

Editorial

The natural iron fertilization experiment KEOPS (Kerguelen Ocean and Plateau compared Study): An overview

1. The concept of a natural iron fertilization experiment

When the first scientific voyages went to the Southern Ocean, high levels of living biomass were observed in the vicinity of islands. [Hart \(1942\)](#) was the first to mention that the abundant biomass might be due to the release of oligo-elements like iron from the island. This hypothesis, however, remained unverified for more than half a century because of the experimental difficulties in properly manipulating water with subnanomolar iron concentrations. When John Martin formulated the iron hypothesis ([Martin, 1990](#)) and provided the first supporting evidence of it, he also suggested using the chlorophyll plume observed westward of the Galapagos Island in the Equatorial Pacific as a natural iron fertilization experiment. This was partly realized during PlumEX, but at the same time most of the efforts were dedicated to conduct the first artificial iron fertilization experiment (IRONEX1), and the investigations within the Galapagos plume were limited ([Gordon et al., 1998](#)).

In the Southern Ocean, the observation of high biomass in the vicinity of the Antarctic and Subantarctic islands has been confirmed by a large number of expeditions. Today, ocean-color satellite images provide daily information on the concentration of chlorophyll in surface waters, revealing the exact extent and the temporal variability of these blooms.

Although Martin proposed natural and artificial fertilization as fruitful strategies to verify the iron hypothesis, most of the effort has been focused on artificial fertilization experiments. Indeed considerable knowledge has been gained using this strategy ([Boyd et al., 2007](#); [De Baar et al., 2005](#)). However, despite the impressive success of these experiments, it has been noted that they are prone to several artefacts, for example, the exchange of water between the inside and outside of the patch ([Boyd et al., 2002](#)). The duration of the experiment and thus the time period of observation following the enrichments are also limited. Some important questions remain therefore unresolved. This is the case for carbon export and for possible side effects, like the emission of dimethylsulfide (DMS).

The cornerstone of a natural iron fertilization experiment is the demonstration that the iron supply is enhanced in the fertilized region compared to a reference region. This requires a careful determination of the dissolved iron distribution that subsequently allows the identification of the natural iron sources. Following this prerequisite, further investigations on the nature and the magnitude of the natural fertilization, on the impact on the ecosystem structure and on the consequences for biogeochemical cycles constitute the general framework of a natural fertilization experiment as conducted recently around the Kerguelen plateau ([Blain et al., 2007](#)) and papers in this issue are around Crozet archipelago ([Pollard et al., 2007](#) and references therein).

2. The KEOPS project: implementation and strategy

The bloom above the Kerguelen Plateau is among the largest observed in the Southern Ocean. Based on the annual composite images this bloom is present every year with some interannual variability ([Mongin et al., 2008](#)). A more detailed examination reveals two distinct regions within the bloom. A long chlorophyll plume extends eastward of Kerguelen island in the region where the Polar and Subantarctic Fronts are in close proximity ([Blain et al., 2001](#)). This plume is therefore strongly impacted by mesoscale activity. In the Southeast of Kerguelen Island another bloom develops from mid November to late February. This bloom covers an area of 45,000 km² and is roughly constrained by the bathymetry of the plateau between the Kerguelen and Heard Islands. The KEOPS program location was chosen due to the lower interannual and mesoscale variability of the southeastern bloom as revealed by satellite imagery.

The three major objectives of KEOPS were (1) to demonstrate the occurrence of natural iron fertilization above the Kerguelen plateau, (2) to describe the functioning of the ecosystem, and (3) to study the consequences of natural fertilization on the biogeochemical cycles with a special focus on carbon. The general strategy involved a comparison between two typical stations, one

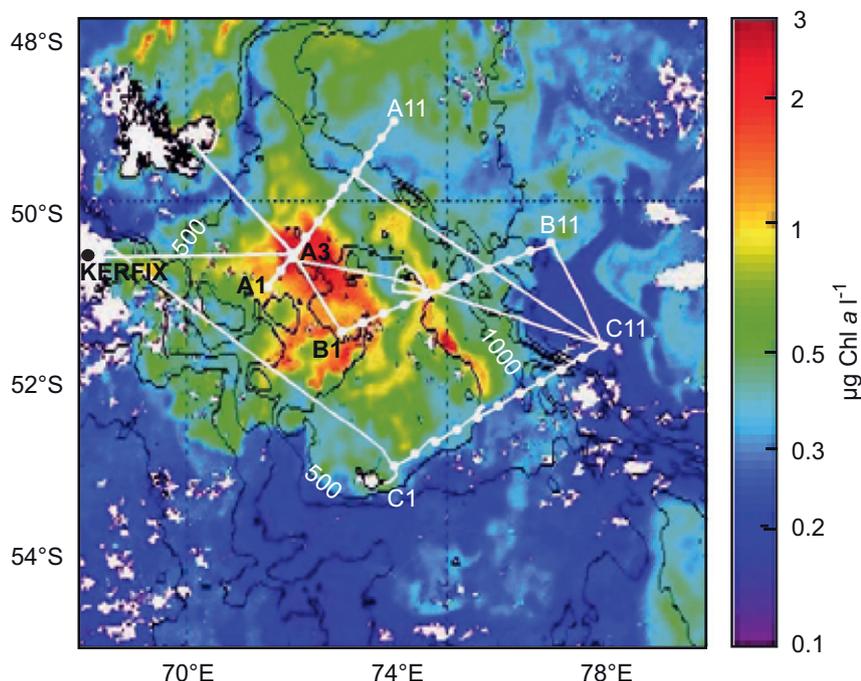


Fig. 1. Map of KEOPS study area showing transects and stations.

representative of the phytoplankton bloom and the other illustrative of HNLC conditions.

