l}^{-1} \text{ d}^{-1}$, and from 0.017 to $0.039 \mu\text{mol Si l}^{-1} \text{ d}^{-1}$ respectively, with maximum values being reached at Stn B5 for carbon and at Stn B6 for silica.

Integrated vertically for the photic zone, biogenic silica and carbon production rates show little spatial variability (Table 3). The integrated BSi production rates are the lowest ever reported for the Southern Ocean, averaging about 30 % lower than those obtained by Nelson & Gordon (1982) in the Antarctic Circumpolar Current (ACC) in very early spring, whereas those of carbon are comparable to those from Tréguer et al. (unpubl.) in autumn in the SIZ of the Weddell Scotia Sea. Carbon production rates were 3 to 10 times

Table 2. Cell counts (cells l^{-1}) in surface water samples from 6 stations. nd: not determined

Stn	Nanophyto- plankton	Microphyto- plankton	% empty frustules of total diatoms	% diatoms of total micro- phytoplankton
B1	2.54×10^5	1.75×10^4	nd	94
B5	3.29×10^5	1.83×10^4	nd	83
B6	2.27×10^5	1.50×10^4	37	78
B9	2.22×10^5	1.02×10^4	40	82
B10	6.78×10^4	2.80×10^3	49	56
B11	1.68×10^5	2.68×10^4	43	49

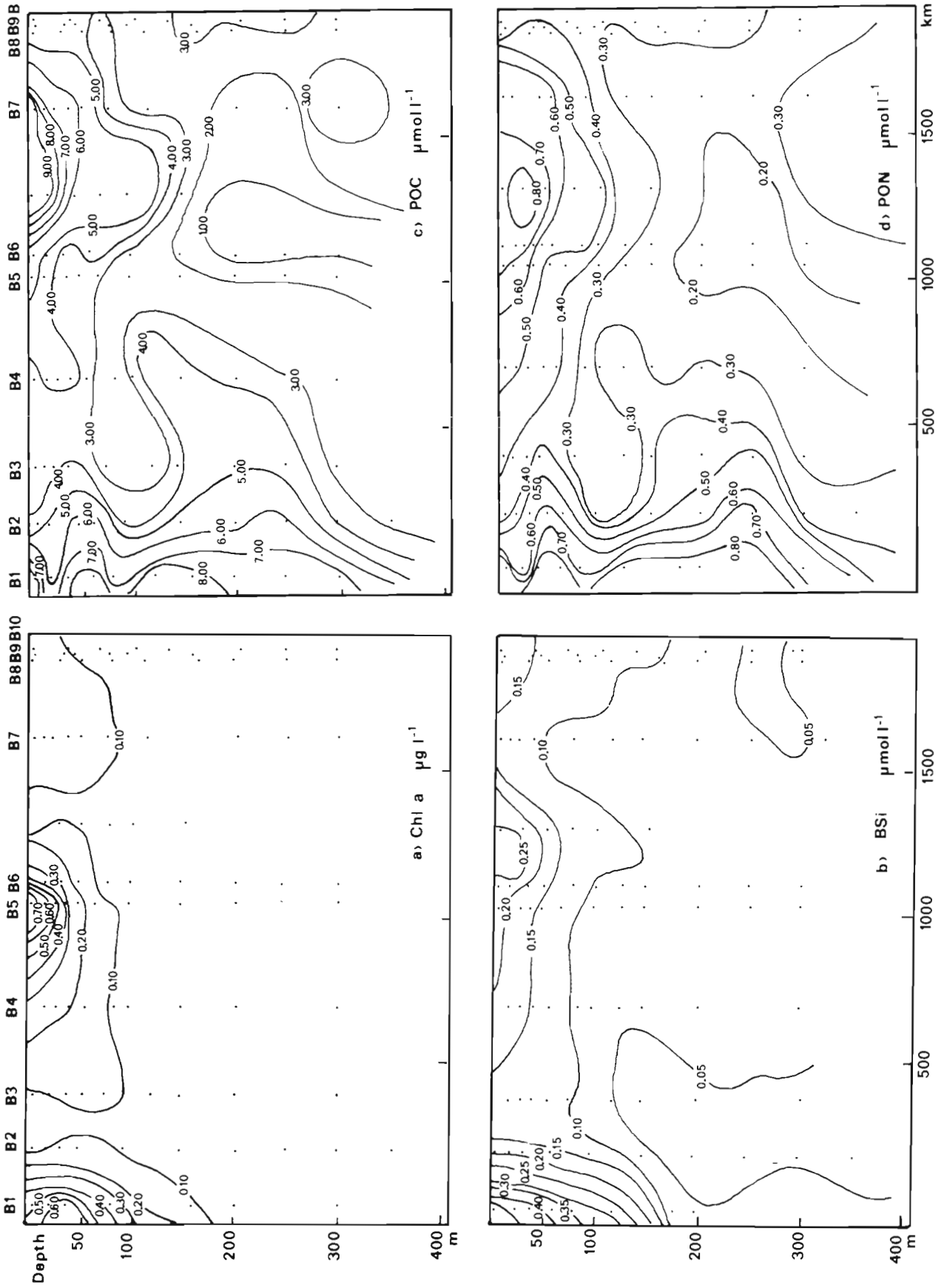


Fig. 3. Distribution of the particulate organic matter in the upper 400 m during the study period along a transect across the Weddell Sea: (a) chl a ($\mu\text{g l}^{-1}$); (b) biogenic silica ($\mu\text{mol l}^{-1}$); (c) particulate organic carbon ($\mu\text{mol l}^{-1}$); (d) particulate organic nitrogen ($\mu\text{mol l}^{-1}$)

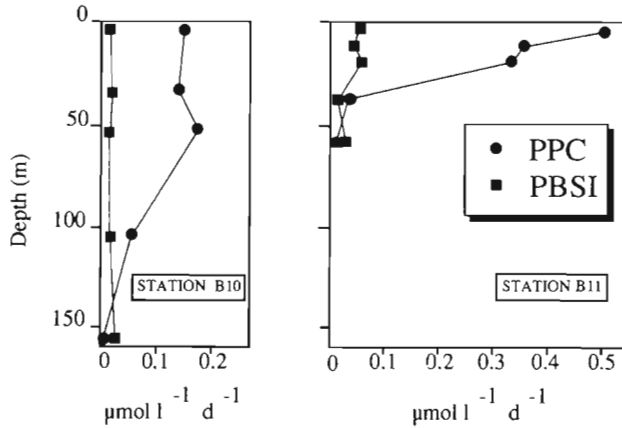


Fig. 4. Vertical profiles of biogenic silica production (PBSi) and carbon primary production rates (PPC) at Stns B10 & B11

higher than those observed in the Weddell Sea in winter (Cota et al. 1992).

