Intense summer Si-recycling in the surface Southern Ocean

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[1] Si-cycle in surface waters was investigated in summer 2003 during a transect conducted from south-Australia to Antarctica. Diatoms dominated the microphytoplankton. Silicic acid was depleted up to 60°S; a subsurface maximum of biogenic silica (= biosilica) was observed in the Permanent Open Ocean Zone. In the 100–0.01% light zone, the ratio of depth-integrated biosilica dissolution rate (D) to depth-integrated biosilica production rate (P) ranged between 0 to 3.1, being >1 for 5 of our 6 stations. The biosilica dissolution was related to the percentage of dead diatoms but not to the temperature and might be, at least partially, under bacteria mediation. This study shows that during summer the Southern Ocean silicate pump can be much less efficient than usually expected. Existence of scenarios with intense surface Si-recycling in the Southern Ocean has major consequences both for modelers and paleoceanographers. *INDEX TERMS:* 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 1615 Global Change: Biogeochemical processes (4805); 4855 Oceanography: Biological and Chemical: Plankton; 4207 Oceanography: General: Arctic and Antarctic oceanography; 4870 Oceanography: Biological and Chemical: Stable isotopes. **Citation:** Beucher, C., P. Tréguer, A.-M. Hapette, R. Corvaisier, N. Metzl, and J.-J. Pichon (2004), Intense summer Si-recycling in the surface Southern Ocean, *Geophys. Res. Lett.*, *31*, L09305, doi:10.1029/2003GL018998.

1. Introduction

[2] The Southern Ocean plays a key role in the global marine biological pump of carbon [e.g., *Tréguer and Pondaven*, 2002]. Diatoms are major players of the biological pump of the Southern Ocean, that is why the biogeochemical cycle of Si in the Southern Ocean is receiving much attention [e.g., *Pondaven et al.*, 2000]. This cycle is not well constrained, especially because only few measurements of Si-recycling are available. In the euphotic zone, the ratios of the depth-integrated biosilica dissolution rate to the depth-integrated biosilica production rate can double from a bloom period to a post-bloom period [*Brzezinski et al.*, 2003]. Currently, mostly because of abundant opal abyssal deposits, the Southern Ocean is viewed as a strong exporter of biosilica. We herein show that during austral summer, the integrated dissolution rate can exceed the integrated production rate in the euphotic layer for various Antarctic subsystems, suggesting almost no export of opal to the deep ocean.

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2. Methods

[3] The CADO/OISO cruise was conducted during austral summer 2003 (23 January–17 February 2003), south of Australia (Figure 1a). Hydrological fronts were located according to *Chaigneau and Morrow* [2002]. The latitude of maximal winter extent of sea ice was 63°30 S (http://www.natice.noaa.gov/). Our stations were distributed in different subsystems: the SAZ, the POOZ, the SIZ and the CCSZ. At each station, water sampling was performed at 6 depths (corresponding to 100, 50, 25, 10, 1 and 0.01 % of surface PAR).

[4] The concentrations of $Si(OH)_4$, (NO_3 + NO_2) and biosilica ($bSiO_2$), and the microphytoplankton (2 per station) counting, determination (species) and characterization (full = alive, empty or broken = dead) were determined as described in *Beucher et al.* [2004]. Total bacteria (i.e., free-living and attached bacteria) protease activity (PA) was measured using commercially available substrate that employs amino-4-methylcoumarine (AMC) as the fluorophore [*Hoppe*, 1983]. Fluorogenic analog substrate (Leucine-AMC) was added at 20 μM final concentration.

[5] Biosilica production and dissolution rates were measured as described in *Beucher et al.* [2004]. Incubations were carried out 24 hours in a deck incubator cooled by running sea-surface water. Incubation flasks were fitted out with neutral photographic screens to simulate in situ light conditions. The method used is quite similar to that developed by *Nelson and Goering* [1977a, 1977b]; the sample was spiked by $^{29}Si(OH)_4$ so that the increase of the in situ concentration did not excess 10 %. The improvement of our method stands in the direct measurement of SiO_2^- (not of SiF_3^+ avoiding using the hazardous HF). Dissolved Si was recovered by precipitation with a TEA/molybdate reagent [*De La Rocha et al.*, 1996] and purified by combustion up to 1100°C. For detailed chemical and analytical procedures, see R. Corvaisier et al. (Determination of the rate of production and dissolution of biosilica in marine waters by thermal ionisation mass spectrometry, submitted to *Analytica Chimica Acta*, 2004). Isotopic abundances were measured on a THQ Finnigan mass spectrometer with precision = 1 part in 10000 for the atom % of ^{29}Si and average blank = 9 nmol. The biosilica production (ρ_P) and dissolution (ρ_D) rates were constrained by the requirement