The KEOPS mission took place in January–February 2005 aboard the *R/V Marion Dufresne*. During the transit from La Réunion to Kerguelen island (11/01/05–18/01/05) quasi-real-time satellite images (composite of MODIS and MERIS products provided by the ACRI company, Fig. 1) were carefully examined to finalize the position of the two reference stations (A3 and C11) and of the three transects (A, B, C) (Fig. 1). The reference stations were visited at different dates (Table 1) to provide insights into the temporal variability of the bloom. The time series station KERFIX (K1) (Jeandel et al., 1998) was also visited, providing information on the conditions prevailing on the western flank of the plateau.

3. Overview of the results

3.1. Mechanisms of natural iron fertilization

The three-dimensional distribution of dissolved iron (DFe) (Blain et al., 2008) revealed low (~ 0.1 nM) DFe concentrations in the upper 150 m at almost all stations. A clear enrichment in DFe below 150 m was seen in stations above the plateau compared to stations off-plateau. The dissolved organic ligands (LFe) were always in excess of DFe, increasing the residence time of DFe in the water column and its potential availability for phytoplankton (Gerringa et al., 2008). Diapycnal mixing enhanced by internal wave activity is one of the mechanisms that made the deep iron seen over the plateau available for phytoplankton in surface waters (Park et al., 2008a). It is important to note that this mechanism also supplied the

surface waters with major nutrients. The short-term budget of iron indicates that this process alone could not match the phytoplankton DFe demand as determined from ^{55}Fe uptake experiments (Sarhou et al., 2008). The utilization of the winter stock brought into the water column and the dissolution of lithogenic iron are other most probable mechanisms that could explain the natural iron fertilization. Culture experiments of the natural phytoplankton assemblage of open-ocean with plateau deep-water collected close to the sea-floor above the plateau significantly increased the carbon assimilation mainly by the larger-sized phytoplankton (Timmermans et al., 2008). This provides complementary evidence of the fertilization from below as the cause of the Kerguelen bloom.

The large-scale circulation above and around the Kerguelen plateau (Park et al., 2008b) shows that the bloom region was characterized by weak currents, leading to a water-mass residence time of several months. This enhanced residence time allows the bloom to develop and persist in response to natural iron fertilization throughout the entire season (Blain et al., 2008).

The multi-geochemical tracer study carried out during KEOPS additionally identified the water-mass pathways for the transport of dissolved and particulate material. The distribution of the rare-earth elements (REE) (Zhang et al., 2008) identifies Heard Island as a significant source of lithogenic material for the water column above the plateau. The partial dissolution of this basaltic material could be a significant source of DFe. The advection of water masses that has been in contact with the sediment in the vicinity of Heard Island are liable for the elevated ^{228}Ra activities observed in the upper 150 m above the plateau (Van Beek et al., 2008). These processes, and possibly also isopycnal