Stn B10, located in a narrow polynya, has a very deep photic zone (158 m) and is of particular interest: although very low biomass concentrations were found

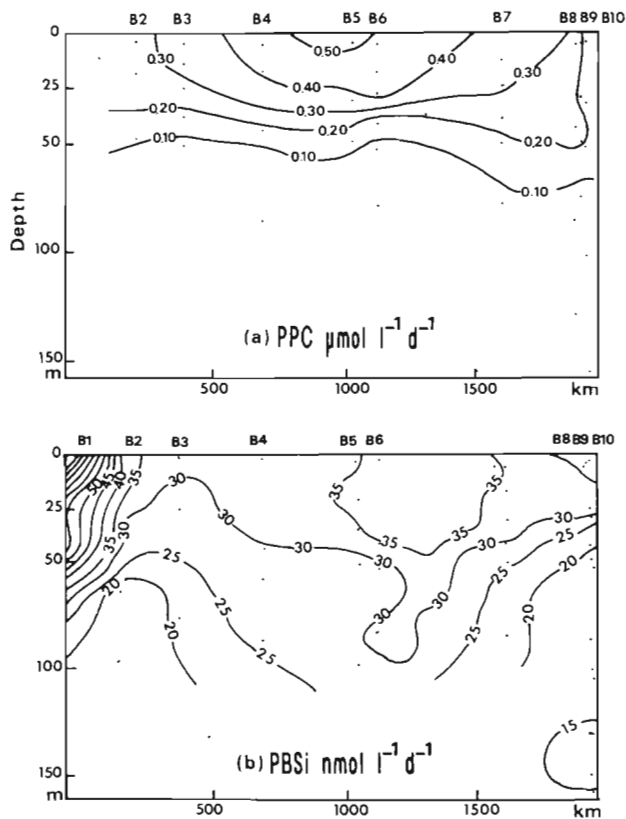


Fig. 5. Distribution of biogenic silica production (PBSi) and carbon primary production rates (PPC) in the photic layer, along a transect across the Weddell Sea during ANT IX/2 cruise

Table 3. Vertically integrated (in the photic depth) rates of biogenic silica production (PBSi) and carbon production (PPC). Specific growth rates are calculated as:

$$\mu = \log[(BSi + PBSi)/BSi] \times 1/t \times 1/\log(2)$$

Stn	PBSi (mmol m ⁻² d ⁻¹)	μ (db d ⁻¹)	PPC (mmol m ⁻² d ⁻¹)
B2	2.31	0.25	13.95
B3	2.06	0.29	13.13
B4	2.59	0.28	17.35
B5	2.91	0.28	22.00
B6	2.84	0.24	18.12
B8	2.75	0.19	17.25
B9	2.69	0.18	20.05
B10	3.18	0.24	15.20
B11	1.97	0.12	10.05
Mean	2.59	0.23	16.34
SD	0.38	0.05	3.46

and the lowest production rates of the cruise reported (0.15 $\mu\text{mol C l}^{-1} \text{d}^{-1}$ and 0.017 $\mu\text{mol Si l}^{-1} \text{d}^{-1}$, at 0 m) the magnitude of the production rates, when integrated to the photic layer, was similar to those at the other stations. This suggests that deeper mixing causes a dilution of phytoplankton biomass by mixing it more evenly through the upper water column, with relatively little effect on the integrated productivity, as suggested by Wilson et al. (1986) for the Ross Sea. We observed an abundance of algae in the brown ice at this station, suggesting a very pre-bloom situation in which most of the autotrophic biomass and productivity are located in the ice rather than in the water.

The measured rates of biogenic silica production per unit of biomass indicate growth rates ranging from 0.12 to 0.29 doublings d^{-1} for the diatom assemblage (Table 3). The overall mean division rate of 0.23, although significantly lower than the maximum division rate to be expected at -2°C (ca 0.7 doublings d^{-1} ; Eppley 1972), is in good agreement with previous estimates reported from ice-edge phytoplankton blooms in the Ross Sea (Nelson & Smith 1986, Nelson et al. 1991) and in the Weddell Sea (Quéguiner et al. 1991). We are aware of the potential inaccuracies and biases introduced by this procedure, but it does provide a means by which growth rates can be compared within the bloom. Underestimates of growth rates will occur if significant amounts of detrital silica are present.

DISCUSSION

Chemical composition of particulate organic matter

In early spring the particulate organic matter was characterized by especially high POC/chl *a* ratios, ranging from 73 to 823 (g/g) in the photic layer, the

lowest values being found in the center of the gyre. The overall mean of 370 suggests that microheterotrophs and detritus comprised a significant fraction of the particulate organic material (Banse 1977). Previous studies have also reported large ranges of variations for POC/chl *a* ratios for Antarctic particulate matter, from 31.8 in a spring bloom (Nelson et al. 1987) to 530 in mid-winter (Cota et al. 1992).

The mean POC/PON mole ratio was 8.2 ± 0.6 (Fig. 6), which is somewhat higher than the typical value of 6.6 found by Redfield et al. (1963). It is considerably lower than the ratio of 10.2 reported by Cota et al. (1992) for the Weddell Sea marginal ice zone in winter and comparable to that measured by von Bodungen et al. (1986) for the photic zone of the marginal ice zone of the Antarctic Peninsula in spring.

BSi/POC mole ratios reached 0.1 in the upper layer at Stns B1 (coastal station) and B11 (open water) but were <0.06 elsewhere. There is no evidence that the BSi/POC ratio changed systematically with depth; values were very uniform through the water column and showed little variability throughout the transect. Ratios of vertically integrated BSi to vertically integrated POC in the photic layer (Table 4) ranged between 0.02 and 0.06, with a mean of 0.04. They are in the same range as those reported by Cota et al. (1992) who found a mean BSi/POC ratio of 0.05 in the marginal ice zone of the Weddell Sea in winter. This value is lower than any BSi/POC ratio reported for productive seasons in the Southern Ocean (e.g. Nelson & Smith 1986, Nelson et al. 1987, 1989, Leynaert et al. 1991). Low BSi/POC ratios reflect the importance of non-siliceous phytoplankton (Table 2) and the presence of non-siliceous microheterotrophs in suspended matter, as evidenced by the high POC/chl *a* ratios.