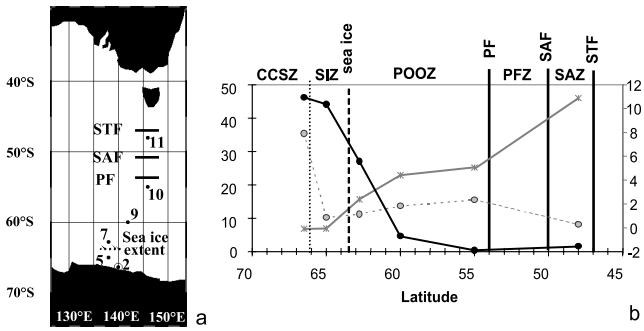

Figure 1. (a) Localization of stations sampled. Sub-Tropical Front (STF), Sub-Antarctic Front (SAF), Polar Front (PF), Sub-Antarctic Zone (SAZ), Permanent Open Ocean Zone (POOZ), Seasonal Ice Zone (SIZ) and Coastal and Continental Shelf Zone (CCSZ). (b) Distribution of temperature (°C, stars, right scale), $Si(OH)_4$ (μM, black circles, left scale) and $bSiO_2$ (μmol l^{-1}, grey circles, right scale) in surface waters versus latitude.

to fit mass and isotopic balances of the dissolved and the particulate phases (i.e., 4 equations for 2 unknowns); the best solution being found iteratively by minimizing the cost function [*Elskens et al.*, 2002; *Beucher et al.*, 2004]. Average specific production (∇_P) and dissolution (∇_D) rates were calculated for each profile (specific rate = absolute rate divided by biosilica concentration).

3. Results

[6] $NO_3 + NO_2$ concentrations in surface waters ranged from 7.5 to 53 μM, i.e. were everywhere sufficient to prevent from N-limitation. Microphytoplankton was everywhere diatom-dominated.

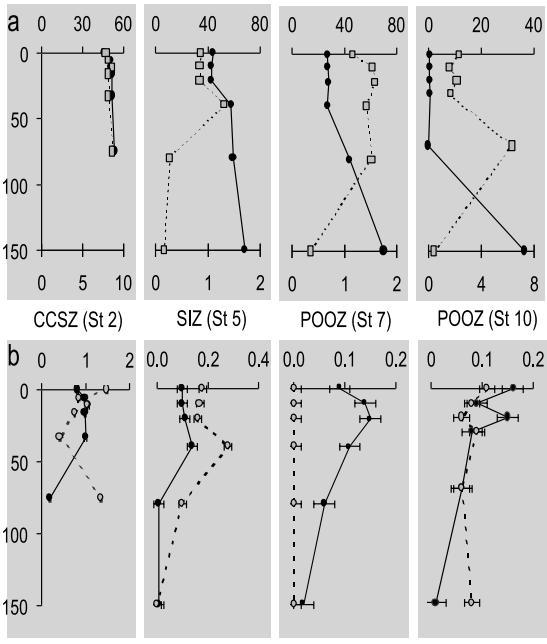

Figure 2. (a) Profiles of $Si(OH)_4$ concentrations (μM, black, high scale) and $bSiO_2$ concentrations (μmol l^{-1}, grey, low scale). (b) Profiles of biosilica production (black, ±0.02 μmol l^{-1} d^{-1}) and dissolution (grey, ±0.015 μmol l^{-1} d^{-1}) rates (error on replicates).