Table 1
Table of stations: bold characters denote station located on the plateau

Station	Start				End			
	Date	Time (UT + 5 h)	Latitude	Longitude	Date	Time (UT + 5 h)	Latitude	Longitude
A03	18/01/2005	20:06	50° 37.80' S	72° 04.80' E	19/01/2005	18:49	50° 37.88' S	72° 04.69' E
A11	20/01/2005	04:42	49° 08.90' S	74° 00.10' E	21/01/2005	12:28	49° 09.00' S	74° 00.60' E
A10	21/01/2005	14:08	49° 20.00' S	73° 45.90' E	21/01/2005	16:00	49° 19.90' S	73° 45.20' E
A09	21/01/2005	17:27	49° 31.20' S	73° 30.30' E	21/01/2005	23:40	49° 31.90' S	73° 30.90' E
A08	22/01/2005	01:56	49° 42.30' S	73° 16.90' E	22/01/2005	09:00	49° 42.03' S	73° 16.63' E
A07	22/01/2005	10:34	49° 53.39' S	73° 02.42' E	22/01/2005	14:46	49° 53.90' S	73° 00.60' E
A06	22/01/2005	16:40	50° 04.80' S	72° 48.20' E	22/01/2005	17:20	50° 05.10' S	72° 00.06' E
A05	22/01/2005	18:41	50° 15.60' S	72° 34.29' E	22/01/2005	22:06	50° 15.60' S	72° 34.00' E
A04	22/01/2005	22:41	50° 26.70' S	72° 19.30' E	23/01/2005	00:22	50° 26.50' S	72° 19.10' E
A03	23/01/2005	01:50	50° 37.80' S	72° 04.80' E	23/01/2005	06:12	50° 36.91' S	72° 04.84' E
A02	23/01/2005	07:42	50° 48.80' S	71° 50.60' E	23/01/2005	08:25	50° 48.77' S	71° 50.66' E
A01	23/01/2005	09:47	50° 59.93' S	71° 36.11' E	23/01/2005	12:46	50° 59.80' S	71° 35.60' E
A03	23/01/2005	16:30	51° 00.00' S	72° 02.96' E	24/01/2005	15:56	50° 41.90' S	72° 01.50' E
C11	25/01/2005	09:34	51° 38.05' S	78° 07.10' E	28/01/2005	18:00	51° 37.75' S	77° 58.51' E
B11	28/01/2005	23:22	50° 29.90' S	77° 00.10' E	29/01/2005	00:10	50° 30.10' S	76° 59.80' E
B09	30/01/2005	00:08	50° 41.90' S	76° 12.10' E	30/01/2005	04:27	50° 41.51' S	76° 11.80' E
B08	30/01/2005	06:28	50° 47.94' S	75° 48.00' E	30/01/2005	09:30	50° 46.72' S	75° 47.37' E
B07	30/01/2005	10:58	50° 53.63' S	75° 23.57' E	30/01/2005	14:20	50° 54.00' S	75° 23.70' E
B06	30/01/2005	20:42	51° 00.30' S	75° 00.70' E	30/01/2005	21:24	51° 00.50' S	75° 00.30' E
B05	30/01/2005	23:28	51° 06.10' S	74° 35.90' E	02/02/2005	02:00	51° 05.70' S	74° 35.90' E
B04	02/02/2005	03:58	51° 11.70' S	74° 12.30' E	02/02/2005	04:31	51° 11.59' S	74° 12.25' E
B03	02/02/2005	06:14	51° 17.11' S	73° 48.15' E	02/02/2005	09:14	51° 17.88' S	73° 47.23' E
B02	02/02/2005	10:51	51° 23.96' S	73° 24.06' E	02/02/2005	11:24	51° 17.79' S	73° 47.37' E
B01	02/02/2005	13:03	51° 30.00' S	73° 00.10' E	02/02/2005	19:46	51° 29.42' S	73° 00.14' E
A05	04/02/2005	23:18	50° 15.60' S	72° 34.00' E	04/02/2005	23:22	50° 15.43' S	72° 34.11' E
A03	03/02/2005	01:00	50° 38.00' S	72° 05.00' E	04/02/2005	20:19	50° 15.60' S	72° 34.00' E
A08	05/02/2005	02:41	49° 45.20' S	73° 13.80' E	05/02/2005	05:16	49° 44.52' S	73° 12.16' E
C11	05/02/2005	20:41	51° 39.00' S	78° 00.00' E	06/02/2005	13:20	51° 46.50' S	77° 33.70' E
C09	06/02/2005	16:14	51° 55.35' S	77° 12.18' E	06/02/2005	19:24	51° 54.76' S	77° 11.71' E
C08	06/02/2005	21:00	52° 03.30' S	76° 48.00' E	06/02/2005	22:22	51° 03.40' S	76° 47.90' E
C07	07/02/2005	00:03	52° 11.40' S	76° 24.00' E	07/02/2005	03:02	52° 11.20' S	76° 23.40' E
C06	07/02/2005	04:32	52° 19.66' S	76° 00.80' E	07/02/2005	05:18	52° 19.86' S	75° 59.93' E
C05	07/02/2005	07:21	52° 27.43' S	75° 36.06' E	08/02/2005	07:45	52° 13.87' S	75° 43.67' E
C04	08/02/2005	10:38	52° 35.32' S	75° 12.37' E	08/02/2005	10:57	52° 35.32' S	75° 12.37' E
C03	08/02/2005	12:56	52° 43.40' S	74° 48.68' E	08/02/2005	15:55	52° 40.88' S	74° 44.04' E
C02	08/02/2005	17:48	52° 52.12' S	74° 24.54' E	08/02/2005	18:05	52° 52.40' S	74° 24.90' E
C01	08/02/2005	20:15	52° 59.90' S	74° 00.10' E	09/02/2005	05:06	53° 11.19' S	73° 52.84' E
KERFIX	10/02/2005	12:25	50° 40.00' S	68° 25.00' E	11/02/2005	13:05	50° 40.16' S	68° 24.99' E
A03	11/02/2005	22:31	50° 37.80' S	72° 05.40' E	13/02/2005	13:17	50° 38.15' S	72° 05.16' E

stirring above the plateau, contributed to the maintenance of a vertical gradient of DFe between 150 m and the seafloor. The flux of iron delivered by dust deposition was negligible (Wagener et al., in press).