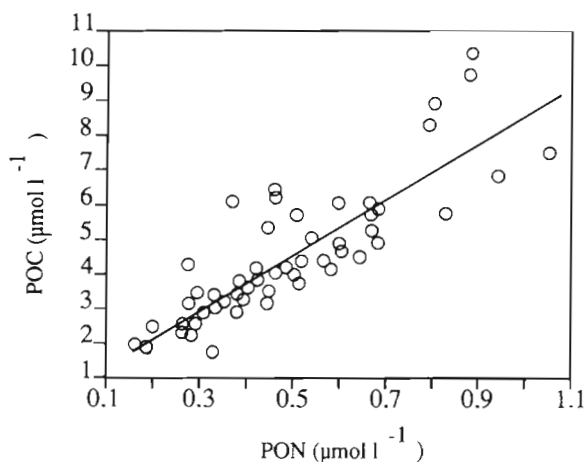


Fig. 6. Particulate organic carbon (POC, $\mu\text{mol l}^{-1}$) versus particulate organic nitrogen (PON, $\mu\text{mol l}^{-1}$). Regression line (see text)

Table 4. Biogenic silica and particulate organic carbon: comparison of biomasses (BSi/POC) and production (PBSi/PPC) molar ratios. nd: not determined

Stns	BSi/POC	PBSi/PPC
B1	0.05	nd
B2	0.03	0.17
B3	0.04	0.16
B4	0.04	0.15
B5	0.04	0.13
B6	0.04	0.16
B8	0.03	0.16
B9	0.04	0.13
B10	0.02	0.21
B11	0.06	0.20
Mean	0.04	0.16
SD	0.01	0.03

The ratio of BSi production to carbon production (PBSi/PPC) was significantly higher than that for standing stock (Table 4). Large variations in BSi/POC ratios for both standing stocks and primary production have been reported in the Antarctic ecosystems (Nelson & Smith 1986, Tréguer et al. 1991). To interpret these variations, we advance the following hypothesis:

During winter, phytoplankton is dominated by non-siliceous species, such as small autotrophic nanoflagellates (Nöthig et al. 1991). Si/C ratios are low (generally <0.06 ; Cota et al. 1992). In early spring, ice melting enhances water-column stability and releases ice algae, some of which survive in the water column (Garrison et al. 1987) and could act as an efficient inoculum to initiate a phytoplankton bloom (Lancelot et al. 1991). But since water-column biomass is still low, Si/C biomass ratio is largely influenced by the biogenic matter released from the melting ice, and a large range of variations has been observed: 0.04 to 0.46 (Leynaert unpubl.). This could reflect variations in taxonomic composition of epontic algae or their physiological state (release of dead or senescent phytoplankton). As the phytoplankton bloom develops, Si/C production ratios increase (Nelson & Smith 1986, Tréguer et al. 1991, this study) and become >0.13 , the average found by Brezinski (1985) for diatoms in culture grown in nutrient-replete conditions, indicating a shift toward an actively growing, mostly siliceous population. Epontic algae, such as *Nitzschia* spp., often proliferate (Smith & Nelson 1985, Wilson et al. 1986, this study).

Then during spring, ecological succession usually leads to a dominance of highly silicified diatoms (*Chaetoceros neglectum*, *Corethron criophilum*, *Thalassiosira gravida*, with mean size $>10 \mu\text{m}$; Jacques & Panouse 1991). This step of phytoplankton succession corresponds to maximum values of Si/C ratios. Mean values reaching 0.65 for biomass and 0.57 for

production have been encountered in the western Ross Sea during a diatom-dominated ice edge bloom (Nelson & Smith 1986, Nelson et al. 1987).

In the final step of the succession, we can distinguish 2 different cases:

(a) Intense grazing (Weddell Sea): due to selective feeding by krill on larger cells (Quentin & Ross 1985), large diatoms are preferentially eaten and biogenic silica is rapidly exported to depth via fecal pellets. Heavy grazing pressure may cause the decline of the bloom and a shift in the species composition of phytoplankton from a diatom-dominated to a nanoflagellate-dominated community (Jacques & Panouse 1991). Si/C ratios diminish. This situation has been clearly observed during Epos2, where the Si/C biomass ratio fell from 0.30 to 0.17 (Leynaert et al. unpubl.) after intense grazing by krill. Cryptophyceans, prymnesiophytes, naked flagellates, green flagellates and small diatoms were identified and 78 % of the total silicic uptake rate was in the <10 μm fraction of suspended matter, indicating that only small diatoms were allowed to remain abundant (Jacques & Panouse 1991).

(b) Low grazing pressure (Ross Sea): low zooplankton stocks allow large phytoplankton blooms with very high BSi levels (up to 40 $\mu\text{mol Si l}^{-1}$; Nelson & Smith 1986). Because of micronutrient limitation (Martin et al. 1990) and/or self shading (Nelson & Smith 1991), growth rates become lower as the physiological state of the phytoplankton changes. The Si/C production and biomass ratios remain high. This could be explained by the fact that light and micronutrient limitations could both be expected to affect photosynthesis and carbon metabolism more severely than silicification, producing cells with high Si/C ratios as a result of organic matter deficiency. Mass sedimentation may cause the decline of the bloom (Smetacek 1985, von Bodungen et al. 1986 in the Bransfield Strait) and the removal of biogenic silica stock from the photic layer.

Estimated annual production of biogenic silica in the northern Weddell Sea

Table 3 presents the first data on production rates of biogenic silica in partially ice-covered surface waters in the Southern Ocean. Because these data were obtained during the period of maximum solar irradiance (November and December) and show relatively little variability in vertically integrated production rates (Table 3), the mean value of 2.59 $\text{mmol m}^{-2} \text{d}^{-1}$ provides the best available estimate of the rate of silica production in areas of significant partial ice cover in summer. These rates can be combined with available data from the marginal ice zone (Quéguiner et al. 1991, Tréguer et al. 1991) and from open ocean areas remote

from the ice edge (Nelson & Gordon 1982) to derive an estimate of the annual production of biogenic silica at 60 to 62°S. The resulting annual estimate can be compared with data on seasonal nutrient depletion (Jennings et al. 1984), annual primary productivity (Smith & Nelson 1986, Smith et al. 1988) and the seasonal cycle of particulate opal flux (Fischer et al. 1988) from the same region to characterize the major feature of the biogenic silica cycle in the Weddell Sea.