Table 1. Sampling Date (2003) of Stations, 0.01% Light Depth (m), Biosilica Parameters and Protease Activity of Total Bacteria

St.	date	0.01%	$\int bSiO_2$	$\int \rho_P$	$\int \rho_D$	$\int D:\int P$	∇_P	∇_D	$\int PA$
2	02–05	75	622	57.6	63.1	1.1	0.10	0.12	19.0
5	02–08.	150	85	7.9	18.8	2.4	0.09	0.20	2.4
7	02–11	150	184	11.4	0.0	0.0	0.07	0.00	3.9
9	02–03	150	370	10.0	12.6	1.3	0.04	0.04	4.5
10	02–01	150	488	9.2	11.0	1.2	0.05	0.06	13.0
11	01–30	80	31	1.7	5.2	3.1	0.06	0.13	4.9

$\int bSiO_2$: depth-integrated biosilica concentration (mmol m^{-2}), $\int \rho_P$ and $\int \rho_D$: depth-integrated biosilica production and dissolution rates (mmol m^{-2} d^{-1}). $\int D:\int P$: ratio of $\int \rho_D$ to $\int \rho_P$. ∇_P and ∇_D: average specific biosilica production and dissolution rates (d^{-1}). $\int PA$: depth-integrated protease activity of total bacteria (μmol m^{-2} h^{-1}).

[7] Station N°2, situated in the CCSZ, presented high concentrations of nutrients and biosilica (Figure 2, Table 1). The total percentage of dead diatoms was lower than in others stations (14%) (Table 2) and differed also by a large range among species. The small *Fragilariopsis curta* were dominant and mostly living (14% dead) whereas the big *Corethron criophilum* (220–300 μm) were mostly dead (60%). This suggests that the dominant small living diatoms ensured the production of biosilica whereas the dissolution was mostly due to the large dead cells. Very high biosilica production and dissolution rates were measured in this coastal station (Figure 2), in accordance with *Nelson et al.*'s study in the Ross Sea [1991]. The ratio of the depth-integrated dissolution to the depth-integrated production of biosilica ($\int D:\int P$) was 1.1. This station presented the highest integrated bacterial protease activity ($\int PA$, Table 1).

[8] Station N°5, situated in the SIZ, was characterized by low biosilica concentration (Figure 2) and low biosilica production rate compared to POOZ stations. 31% of diatoms were dead (Table 2). This station was also characterized by the presence (5%) of *Corethron criophilum* mostly dead (60%). The specific dissolution rate reached a maximal value of 0.38 d^{-1}. A net dissolution (dissolution overwhelming production) occurred at the 6 depths sampled: $\int D:\int P$ was 2.4. $\int PA$ was the lowest of this study (almost 10 times less than in the CCSZ, Table 1).

[9] The POOZ presented a $Si(OH)_4$ gradient (Figure 1), with surface concentrations decreasing from south to north.

Table 2. Percentage of Dead Diatoms and of Major Diatom Species

St	% dead	3 major species
2	14	*F. curta (39%), Nitzschia sp. (19%), Corethron criophilum (12%)*
5	31	*F. curta (51%), F. cylindrus (20%), Pseudonitzschia heimii (11%)*
7	28	*Fragilariopsis sp. (27%), F. curta (19%), F. kerguelensis (18%)*
9	29	*F. kerguelensis (64%), Fragilariopsis sp. (9%), Pseudonitzschia heimii (6%)*
10	19	*Fragilariopsis sp. (27%), F. kerguelensis (24%), Pseudonitzschia heimii (18%)*
11	35[a]	*Pseudonitzschia heimii (36%), Thalassiosira (21%), Fragilariopsis sp. (18%)*

F.: *Fragilariopsis*,
[a]: calculated excluding *Pseudonitzchia lineola* (see text).

In parallel, $bSiO_2$ concentrations increased from south to north such as the integrated protease activity (Table 1). Diatoms were dominated by the genus *Fragilariopsis* (Table 2).

[10] In the south part of the POOZ (station N°7), silicic acid was not at limiting concentrations (Figure 2). Diatoms ranged from 10 to 50 μm and appeared relatively highly silicified (average $bSiO_2$/cells = 105 pmol Si $cell^{-1}$). The dissolution rate at the 6 depths was never analytically different from 0 (i.e., in that case < 0.05 μmol l^{-1} d^{-1}), indicating no (or very low) recycling of Si at this station.