3.2. Ecosystem structure

The three-dimensional distribution of pigments (Uitz et al., in revision; see also Fig. 1 in Belviso et al., 2008) as well as direct microscopic observations performed during the cruise on samples collected with Niskin bottles and net hauls (Armand et al., 2008a) demonstrated that the Kerguelen bloom was dominated by micro-phytoplankton (diatoms). These observations were in contrast to the off-plateau HNLC area, where both nano- and micro-

phytoplankton were important contributors. At the plateau stations, the relative contribution of micro-phytoplankton was >90% of total phytoplankton biomass and in the off-plateau stations it decreased to >70%. Pico-phytoplankton were negligible throughout the study area. A detailed description performed at stations A3 and C11 revealed that diatoms dominated the phytoplankton community in terms of carbon biomass at both sites. (Armand et al., 2008a; Cornet-Barthau et al., 2007). At station A3, two chain-forming diatom taxa, small *Chaetoceros* spp. from the subgenus *Hyalochaete* and *Eucampia antarctica*, dominated diatom cell abundance as well as diatom carbon biomass, but a distinct change in dominance from *Chaetoceros* spp. subgen. *Hylochaete* spp. to *E. antarctica* occurred during the course of the study. In contrast, at C11 the minute

Fragilariopsis pseudonana was the most abundant diatom but the open-ocean species *Fragilariopsis kerguelensis* was more important to the diatom carbon biomass at this location distinguished from its minor abundance. The low abundance of *F. kerguelensis* at A3 contrasts with its strong increase in abundance during the SOIREE mesoscale iron fertilization in the polar Southern Ocean (Gall et al., 2001). Sea-floor sediments under station A3 were dominated in order by *F. kerguelensis*, *Thalassionema nitzschioides* and *Chaetoceros* subgen. *vs* leave in, whereas those under the C11 location represent a typical open-ocean assemblage, dominated by *F. kerguelensis* and *Thalassiosira lentiginosa* (Armand et al., 2008b). These results suggest that the use of sediment abundances of *Chaetoceros* subgen. *Hyalochaetae* resting spores and *F. kerguelensis* to determine past productivity events as proposed by Abelman et al. (2006) may need re-evaluation.

Heterotrophic prokaryotes (*Bacteria* and *Archaea*) responded markedly to the Kerguelen bloom in terms of abundance, production and respiration (Christaki et al., 2008; Obernosterer et al., 2008). Flow cytometry analysis revealed that the bacterial community associated with the bloom was dominated (80% of total bacterial abundance) by high nucleic acid-containing (HNA) cells, in contrast to off-plateau HNLC waters where the relative contribution of HNA-cells remained low (45% total bacterial abundance) (Obernosterer et al., 2008). These observations indicate that the Kerguelen bloom bacterial community exhibited distinct features. This finding was further supported by contrasting results between A3 and C11 on the diversity and the activity of the bacterial communities, as determined from clone libraries and DNA and RNA CE-SSCP profiles (West et al., 2008).

Heterotrophic flagellates revealed similar abundances within and outside the bloom (Christaki et al., 2008). Grazing by heterotrophic flagellates was the predominant control mechanism of heterotrophic bacterial production at C11, but at station A3 heterotrophic flagellates consumed only 35% of the bacterial production (Christaki et al., 2008). Viral abundance and production were substantially higher at A3 (2.7- and 7-fold, respectively) than at C11 (Bonilla-Findji et al., 2008; Brussaard et al., 2008; Malits, unpublished data), indicating that viruses played an important role in the regulation of heterotrophic bacterial biomass in the Kerguelen bloom. By contrast, viral lysis of phytoplankton cells (<10 µm) appeared to be of minor importance (Brussaard et al., 2008). Ciliate abundance and biomass were low over the study area (Christaki et al., 2008), most likely due to strong top-down control by mesozooplankton. Depth-integrated (0–200 m) mesozooplankton biomass was roughly four times higher at A3 than at C11, and the communities were dominated by copepods, in particular large and medium size Calanoidea and small Oithinidae (Carlotti et al., 2008). Gut content observations suggested that direct mesozooplankton grazing on phytoplankton played a minor role in the control of primary production within the bloom (Carlotti et al., 2008).

3.3. Biogeochemical cycles

3.3.1. The case of carbon

One of the central objectives of KEOPS was to investigate in detail the carbon cycle within and outside the bloom, and to quantify the impact of natural iron fertilization on carbon dioxide (CO₂) uptake and the subsequent export of carbon into the deep ocean. Jouandet et al. (2008) found the bloom area to be a deep CO₂ sink compared to the HNLC waters that were close to equilibrium with the atmosphere. The depletion in dissolved inorganic carbon was higher in surface waters above compared to off the plateau. Combined with rapid phytoplankton growth, this led to higher δ¹³C of suspended particulate matter (Trull et al., 2008). Different approaches were applied to determine primary production (Lefèvre et al., 2008; Mosseri et al., 2008; Uitz et al., in revision). Overall, the mixed-layer-depth integrated primary production was substantially higher at A3 (72–200 mmol C m⁻² d⁻¹) than at C11 (14–35 mmol C m⁻² d⁻¹) see Table 3 in Lefèvre et al. (2008). Net community production measurements revealed that autotrophic metabolism dominated the Kerguelen bloom at the time of the cruise, indicating that a large fraction of photosynthetically fixed carbon was available for mesozooplankton grazing and export to the ocean interior. Observations of the forms of sinking particles recovered with sediment traps filled with polyacrylamide gel confirmed a major role for zooplankton fecal pellets in the control of export at the date of deployment (Ebersbach and Trull, 2008).