We have estimated the annual silica production in the northern Weddell Sea in a manner similar to that employed in the carbon productivity estimates for the same region derived by Smith & Nelson (1986) and Smith et al. (1988). The year is divided into 4 characteristically different periods: a winter period of negligible productivity, a well-lit but partially ice-covered period, a bloom period developing after the ice edge has passed, and an open-ocean, deep mixed period in late summer.

Winter

At 60 to 62°S, the maximum daily irradiance under cloudless skies would be <15 $\text{E m}^{-2} \text{d}^{-1}$ from 1 April through 1 October (Campbell & Aarup 1989) and clouds further reduce irradiance to an average of ca 5 $\text{E m}^{-2} \text{d}^{-1}$ for most of this period (Cota et al. 1992), resulting in a light/mixing regime that is highly unfavorable to phytoplankton growth (Nelson & Smith 1991). In addition, the 60 to 62°S zonal band in the Weddell Sea is typically ice-covered from May through September (Zwally et al. 1983), diminishing the light availability in the water column to virtually zero. Our annual silica budget thus assumes negligible production for a 6 mo (April to October) period.

Spring–summer under partial ice cover

The northern limit of >15 % ice cover in the Weddell Sea is typically ca 57°S, with the 60 to 62°S zone remaining >80 % covered from June to September (Zwally et al. 1983). The ice edge begins to retreat in late September or early October, and in 1983 the mean rate of retreat was 5 km d^{-1} through the October to early January period (Nelson et al. 1987). In 1988, a similar rate of retreat (ca 5.5 km d^{-1}) was observed during December (Leynaert et al. 1991). The mean rate of ice retreat apparently increases significantly during January of most years (Smith et al. 1988). Throughout the October–January period the zone of significant partial ice cover (20 to 80 %) is approximately 300 km in north-south extent (Zwally et al. 1983); thus a given location in the northern Weddell Sea would be under significant partial ice cover for approximately 60 d (300 km at 5 km d^{-1}) each spring. This period would commence on about 1 October at 60°S, and later at

Table 5. Estimated annual production of biogenic silica in the Weddell Sea (estimates for the northern and southern parts calculated separately)

Period	Duration (d)	Production (mmol m ⁻² d ⁻¹)	Total (mol m ⁻²)
Between 60 and 65° S (4.9 × 10 ⁶ km ²)			
Partial ice cover	60	2.60	0.16
Ice-edge bloom	40	10.90	0.44
Post-bloom	70–90	3.00	0.44
Total	170–190	4.58–4.76	0.81–0.87
South of 65° S (1.2 × 10 ⁶ km ²)			
Partial ice cover	60	2.60	0.16
Ice-edge bloom	30	10.90	0.33
Post-bloom	60	3.00	0.18
Total	150	4.47	0.67
Total Weddell Sea			0.78–0.83

more southerly locations. The mean rate of silica production in this zone is taken to be 2.6 mmol m⁻² d⁻¹ (see Table 3), resulting in an integrated silica production of ca 160 mmol m⁻² for the 60 d period (Table 5).

Ice-edge phytoplankton bloom

As is the case in many other seasonally ice-covered regions of the ocean (e.g. Niebauer & Alexander 1985, Smith & Nelson 1985), a phytoplankton bloom typically develops in the open water seaward of the receding ice edge in the Weddell Sea (Nelson et al. 1987). The north-south extent of this bloom was ca 200 km in 2 spatial studies of biomass distributions in different years (Nelson et al. 1987, Leynaert et al. 1991). Silica production rates have been measured in ³⁰Si and ³²Si tracer studies in the marginal ice zone of the Weddell Sea in spring (Quéguiner et al. 1991, Tréguer et al. 1991), and are significantly higher than those we report here for the zone of partial ice cover; they range from 6.0 to 20.0 mmol m⁻² d⁻¹, with a mean of 10.9. Using the 5 km d⁻¹ rate of ice retreat discussed above, the bloom would be present at any fixed location for approximately 40 d (200 km at 5 km d⁻¹), resulting in an integrated production of ca 440 mmol m⁻² during the bloom.

Post-bloom period

Using the approximations developed above, the ice edge and associated bloom have typically moved to the south of 60° S by early January, and to the south of 62° S by late January. Phytoplankton blooms are exceptionally rare or absent in open water remote from the ice edge (e.g. Holm-Hansen et al. 1977, Lancelot et al. 1991), and recent calculations suggest that chloro-

phyll concentrations exceeding ca 1 µg l⁻¹ may not be sustainable because of the relatively deep mixed surface layers present (Smith & Nelson 1986). However, the integrated daily solar irradiance is near its annual maximum in early January and does not begin to decrease rapidly until late February (e.g. Campbell & Aarup 1989). Thus, some production of biogenic silica almost undoubtedly continues in the open-ocean regions of the Weddell Sea through the late summer. No data on silica production rates in this portion of the system are available, and the production during the open-ocean period following the bloom is the most uncertain term in our annual budget. However, Nelson & Gordon (1982) reported silica production rates ranging from 0.9 to 6.8 mmol m⁻² d⁻¹ (mean 3.0) in the open waters of the Pacific sector of the ACC in October. October is seasonally symmetrical with February with respect to solar irradiance, and we will use the 3.0 mmol m⁻² d⁻¹ as a provisional mean rate. The open-ocean period lasts approximately 90 d (early January through late March) at 60° S, and 70 d (late January through late March) at 62° S as a result of the later passage of the ice edge. Thus our estimate of the integrated silica production in open water following the ice-edge bloom ranges from 210 mmol m⁻² at 62° S to 270 mmol m⁻² at 60° S.