[11] Stations N°9 and N°10 were characterized by a subsurface maximum of biosilica at the 1% PAR depth (75 and 70 m, respectively) with concentrations of 3.4 and 6.3 μmol l^{-1}. ∇_P and ∇_D were low and of similar magnitude. At the two stations, a net production of biosilica occurred in the first 40 meters and a net dissolution below. $\int D:\int P$ ratios were 1.3 and 1.2, respectively.

[12] At station N°11 located in the SAZ, nutrient concentrations were typical of an HNLSLC (High Nutrient Low Si low Chlorophyll) system ($Si(OH)_4$ < 2 μM and NO_3 + NO_2 > 10 μM). Excepting *Pseudonitzschia lineola* cells for which the characterization was impossible, the total percentage of dead diatoms was 35% (Table 2). Fluorescence values were comparable to those found in the POOZ or the CCSZ but $bSiO_2$ (Table 1) and diatom abundance were very low. This suggests that, during our study, the SAZ was dominated by small phytoplankton (pico- and nano- not observable by microscopy, i.e., <5 μm), in agreement with previous observations in the same area [*Kopczynska et al.*, 2001]. A net dissolution of biosilica occurred at the 6 depths; $\int D:\int P$ was 3.1.

4. Discussion

[13] In the Southern Ocean, during winter, the Polar Front (PF) usually coincides with a silicic acid gradient [*Jones et al.*, 1990]. In our study $Si(OH)_4$ was depleted up to 60°S (<5 μM at station N°9) whereas PF was centered at 54°S. This suggests a south spring/summer migration of the $Si(OH)_4$ gradient as already shown in the Indian and Pacific sectors [*Pondaven et al.*, 2000; *Brzezinski et al.*, 2001]. The subsurface $bSiO_2$ maximum in the POOZ is typical of this area during summer [*Parslow et al.*, 2001]. As reported for 1998 [*Jabaud-Jan et al.*, 2004] the POOZ was more productive than the SIZ. Actually, both for 1998 and 2003, sea surface temperatures in the POOZ show positive anomaly compared to the two-decade average (interpreted by *Jabaud-Jan et al.* [2004] as resulting from an indirect El Nino connection) which might have positively impacted the POOZ productivity.

[14] Compared to spring studies [*Nelson and Gordon*, 1982; survey I in *Brzezinski et al.*, 2001] our study shows relative low specific production rates (∇_P < 0.1 d^{-1}) suggesting non-optimal conditions for the growth of diatoms. This was probably due to low Fe availability in surface waters during summer (although low $Si(OH)_4$ availability might also be involved at least in the northern part of the study area, *cf. Franck et al.*, 2000).

[15] Interestingly, excluding station N°2 (for which the percentage of dead cells is not homogeneously distributed), the specific biosilica dissolution rate was correlated to the percentage of dead diatoms (N = 10, R^2 = 0.48, p = 0.015). So why was the dissolution of dead diatom frustules so active during our summer cruise? For the whole data set no correlation was found between specific biosilica dissolution rate and temperature (Figure 3), indicating that other processes have to be involved. Actually, any process that results in increasing silica specific surface and/or in building up small amorphous silica objects of long residence time in surface waters favors biosilica dissolution. Mechanical breakage of diatom frustules during crustacean zooplankton mastication is a first process that has the potential to do it, but grazing has also a negative effect by embedding siliceous materials in fecal pellets that settle down rapidly. Microscopic observations of diatoms at our stations does not give evidence of intense grazing activity of microphytoplankton during our study period, in agreement with previous studies [e.g., *Voronina*, 1998] that show usual low grazing pressure by micronekton (krill) in this area. *Bidle and Azam* [1999] have pointed out the importance of a second process, they showed evidence of attached-bacteria mediated biosilica dissolution through hydrolytic attack on organic matrix of biosilica frustules. During our study, we measured the total activity of bacteria (i.e., of free + attached bacteria). Interestingly, for the stations where diatoms dominated phytoplankton (SAZ excluded), the integrated bacteria protease activity ($\int PA$) was correlated with integrated $bSiO_2$ concentrations ($\int bSiO_2$) (R^2 = 0.85, p = 0.025), suggesting that the dynamic of total bacteria and of diatoms were linked during this austral summer. In the open-ocean, most of bacteria are free but the number of attached bacteria increases with biomass density [e.g., *Bidle and Fletcher*, 1995]. Attached-bacteria have a stronger activity than free bacteria [e.g., *Becquevort and Smith*, 2001] and most of free bacteria are enzymatically inactive [e.g., *Chrøst*, 1991]. Station 5 (SIZ) distinguishes with relative low $bSiO_2$ (compared to the POOZ or the CCSZ) and low protease activity suggesting either that bacteria were not abundant or that they were mostly free-living. Ignoring this station 5, the average specific biosilica dissolution rate was linearly correlated with the protease activity of total bacteria (N = 4, R^2 = 0.85, p = 0.06). So, although the bacterial activity measured during our cruise was not diatom-specific, these results seem to support the new perspective of *Bidle and Azam* [1999].