The carbon export derived from ²³⁴Th inventories in the water column was variable both above and off the Kerguelen plateau (9.0–38.4 mmol C m⁻² d⁻¹ and 1.6–4.8 mmol C m⁻² d⁻¹, respectively) (Savoie et al., 2008), but within in the range of values reported for other Southern Ocean sites. The efficiency of the export, defined as the ratio of the particulate organic carbon (POC) to primary production, was variable above the plateau, but on average lower (28%) than in surrounding HNLC waters (58%). The excess of POC export at 100 m estimated from the difference of the export flux between station A3 and C11 amounted to 10.8 ± 4.9 mmol C m⁻² d⁻¹ and was only slightly higher than during SOFEX (7.1 mmol C m⁻² d⁻¹ at 100 m) (Buesseler et al., 2004).

The excess of iron supply due to natural iron fertilization was estimated at 204 ± 77 nmol m⁻² d⁻¹. The C/Fe sequestration efficiency of natural iron fertilization was then calculated as the excess of POC export divided by the excess of iron supply, yielding 70,000 ± 40,000 mol mol⁻¹ (Blain et al., 2008). Based on seasonal C and Fe budgets an efficiency of 668,000 mol mol⁻¹ was obtained (Blain et al., 2008; Jouandet et al., 2008). This result contrasts with the low carbon-export efficiency obtained by artificial iron fertilization experiments (De Baar et al., 2005). Using a one-dimensional biogeochemical model, Mongin et al. (2008) obtained a C/Fe sequestration efficiency 2 orders

of magnitude lower than those calculated by Blain et al. (2007, 2008). The large discrepancies among these three different approaches, i.e. the model (Mongin et al., 2008), the field data (Blain et al., 2008) and the seasonal budget calculations (Jouandet et al., 2008), derives from different estimate approaches determining the amount of iron supplied to the surface water and also the fate of particulate iron.

The excess of biogenic particulate barium was used as a proxy for organic matter mineralization in the mesopelagic zone (125–450 m) (Jacquet et al., 2008). Based on this approach, the fraction of POC exported at 100 m (Savoye et al., 2008) that was mineralized between 125 and 450 m was lower above (9–13%) compared to off the plateau (18–39%). These results are compatible with the particle settling velocity (3000 m yr^{-1}) derived from ^{230}Th and ^{232}Th measurements above the plateau (Vencharutti et al., in revision). Combining the export efficiency at 100 m and the percent mineralization between 125 and 450 m, roughly 25% of the amount of carbon fixed in surface waters at A3 reach the Kerguelen Plateau (450 m), amounting to a flux of $18\text{--}50 \text{ mmol C m}^{-2} \text{ d}^{-1}$ during the cruise. For comparison, at C11, the percentage of the primary production that reached 450 m was 40%, corresponding to a flux of $5.6\text{--}14 \text{ mmol C m}^{-2} \text{ d}^{-1}$. Loss of deep sediment traps moored at C11 and A3 precluded direct validation of these estimates, although recent recovery of the mooring from the A3 site may yield some information in the future.

3.3.2. Major nutrient cycling

A large stock of unused nutrients is one of the criteria that define an HNLC system. It therefore can be expected that the relief of iron limitation results in a depletion in the concentration of major nutrients in surface waters. Surprisingly, during KEOPS, although silicic acid was very low ($1\text{--}2 \mu\text{M}$) in the core of the bloom, the concentrations of nitrate never went below $20 \mu\text{M}$ (Mosseri et al., 2008) in surface waters. As expected for diatoms growing in favorable nutrient conditions, the $\text{Si(OH)}_4\text{:NO}_3^-$ uptake rate ratio in surface waters of the plateau was close to 1:1. The decoupling in the remineralization of N and Si, due to differential remineralization rates, maintained a very efficient silica pump that depleted Si(OH)_4 in surface waters, while building a sufficiently large stock of ammonium supporting diatom growth (Mosseri et al., 2008).

Nitrate uptake determined by ^{15}N uptake experiments accounted for 61 to 23% (Mosseri et al., 2008) of the total nitrogen uptake above the plateau with a clear decline of the f -ratio from mid January to mid February when it reached values similar to those in the HNLC region. Enhanced levels of new production over the plateau were also inferred from the determination of the natural abundance of ^{15}N in particulate organic nitrogen and nitrate, which yielded f -ratios of 0.7–0.9 above the plateau and 0.4–0.6 outside. This confirms the enhancement of NO_3^- assimilation in response to the natural iron fertiliza-

tion (Trull et al., 2008). The $\delta^{15}\text{N}\text{--NO}_3^-$ values also yielded indistinguishable isotopic fractionation factors on and off the plateau. This suggests that variations in iron availability may not bias the interpretation of paleo-environmental ^{15}N records (Trull et al., 2008).