The calculations described above are summarized in Table 5. The resulting estimate of the annual rate of biogenic silica production in the northern Weddell Sea is 810 to 870 mmol m⁻² yr⁻¹. We believe this estimate is conservative because it assumes zero production from April through September and because no production rate data are available from the marginal ice zone in late summer, when the bloom is likely to be more intense than it is in November and December. Jennings et al. (1984), using data on seasonal nutrient depletion, calculated an integrated silica production rate of 850 mmol m⁻² in the Weddell Sea at 60° S for the period from the first appearance of open water until late January. We believe that estimate and ours to be in good agreement. The annual rate of silica production that we estimate for the northern Weddell Sea is about one third as high as has been estimated for the Ross Sea, where a very intense ice-edge diatom bloom develops and silica production rates often exceed 30 mmol m⁻² d⁻¹ in summer (Jones et al. 1990, Nelson et al. 1991).

Cycling of biogenic silica in the Weddell Sea: an anomaly in the Southern Ocean?

The estimate of annual production of biogenic silica in the northern Weddell Sea that we have derived from ²⁹Si, ³⁰Si and ³²Si tracer data (Table 5) and the earlier

estimate made by Jennings et al. (1984) from seasonal nutrient depletion in the surface layer both indicate that the production rate must exceed $810 \text{ mmol m}^{-2} \text{ yr}^{-1}$. In contrast, studies of the vertical flux of opal through the water column based on long-term deployment of sediment traps at several locations in the Weddell Sea indicate that the flux to depths of 800 to 900 m is no more than $5 \text{ mmol m}^{-2} \text{ yr}^{-1}$ (e.g. Fischer et al. 1988, Honjo 1991). The seasonality of the particle flux collected by traps matches the apparent seasonal cycle of biogenic silica production to a certain degree: there is a single strong maximum in summer, although the flux maximum appears to occur 1 to 2 mo later than the calculated maximum in productivity. The quantitative picture of the regional silica cycle that emerges from these studies, when taken together, is that $< 1\%$ of the silica produced annually by phytoplankton in the upper ocean reaches a depth of 800 m. Although benthic fluxes of silicic acid calculated by Rutgers van der Loeff & van Bennekom (1989) do not match these sediment trap data, these authors also support the idea that biogenic silica fluxes in the central Weddell Sea are significantly lower than in other areas of the ACC.

This relationship between production and flux suggests that the recycling of biogenic silica in the Weddell Sea must be dramatically different from that in the rest of the Southern Ocean (Table 6). Nelson & Gordon (1982) compared rates of silica production measured in the surface waters of the ACC with DeMaster's (1981) data on opal accumulation rates in Southern Ocean sediments and concluded that at least 20% of the annual silica production must reach the sea floor (typically at depths of 3000 to 5000 m). A recent coordinated study of biogenic silica cycling in the water column and sediments of the western Ross Sea has developed a regional silica budget which suggests that over 25% of the silica produced annually by diatoms, and ca 65% of the net silica production (production in excess of redissolution in the upper 50 m), is delivered to the seabed at depths of 600 to 700 m (Nelson et al. 1991, DeMaster et al. in press). Particle flux data from long-term sediment-trap deployments on the Ross Sea shelf also indicate that the annual opal flux to depths 35 m above the bottom is in the range of

25 to 50% of the annual surface production (DeMaster et al. in press). On a large scale, sediment south of the Antarctic Polar Front has been identified as the main present site of opal accumulation in the oceans (e.g. DeMaster 1981, Ledford-Hoffman et al. 1986), despite the fact that the annual primary productivity of the Southern Ocean is quite low (El-Sayed 1978, Smith et al. 1988). This relationship would not be possible unless the fraction of surface-produced silica reaching the sea floor is considerably higher than the global average, which has been estimated to be 2 to 5% (Calvert 1983).

The modern sediments of the Southern Ocean are rich in opal (50 to 80% by weight) in a circumpolar band extending 80% of the distance around the ACC, with one notable gap from ca 25 to 85° W (DeMaster 1981). The gap is in the region of the Drake Passage, Scotia and western Weddell Seas, and thus includes the area where we calculate that $< 1\%$ of the annual silica production reaches a depth of 800 m. The available data on biogenic silica production in the Weddell Sea (Quéguiner et al. 1991, Tréguer et al. 1991, this study) indicate that silica production by diatoms proceeds at rates that are reasonably high for the Southern Ocean, especially in the marginal ice zone. Thus, the low opal content of sediments in the Weddell Sea appears to result from the almost complete redissolution of silica in the upper kilometer of the ocean, rather than from low rates of production in the euphotic zone or from near-bottom processes.

It is not immediately clear what conditions in the Weddell Sea might make the biogeochemistry of siliceous material so very different from that in the Ross Sea and in most of the ACC. It is known that there is a complex microheterotrophic food web in the marginal ice zone of the Weddell Sea in summer (e.g. Hewes et al. 1985, Garrison & Buck 1989), and microzooplankton grazing on heavily silicified diatoms could result in much more intense recycling (and hence less vertical transport) of both organic and siliceous material than would be the case if most grazing were carried out by larger metazoans. Honjo (1991) noted that most of the biogenic particle flux in the northern Weddell Sea is in the form of 'relatively fast-sinking, more protected fecal pellets', and that this flux is very low in comparison with that in the other major oceans. The relative importance of micro- and macroheterotrophic grazers is not clearly understood in any subsystem of the Southern Ocean, but if microzooplankton are far more important in the Weddell Sea than in the Ross Sea or the ACC at large it would help to explain the unusually intense recycling suggested by the relationship between silica production and vertical silica flux.

Alternatively, van Bennekom et al. (1991) have suggested that the dissolution rate of biogenic silica in the

Table 6. Cycling of biogenic silica in the Southern Ocean. Is the Weddell Sea atypical?

	Production ($\text{mol m}^{-2} \text{ yr}^{-1}$)	Accumulation ($\text{mol m}^{-2} \text{ yr}^{-1}$)	Acc./prod. (%)
Weddell Sea	0.8	0.005	$< 1\%$
Ross Sea	2.0–3.0	1.060	35–50%
ACC	0.5–0.8	0.200	25–40%

water column of the Southern Ocean may be considerably higher than expected for cold water because of a low Al/Si ratio in the siliceous particles. Their data and experimental materials were obtained entirely from the Weddell and Scotia Seas: if the Al/Si ratio of diatoms in this region is significantly lower than in other areas of the Southern Ocean the lower ratio could, in principle, result in less efficient preservation of silica through the water column.