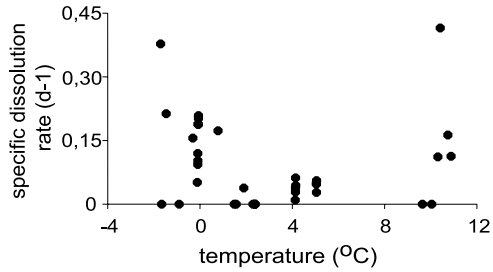

Figure 3. Specific biosilica dissolution rate (d^{-1}) *versus* temperature (°C).

[16] In previous studies production and dissolution rates have been integrated in the 100–0.1% layer (no 0.01% light depth as done in our study). This raises the question of the appropriate integration layer as, both dissolution and production might occur below the 0.1% light depth. Anyway,

Table 3. $\int D:\int P$ Ratios in the Southern Ocean 100–0.1% Light Layer From Which Vertically Integrated Data are Available (N = Number of Stations)

Season		N	low	mean	high
Austral spring					
O-N 1978	Pacific[a]	6	0.18	0.34	0.58
O-N 1997	Pacific survey I[b]	3	0.61	0.64	0.69
D 1997	Pacific Process I[b]	7	0.01	0.27	0.72
	total	16		0.37	
Austral summer					
J-F, 1990	Ross Sea[c]	9	0.41	0.65	1.1
F-M, 1998	Pacific Process II[b]	6	0.04	0.83	2.71
J-F, 2003	East Indian[d]	6	*0.0*	*1.4*	*3.2*
	total	21		0.9	

Data from:
[a]*Nelson and Gordon* [1982].
[b]*Brzezinski et al.* [2001].
[c]*Nelson et al.* [1991].
[d]This study (using 0.1% data estimated).

in order to compare previous studies to our, we have estimated, from our results, ρ_P and ρ_D at the 0.1% depth and calculated $\int D:\int P$ in the 100–0.1% layer. These estimated ratios are 0.8, 2.3, 0, 1.3, 0.9 and 3.2 for stations 2, 5, 7, 9, 10 and 11, respectively (Table 3). Now, Table 3 offers a new vision of the Si-cycle in the surface waters of the Southern Ocean, and delivers a clear message: a higher Si-recycling occurs during summer ($\int D:\int P$ average = 0.9) as opposed to spring ($\int D:\int P$ average = 0.37). Although the Si-recycling varies within a large range during a given season, it is remarkable that during spring $\int D:\int P$ never exceeds unity whereas in summer ratios >1 are found for different systems of the Southern Ocean. In other words, this suggests that the silicate pump (a concept described by *Dugdale et al.* [1995]) is more efficient in the Southern Ocean during spring than during summer.

5. Conclusion

[17] This study clearly confirms that temperature alone does not control the biosilica dissolution in surface waters of the Southern Ocean, and supports Bidle and Azam's view on bacteria-mediated biosilica dissolution. This has strong implications for modelers who should take into account the role of the microbial loop on biosilica dissolution. Our results also show that a complete recycling of biosilica produced in the euphotic layer can occur during summer. This has strong implications for paleo-reconstructions, as diatom oozes apparently may mostly represent the spring production.

[18] **Acknowledgments.** This work is dedicated to the memory of J. J. Pichon. It was supported by INSU/CNRS/IPEV, France. We thank the captain and crew of the *R.V. Marion-Dufresne*, the chief scientists: X. Crosta and E. Michel and E. Follenfant for (NO_3 + NO_2) analyses. Contribution No 908 of European Institute for Marine Studies, Brest, France.

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