3.3.3. Dimethyl sulfide cycling

During the artificial iron experiment SOIREE, the iron-mediated bloom was a source of DMS. Extrapolating these results from short-term experiments to longer time scales would suggest that iron-enhanced production of DMS, and subsequent clouds formation, would reinforce the cooling that results from the enhanced uptake of atmospheric CO_2 resulting from the fertilization. Measurement of DMS and DMSP in the KEOPS study area do not support this idea. No significant differences in DMS and DMSP were observed between surface waters inside and outside the bloom (Belviso et al., 2008). The low production of DMS above the plateau results (i) from the dominance of diatoms that are poor DMS producers as compared to nanophytoplankton, (ii) the high bacterial activity observed above the plateau that most likely lowered the transfer efficiency of DMS to DMSP, and (iii) from enhanced photodegradation of DMS. The production of DMS in the Southern Ocean in response to iron fertilization was explored using a three-dimensional ocean biogeochemical model (Bopp et al., 2008). The model is able to reproduce the decoupling between high primary productivity and DMS production.

4. Epilogue

In the context of the iron hypothesis the results of KEOPS are relevant to palaeo scenarios where more iron would have been supplied by the Antarctic upwelling during the glacial periods (Latimer and Filipelli, 2001; Ridgwell and Watson, 2002). However, the mode of addition of iron above the Kerguelen plateau and the concomitant supply of major nutrients does not correctly represent iron fertilization by episodic dust deposition. For the same reasons the high efficiency observed during KEOPS cannot be used as an argument to assess that the geo-engineering proposals of large-scale Fe fertilization for CO_2 mitigation will obtain a high efficiency.

The findings of KEOPS demonstrate that the impact of natural iron fertilization in the Southern ocean is significantly different from those observed in artificial iron fertilization experiments (Boyd et al., 2007). The continuous fertilization of surface waters drives a complete change in the ecosystem with important consequences for biogeochemical fluxes. These changes are not simply an increase of the rates or the processes observed in the non-fertilized area. The results of KEOPS suggest that new efforts will be needed to explore further the biogeochemical cycles in an iron-fertilized region, and that the potential of a natural laboratory such as the Kerguelen plateau for new findings is large.

Acknowledgments

We thank the captain and the crew of the R/V *Marion Dufresne*. This work was supported by the Institut National des Sciences de L'Univers (INSU) and the Centre National de la Recherche Scientifique (CNRS), l'Institut Paul Emile Victor (IPEV), French-Australian Science and Technology (FAST), the Australian Commonwealth Co-operative Research Centre program through the Antarctic Climate and Ecosystem CRC, and the Belgian Science Policy (BELSPO). The project benefited from the collaboration with N. Metzl and the Service d'Observation OISO also supported by Institut Pierre Simon Laplace (IPSL). We thank all the referees who responded with timely constructive reviews that greatly improved this volume.