The 2 explanations offered above are not mutually exclusive. The unusual quantitative relationship among silica production, vertical silica transport and sediment composition in the Weddell Sea may result from the combined effects of food-web structure and particle chemistry, or from some other condition that has not yet been identified. Regardless of the mechanism, however, it appears that the cycling of biogenic silica in the upper water column of the Weddell Sea is very different from that in the rest of the Southern Ocean and that this difference is accurately recorded in the sediments.

New silica budget for the Southern Ocean

The data on silica production rates in ice-covered waters in early spring (Table 3) enable us to improve estimates of the annual silica production in the Southern Ocean. Table 7 presents a revised estimate of the annual BSi production in the Southern Ocean, based on information from 3 characteristically different systems: the Weddell Sea, the Coastal and Continental Shelf Zone (CCSZ) (both of which experience seasonal ice cover), and the permanently ice-free waters of the ACC.

To estimate a budget, the Weddell Sea is somewhat arbitrarily defined as the entire oceanic region adjoining the Antarctic continent between 60°W and 20°E and south of 60°S. The northern limit coincides reasonably well with the maximum extent of >80% ice cover in September in this area (Zwally et al. 1983).

Table 7. New silica budget for the Southern Ocean

Area	Surface (km ²)	Production (mol m ⁻² yr ⁻¹)	Total (Tmol yr ⁻¹)	% Total
Weddell Sea	6.10 × 10 ⁶	0.8	4.9	15–43
Continental shelves	9.20 × 10 ⁵	3.5	0.6–3.2	3–23
ACC	3.00 × 10 ⁷	0.2–0.8	6.0–24.0	42–81
Antarctic Ocean	3.70 × 10 ⁷	0.3–0.8	11.5–32.1	

This definition reflects more a biological ensemble than any regime of circulation or hydrography. The method described above to estimate annual BSi production can be extended as far south as 65°S (see Table 5). However, south of 65°S the ice-free period is shorter and the length of each different period of productivity is thus affected. This area is mostly ice-covered until early January, and is permanently ice-covered in the western part. In February, after having reached its minimum extent, the ice begins to advance again, cutting short the ice-edge bloom and the after-bloom periods to about 30 and 40 d respectively. Calculations are summarized in Table 5 and give an estimated annual BSi productivity ranging from 0.81 to 0.87 mol m⁻² yr⁻¹ for the northern Weddell Sea and of 0.67 mol m⁻² yr⁻¹ for the southern part. Accounting for the permanently ice-covered region in the southwestern Weddell Sea, where productivity must remain very low at all times, these rate estimates yield a total BSi production of 4.7 to 5.0 Tmol Si yr⁻¹ for the Weddell Sea.

BSi production data for the CCSZ come only from the Ross Sea, which is the only continental-shelf area in the Antarctic that has been extensively studied. Nelson & Smith (1986) reported the highest BSi production rates ever encountered in the Southern Ocean: 2.3 mol m⁻² yr⁻¹, and this estimate has now been revised upward to 3.5 mol m⁻² yr⁻¹ by including data from later in the spring production season (DeMaster et al. in press). Thus if the Ross Sea is typical of the CCSZ with respect to silica production, this region is a significant term in the Southern Ocean total in spite of its small surface area (Table 7). We have estimated the overall annual silica production in the CCSZ by assuming that it ranges between 2 limits: the lower limit is obtained taking into account only the production in the Ross Sea and assuming that the production is negligible anywhere else in the CCSZ (i.e. by applying the 3.5 mol m⁻² yr⁻¹ value only to the 1.6 × 10⁵ km² area of the Ross Sea shelf). The upper limit is obtained by extrapolating the BSi production of the Ross Sea to the entire CCSZ, an area of approximately 9.2 × 10⁵ km².

The ACC is known to be an area of low productivity and many satellite images have confirmed that idea (e.g. Smith & Sakshaug 1990, Mitchell et al. 1991). The only data available on silica production rates in the open waters of the ACC were obtained in October (Nelson & Gordon 1982), and these averaged 3 mmol m⁻² d⁻¹. Without more seasonal information, especially from mid summer, it is virtually impossible to derive an annual estimate from the available direct measurements, so we have attempted to place upper and lower limits on this term from indirect information. As a first approximation, we can consider that the maximum annual rate of silica production in the

oceanic region influenced by the seasonal ice retreat should not be higher than that it is in areas that experience an ice-edge phytoplankton bloom. Thus, we took our estimate of the annual silica production in the northern Weddell Sea ($0.8 \text{ mol Si m}^{-2} \text{ yr}^{-1}$; see previous section) as an upper limit. As a lower limit, we took primary productivity data from El Sayed (1978) $16 \text{ gC m}^{-2} \text{ yr}^{-1}$ ($= 1.3 \text{ mol C m}^{-2} \text{ yr}^{-1}$) and converted this value to an estimated rate of silica production using a BSi/POC ratio of 0.13 (Brzezinski 1985). The resulting lower limit is $0.2 \text{ mol Si m}^{-2} \text{ yr}^{-1}$, or one-fourth of the maximum estimate. The culture-derived BSi/POC ratio of 0.13 pertains only to diatoms (Brzezinski 1985), and still lower estimates of silica production in the ACC could be obtained by using a lower ratio to characterize the mixed phytoplankton assemblages of the region. However, BSi/POC ratios <0.13 in Southern Ocean surface waters have been reported only in the unproductive winter period and in ice-covered waters (e.g. Cota et al. 1992; see also Table 4), and considerably higher values are commonly observed in spring and summer (e.g. Nelson et al. 1989).

The resulting annual estimate for the Southern Ocean (Table 7) presents what we believe to be a range that represents the highest and lowest estimates that can be reasonably supported by the available data, rather than a single estimate of the annual BSi production of the Southern Ocean. The range we calculate in this way, ca 11.7 to $32.1 \text{ Tmol Si yr}^{-1}$, is lower than in previous works. For example, it is only about 25 to 65 % of the estimate recently obtained by Tréguer & van Bennekom (1991). If we compare our data to the carbon productivity estimate of Smith et al. (1988; 1 Gt C yr^{-1} , which equates to ca $83 \text{ Tmol C yr}^{-1}$) we obtain a PBSi/PPC ratio for the Antarctic phytoplankton ranging from 0.14 to 0.39. Comparison with the more recent primary production estimate of Lancelot et al. (1991) gives lower ratios, ranging from 0.07 to 0.20. Both of these results are in a range that is consistent with field data. The large uncertainties remaining are primarily a result of uncertainties for the ACC, where we cannot yet estimate the annual rate of silica production from direct measurements, but which appear from indirect estimates (Table 7) to account for about 45 to 80 % of the total.