References

- Abelmann, A., Gersonde, R., Cortese, G., Kuhn, G., Smetacek, V., 2006. Extensive phytoplankton blooms in the Atlantic sector of the glacial Southern Ocean. *Paleoceanography* 21, PA1013 [doi:10.1029/2005PA001199].
- Armand, L., Cornet-Barthau, V., Mosseri, J., Quéguiner, B., 2008a. Late summer diatom biomass and community structure on and around the naturally iron-fertilized Kerguelen plateau in the Southern Ocean. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.031].
- Armand, L., Crosta, X., Quéguiner, B., Mosseri, J., Garcia, N., 2008b. Diatoms preserved in surface sediments northeastern Kerguelen plateau. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.032].
- Belviso, S., Bopp, L., Mosseri, J., Tedetti, M., Garcia, N., Griffiths, B., Joux, F., Obernosterer, I., Uitz, J., Veldhuis, M.J.W., 2008. Effect of natural iron fertilization on the distribution of DMS and DMSP in the Indian sector of the Southern Ocean. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.040].
- Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Martin Jezequel, V., Le Fevre, J., Mayzaud, P., 2001. A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep-Sea Research Part I: Oceanographic Research Papers* 48 (1), 163–187.
- Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, K., Carlotti, F., Christaki, U., Corbière, A., Durand, I., Ebersbach, F., Fuda, J.L., Garcia, N., Gerringa, L.J.A., Griffiths, F.B., Guigue, C., Guillerm, C., Jacquet, S., Jeandel, C., Laan, P., Lefèvre, D., Lomonaco, C., Malits, A., Mosseri, J., Obernosterer, I., Park, Y.H., Picheral, M., Pondaven, P., Remenyi, T., Sandroni, V., Sarthou, G., Savoye, N., Scouarnec, L., Souhault, M., Thuilliers, D., Timmermans, K.R., Trull, T., Uitz, J., Van-BEEK, P., Veldhuis, M.J.W., Vincent, D., Viollier, E., Vong, L., Wagener, T., 2007. Effect of natural iron fertilisation on carbon sequestration in the Southern Ocean. *Nature* 446 (7139), 1070–1075.
- Blain, S., Sarthou, G., Laan, P., 2008. Distribution of dissolved iron during the natural iron fertilisation experiment KEOPS (Kerguelen Plateau, Southern Ocean). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.028].
- Bonilla-Findji, O., Malits, A., Lefèvre, D., Rochell-Newall, E., Lemée, R., Weinbauer, M., Gattuso, J.-P., 2008. Viral effects on bacterial respiration, production and growth efficiency: consistent trends in the Southern Ocean and the Mediterranean Sea. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.004].
- Bopp, L., Aumont, O., Belviso, S., Blain, S., 2008. Modeling the effect of iron fertilization on dimethylsulfide emissions in the Southern Ocean. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.002].
- Boyd, P.W., Jackson, G.A., Waite, A.M., 2002. Are mesoscale perturbation experiments in polar waters prone to physical artefacts? Evidence from algal aggregation modelling studies. *Geophysical Research Letters* 29 (11).
- Boyd, P.W., Jickells, T., Law, C., Blain, S., Boyle, E.A., Buesseler, K.O., Coale, K.H., Cullen, J.J., De Baar, H.J.W., Follows, M., Harvey, M., Lancelot, C., Levasseur, M., Owens, N.J.P., Pollard, D.A., Rivkin, R.B., Sarmiento, J.L., Schoemann, V., Smetacek, V., Takeda, S., Tsuda, A., Turner, D.R., Watson, A., 2007. Mesoscale iron enrichment experiments 1993–2005: synthesis and future directions. *Science* 315, 612–617.
- Brussaard, C.P.D., Timmermans, K.R., Uitz, J., Veldhuis, M.J.W., 2008. Virioplankton dynamics and virally induced phytoplankton lysis versus microzooplankton grazing southeast of the Kerguelen (Southern Ocean). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.034].
- Buesseler, K.O., Andrews, J.E., Pike, S.M., Charette, M.A., 2004. The effects of iron fertilization on carbon sequestration in the Southern Ocean. *Science* 304, 414–417.
- Carlotti, F., Thibault-Botha, D., Nowaczyk, A., Lefèvre, D., 2008. Zooplankton community structure, biomass and role in carbon fluxes during the second half of a phytoplankton bloom in the eastern sector of the Kerguelen shelf (January–February 2005). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.010].
- Christaki, U., Obernosterer, I., Van Wambeke, F., Veldhuis, M.J.W., Garcia, N., Catala, P., 2008. Microbial food web structure in a naturally iron fertilized area in the Southern Ocean (Kerguelen Plateau). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.009].
- Cornet-Barthau, V., Armand, L., Quéguiner, B., 2007. Biovolume and biomass estimates of key diatoms in the Southern Ocean. *Aquatic Microbial Ecology* 48, 295–308.
- De Baar, H.J.W., Boyd, P.W., Coale, K.H., Landry, M.R., Tsuda, A., Assmy, P., Bakker, D.C.E., Bozec, Y., Barber, R.T., Brzezinsky, M.A., Buesseler, K.O., Boyé, M., Croot, P., Gervais, F., Gorbunov, M.Y., Harrison, P.J., Hiscock, M.R., Laan, P., Lancelot, C., Law, C., Levasseur, M., Marchetti, A., Millero, F., Nishioka, J., Nojiri, Y., Van Oijen, T., Riebesell, U., Rijkenberg, M.J.A., Saito, H., Takeda, S., Timmermans, K.R., Veldhuis, M.J.W., Waite, A., Wong, C.S., 2005. Synthesis of iron fertilization experiments: from the iron age in the age of enlightenment. *Journal of Geophysical Research* 110.
- Ebersbach, F., Trull, T., 2008. Sinking particle properties from polyacrylamide gels during KEOPS: zooplankton control of carbon export in an area of persistent natural iron inputs in the Southern Ocean. *Limnology and Oceanography* 53 (1), 212–224.
- Gall, M.P., Boyd, P.W., Hall, J., Safi, K.A., Chang, H., 2001. Phytoplankton processes. Part 1: community structure during the southern ocean iron release experiment (SOIREE). *Deep-Sea Research Part II: Topical Studies in Oceanography* 48 (11–12), 2551–2570.
- Gerringa, L.J.A., Blain, S., Laan, P., Sarthou, G., Veldhuis, M.J.W., Brussaard, C.P.D., Viollier, E., Timmermans, K.R., 2008. Fe binding dissolved organic ligands near the Kerguelen archipelago in the Southern Ocean (Indian sector). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.007].
- Gordon, R.M., Johnson, K.S., Coale, K.H., 1998. The behaviour of iron and other trace elements during the ironEx-I and PlumEx experiments in the equatorial Pacific. *Deep-Sea Research II* 45, 995–1041.
- Hart, T.J., 1942. Phytoplankton periodicity in Antarctic surface water. *Discovery Report*, VIII, pp. 1–268.
- Jacquet, S., Dehairs, F., Savoye, N., Obernosterer, I., Christaki, U., Monnin, C., Cardinal, D., 2008. Mesopelagic organic carbon remineralization in the Kerguelen plateau region tracked by biogenic particulate Ba. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.038].
- Jeandel, C., Ruiz-Pino, D., Gjata, E., Poisson, A., Brunet, C., Charriaud, E., Dehairs, F., Delille, D., Fiala, M., Fravallo, C., 1998. KERFIX, a