Acknowledgements. We thank E. Fahrbach, chief scientist of the ANT IX/2 cruise; the officers and crew of the RV 'Polarstern'; Lou Gordon, Andy Ross and Jim Kress for the nutrient data; Olivier Ragueneau for his help at sea; and Annick Masson and Julie Arrington for their technical assistance.

LITERATURE CITED

- Alpkem Corp. (1986). Silicate, A303-S220. Preliminary RFA/2 Rapid flow analyser operator's manual. Portland, OR
- Banse, K. (1977). Determining the carbon to chlorophyll ratio of natural phytoplankton. *Mar. Biol.* 41: 199–212
- Brzezinski, M. A. (1985). The Si/C/N ratios of marine diatoms: interspecific variability and the effect of some environmental variables. *J. Phycol.* 21: 345–357
- Calvert, S. E. (1983). Sedimentary geochemistry of silicon. In: Aston, S. R. (ed.) *Silicon geochemistry and biogeochemistry*. Academic Press, London, p. 143–186
- Campbell, J. W., Aarup, T. (1989). Photosynthetically available radiation at high latitudes. *Limnol. Oceanogr.* 34(8): 1490–1499
- Carmack, E. C., Foster, T. D. (1975). On the flow of water out of the Weddell Sea. *Deep Sea Res.* 22: 711–724
- Cota, G. F., Smith, W. O. Jr, Nelson, D. M., Muench, R. D., Gordon, L. I. (1992). Nutrient and biogenic particulate distributions, primary productivity and nitrogen uptake in the Weddell-Scotia Sea Marginal Ice Zone in winter. *J. mar. Res.* 50: 155–181
- DeMaster, D. Jr (1981). The supply and accumulation of silica in the marine environment. *Geochim. Cosmochim. Acta* 45: 1715–1732
- DeMaster, D. J., Dunbar, R. B., Nelson, D. M., Nittrouer, C. A., Smith, W. O. Jr (in press). The cycling and accumulation of organic matter and biogenic silica in a high-latitude environment: the Ross Sea. *Oceanography*
- DeMaster, D. J. Jr, Nelson, T. M., Harden, S. L., Nittrouer, C. A. (1991). The cycling and accumulation of biogenic silica and organic carbon in Antarctic deep-sea and continental margin environments. *Mar. Chem.* 35: 489–502
- El-Sayed, S. Z. (1978). Primary productivity and estimates of potential yields of the Southern Ocean. In: McWhinnie, M. A. (ed.) *Polar research*. Westview, New York, p. 141–160
- Eppey, R. W. (1972). Temperature and the regulation of phytoplankton growth in the sea. *Fish. Bull. U.S.* 70: 1063–1085
- Fahrbach, E., Knoche, M., Rohardt, G. (1991). An estimate of water mass transformation in the southern Weddell Sea. *Mar. Chem.* 35: 25–44
- Fischer, G., Fütterer, D., Gersonde, R., Honjo, S., Ostermann, D., Wefer, G. (1988). Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. *Nature* 335: 426–428
- Foster, T. D., Carmack, E. C. (1976). Frontal zone mixing and Antarctic bottom water formation in the southern Weddell Sea. *Deep Sea Res.* 23: 301–307
- Frontier, S. (1969). Méthode d'analyse statistique applicable à l'écologie du plancton. *Doc. Sci. ORSTOM*, Nosy-Bé, 7
- Garrison, D. L., Buck, K. R. (1989). Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice-edge zone. *Polar Biol.* 9: 341–351
- Garrison, D. L., Buck, K. R., Fryxell, G. A. (1987). Algal assemblages in Antarctic pack ice and in ice edge-plankton. *J. Phycol.* 23: 564–572
- Hewes, C. D., Holm-Hansen, O., Sakshaug, E. (1985). Alternate carbon pathways at lower trophic levels in the Antarctic food web. In: Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, p. 277–283
- Holm-Hansen, O., El-Sayed, S. Z., Franceschini, G. A., Cuhel, R. L. (1977). Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: Llano, G. (ed.) *Adaptations within Antarctic ecosystems*. Gulf, Houston, p. 11–50