- time-series station in the Southern Ocean: a presentation. *Journal of Marine Systems* 17 (1–4), 555.
- Jouandet, M.P., Blain, S., Metzl, N., Brunet, C., Trull, T.W., Obernosterer, I., 2008. A seasonal carbon budget for a naturally iron-fertilized bloom over the Kerguelen Plateau in the Southern Ocean. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.037].
- Latimer, J.C., Filipelli, G.M., 2001. Terrigenous input and paleoproductivity in the Southern Ocean. *Paleoceanography* 16 (6), 627–643.
- Lefèvre, D., Guigue, C., Obernosterer, I., 2008. The metabolic balance at two contrasting sites in the Southern Ocean: the iron-fertilized Kerguelen area and HNLC waters. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.006].
- Martin, J.H., 1990. Glacial interglacial CO₂ change: the iron hypothesis. *Paleoceanography* 5, 1–13.
- Mongin, M., Molina, E., Trull, T., 2008. Seasonality and scale of the Kerguelen plateau phytoplankton bloom: a remote sensing and modeling analysis if the influence of natural iron fertilization in the Southern Ocean. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.039].
- Mosseri, J., Quéguiner, B., Armand, L., Cornet-Barthau, V., 2008. Impact of iron on silicon utilization by diatoms in the southern ocean: a case of Si/N cycle decoupling in a naturally iron-enriched area. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.003].
- Obernosterer, I., Christaki, U., Lefèvre, D., Catala, P., Van Wambeke, F., Le Baron, P., 2008. Rapid bacterial remineralization of organic carbon produced during a phytoplankton bloom induced by natural iron fertilization in the Southern Ocean. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.005].
- Park, Y.H., Fuda, J.L., Durand, I., Naveira Garabato, A.C., 2008a. Internal tides and vertical mixing over the Kerguelen Plateau. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.027].
- Park, Y.H., Roquet, F., Durand, I., Fuda, J.L., 2008b. Large scale circulation over and around the Northern Kerguelen Plateau. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.030].
- Pollard, R., Sander, S., Lucas, M., Statham, P.J., 2007. The Crozet natural iron bloom and export experiment (CROZEX). *Deep-Sea Research II*, in press.
- Ridgwell, A.J., Watson, A., 2002. Feedback between aeolian dust, climate, and atmospheric CO₂ in glacial time. *Paleoceanography* 17 (4), 1059.
- Sarthou, G., Vincent, D., Christaki, U., Obernosterer, I., Timmermans, K.R., Brussaard, C.P.D., 2008. The fate of biogenic iron during a phytoplankton bloom induced by natural fertilization: impact of copepod grazing. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.033].
- Savoie, N., Trull, T.W., Jacquet, S., Navez, J., Dehairs, F., 2008. 234Th-based export fluxes during a natural iron fertilisation experiment in the Southern Ocean (KEOPS). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.036].
- Timmermans, K.R., Veldhuis, M.J.W., Brussaard, C.P.D., 2008. Probing natural iron fertilization near the Kerguelen (Southern Ocean) using natural phytoplankton assemblages and diatoms cultures. *Deep-Sea Research II*, this volume [doi:10.1016/j.dsr2.2007.12.008].
- Trull, T., Davies, D., Casciotti, K., 2008. Insights into nutrient assimilation and export in naturally iron-fertilized waters of the Southern Ocean from nitrogen, carbon and oxygen isotopes. *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.035].
- Uitz, J., Claustre, H., Garcia, N., Griffiths, B., Ras, J., Sandroni, V., in revision. A phytoplankton class-specific primary production model applied to the Kerguelen Islands region (Southern Ocean). *Deep-Sea Research I*.
- Van Beek, P., Bourquin, M., Reyss, J.L., Souhault, M., Charette, M., Jeandel, C., 2008. Radium isotopes to investigate the water mass pathways on the Kerguelen Plateau (Southern Ocean). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.025].
- Venchiarutti, C., Jeandel, C., Roy-Barman, M., in revision. Particle dynamics in the wake of Kerguelen Island traced by thorium isotopes (Southern Ocean, KEOPS program). *Deep-Sea Research I*.
- Wagner, T., Guieu, C., Losno, R., Bonnet, S., Mahowald, N., in press. Revisiting atmospheric dust export to the southern hemisphere ocean: biogeochemical implication. *Global Biogeochemical Cycles* [doi:10.1029/2007GB002984].
- West, N., Obernosterer, I., Zemb, O., Le Baron, P., 2008. Major difference of bacterial diversity and activity inside and outside of a natural iron-fertilized phytoplankton bloom in the Southern Ocean. *Environmental Microbiology* 10 (3), 738–756.
- Zhang, Y., Lacan, F., Jeandel, C., 2008. Dissolved rare earth elements tracing lithogenic inputs over the Kerguelen plateau (Southern Ocean). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.029].

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