- Honjo, S. (1991). Particles fluxes and modern sedimentation in the Polar Oceans. In: Smith, W. O. Jr (ed.) Polar oceanography. Academic Press, New York, p. 687–740
- Jacques, G., Panouse, M. (1991). Biomass and composition of size fractionated phytoplankton in the Weddell-Scotia Confluence area. *Polar Biol.* 11: 315–328
- Jennings, J. C., Gordon, L. I., Nelson, D. M. (1984). Nutrient depletion indicates high primary productivity in the Weddell Sea. *Nature* 309: 51–54
- Jones, E. P., Nelson, D. M., Tréguer, P. (1990). Chemical oceanography. In: Smith, W. O. Jr (ed.) Polar oceanography. Academic Press, New York, p. 407–476
- Lancelot, C., Billen, G., Veth, C., Becquevort, S., Mathot, S. (1991). Modelling carbon cycling through phytoplankton and microbes in the Scotia-Weddell Sea area during sea ice retreat. *Mar. Chem.* 35: 305–324
- Ledford-Hoffman, P. A., DeMaster, D. J., Nittrouer, C. A. (1986). Biogenic silica accumulation in the Ross Sea and the importance of Antarctic continental shelf deposits in the marine silica budget. *Geochim. Cosmochim. Acta* 50: 2099–2110
- Leynaert, A., Tréguer, P., Quéguiner, B., Morvan, J. (1991). The distribution of biogenic silica and the composition of particulate organic matter in the Weddell-Scotia Sea during spring 1988. *Mar. Chem.* 35: 435–447
- Martin, J. H., Fitzwater, S. E., Gordon, R. M. (1990). Iron deficiency limits phytoplankton growth in Antarctic waters. *Global biochem. Cycles* 4: 5–12
- Mitchell, B. G., Brody, E. A., Holm-Hansen, O., McClain, C., Bishop, P. (1991). Light limitation of phytoplankton biomass and macronutrient utilization in the Southern Ocean. *Limnol. Oceanogr.* 36: 1662–1677
- Muench, R. D. (1990). Mesoscale phenomena in the Polar Oceans. In: Smith, W. O. Jr (ed.) Polar oceanography. Academic Press, New York, p. 223–286
- Nelson, D. M., Ahern, A. J., Herlihy, L. J. (1991). Cycling of biogenic silica within the upper water column of the Ross Sea. *Mar. Chem.* 35: 461–476
- Nelson, D. M., Brzezinski, M. A. (1990). Kinetics of silicic acid uptake by natural diatom assemblages in two Gulf-Stream warm-core rings. *Mar. Ecol. Prog. Ser.* 62: 283–292
- Nelson, D. M., Goering, J. J. (1977). A stable isotope tracer method to measure silicic acid uptake by marine phytoplankton. *Analyt. Biochem.* 78: 139–147
- Nelson, D. M., Gordon, L. I. (1982). Production and pelagic dissolution of biogenic silica in the Southern Ocean. *Geochim. Cosmochim. Acta.* 46: 491–501
- Nelson, D. M., Smith, W. O. (1986). Phytoplankton bloom dynamics of the western Ross Sea ice edge – II. Mesoscale cycling of nitrogen and silicon. *Deep Sea Res.* 33: 1389–1412
- Nelson, D. M., Smith, W. O. Jr (1991). Sverdrup revisited: Critical depths, maximum chlorophyll levels, and the control of Southern Ocean productivity by the irradiance-mixing regime. *Limnol. Oceanogr.* 36: 1650–1661
- Nelson, D. M., Smith, W. O., Gordon, L. I., Huber, B. A. (1987). Spring distribution of density, nutrients, and phytoplankton biomass in the ice edge zone of the Weddell-Scotia Sea. *J. geophys. Res.* 92: 7181–7190
- Nelson, D. M., Smith, W. O., Muench, R. D., Gordon, L. I., Sullivan, C. W., Husby, D. M. (1989). Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: relationship to hydrography during late summer. *Deep Sea Res.* 36: 191–209
- Neveux, J. (1976). Dosage de la chlorophylle a et de la phéophytine par fluorométrie. *Annls Inst. océanogr., Paris* 52: 165–174
- Niebauer, H. J., Alexander, V. (1985). Observations and significance of ice-edge oceanographic frontal structure in the Bering Sea. *Cont. Shelf Res.* 4: 367–388
- Nöthing, E. M., Bathmann, U., Jennings, J. C., Fahrbach, 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
- Paasche, E. (1973). Silicon and the ecology of marine plankton diatoms. 1. *Thalassiosira pseudonana* (*Cyclotella nana*) grown in a chemostat with silicate as the limiting nutrient. *Mar. Biol.* 19: 117–126
- Quéguiner, B., Tréguer, P., Nelson, D. M. (1991). The production of biogenic silica in the Weddell and Scotia Seas. *Mar. Chem.* 35: 449–459
- Quentin, L. B., Ross, R. M. (1985). Feeding by Antarctic krill, *Euphausia superba*: does size matter? In Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, p. 372–377
- Redfield, A. C., Ketchum, B., Richards, F. A. (1963). The influence of organisms on the composition of seawater. In: Hill, M. N. (ed.) The sea, Vol. 2. Wiley Interscience, New York, p. 26–77
- Rutgers van der Loeff, M. M., van Bennekom, A. J. (1989). Weddell Sea contributes little to silica enrichment in Antarctic bottom water. *Deep Sea Res.* 36: 1341–1357
- Smetacek, V. S. (1985). Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.* 84: 239–251
- Smith, W. O., Nelson, D. M. (1985). Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science* 227: 163–166
- Smith, W. O., Nelson, D. M. (1986). The importance of ice-edge phytoplankton blooms in the Southern Ocean. *BioSci.* 36: 251–257
- Smith, W. O. Jr, Keene, N. K., Comiso, J. C. (1988). Inter-annual variability in estimated primary production of Antarctic marginal ice zone. In: Sahrhage, D. (ed.) Antarctic ocean and resources variability. Springer-Verlag, Berlin, p. 131–139
- Smith, W. O. Jr, Sakshaug, E. (1990). Polar phytoplankton. In: Smith, W. O. Jr (ed.) Polar oceanography, Part B. Academic Press, San Diego, p. 477–525
- Strickland, J. D. H., Parsons, T. R. (1972). A practical handbook of seawater analysis, 2nd edn. *Bull. Fish. Res. Bd Can.* 167
- Tréguer, P., Jacques, G. (1992). Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biol.* 12: in press
- Tréguer, P., Lindner, L., van Bennekom, A. J., Leynaert, A., Panouse, M., Jacques, G. (1991). Production of biogenic silica in the Weddell-Scotia Seas measured with ³²Si. *Limnol. Oceanogr.* 36: 1217–1227
- Tréguer, P., Nelson, D. M., Guezeley, S., Zeyon, C., Morvan, J., Buma, A. (1990). The distribution of biogenic and lithogenic silica and the composition of particulate organic matter in the Scotia Sea and the Drake Passage during autumn 1987. *Deep Sea Res.* 37: 833–851
- Tréguer, P., van Bennekom, A. J. (1991). The annual production of biogenic silica in the Antarctic Ocean. *Mar. Chem.* 35: 477–487
- Utermöhl, H. (1931). Neue Wege in der quantitativen Erfassung des Planktons (mit besonderer Berücksichtigung des Ultraplanktons). *Verh. int. Verein. theor. angew. Limnol.* 5: 567–596
- van Bennekom, A. J., Buma, A. G. J., Nöthing, R. F. (1991).

- Dissolved aluminium in the Weddell-Scotia Confluence and effect of Al on the dissolution kinetics of biogenic silica. *Mar. Chem.* 35: 423–434
- von Bodungen, B. V., Smetacek, V. S., Tilzer, M. M., Zeitzschel, B. (1986). Primary production and sedimentation during spring in the Antarctic Peninsula region. *Deep Sea Res.* 33: 177–194
- Wilson, D. L., Smith, W. O. Jr, Nelson, D. M. (1986). Phytoplankton bloom dynamics of the western Ross Sea ice edge. I. Primary productivity and species-specific production. *Deep Sea Res.* 33: 1375–1387
- Zwally, H. J., Parkinson, C. L., Comiso, J. C. (1983). Variability of Antarctic sea ice and changes in carbon dioxide. *Science* 220: 1005–1012

This article was submitted to the editor

Manuscript first received: July 29, 1992

Revised version accepted: March 15, 1993