



## Diatoms preserved in surface sediments of the northeastern Kerguelen Plateau

Leanne K. Armand<sup>a,\*</sup>, X. Crosta<sup>b</sup>, B. Quéguiner<sup>a</sup>, J. Mosseri<sup>a</sup>, N. Garcia<sup>a</sup>

<sup>a</sup>Aix-Marseille Université, CNRS, LOB-UMR 6535, Laboratoire d'Océanographie et de Biogéochimie, OSU/Centre d'Océanologie de Marseille, France

<sup>b</sup>UMR-CNRS 5805 EPOC, Université de Bordeaux I, Av. des Facultés, 33405 Talence, France

Accepted 8 December 2007

### Abstract

An “island mass effect” was observed from the sedimentary distribution of diatoms on the northeastern Kerguelen Plateau. Five new samples placed in context to species distributions previously reported from the Permanently Open Ocean Zone (POOZ) revealed a plateau community dominated by three species/taxa: *Fragilariopsis kerguelensis*, *Thalassionema nitzschioides* f. *nitzschioides* and *Chaetoceros Hyalochaete* resting spores. Intermediate abundances of *Thalassiosira antarctica* were unique to the plateau sediment signature as were increased abundances of *Eucampia antarctica* v. *antarctica*. The off-plateau sediment sample contained typical POOZ sediment distributions dominated by *F. kerguelensis*, *Thalassiosira lentiginosa* and *Thalassiothrix antarctica*. The role of deposition from the surface waters to the sediments was investigated by comparison to the diatom thanatocoenose observed in surface waters. These results suggest that the use of sediment abundances of *C. Hyalochaete* resting spores and *F. kerguelensis* to determine past productivity events (such as wind-sourced iron enrichment of the Southern Ocean at the Last Glacial Maximum) is not straightforward. The elevated abundance of *T. nitzschioides* f. *nitzschioides* on the plateau did not indicate an iron-deplete regime but the converse. For the evaluation of paleo-productivity hypotheses for the open Southern Ocean, we suggest caution in the use of Subantarctic and Kerguelen Plateau sediment signatures, and emphasize that there is a need to also study Antarctic coastal and especially sea-ice melt-water stimulated blooms.

© 2008 Elsevier Ltd. All rights reserved.

**Keywords:** Bacillariophyceae; Sediments; Fluff layer; Biogenic silica; Chlorophyll *a*; Southern Ocean

### 1. Introduction

Understanding diatom distribution in surface sediments, and subsequently their ecology and distribution in the surface waters, is essential to the evaluation of past sea-surface conditions, such as sea-surface temperature, sea-ice cover, and productivity (e.g., Armand et al., 2005). Enhancing the Southern Ocean diatom sea-floor database for these tasks is difficult because of limited opportunities for sea-floor sampling. Where sampling is possible comparisons between the current database and new data are required. This comparison determines a sample's suitability for the database and divulges evidence on a species distribution and its links to the surface environment in

which it lived. As an example of a samples' unsuitability, it is known that the northeastern flank of the Kerguelen Plateau and the Southeast Indian Ridge act as topographic barriers in the northern pathway of Antarctic Bottom Water (AABW) in the Indian sector of the Southern Ocean, therefore acting as a deposition centre for entrained Antarctic diatoms (Dezileau et al., 2000). This deposition centre subsequently dilutes the diatom signal from overlying open-ocean surface waters. The palaeontological significance is that surface samples from this region may result in material unsuitable for transfer function analysis of sea-surface conditions of the past due to their mixed environmental signals.

To date, diatom distributions in surface sediments in vicinity of Kerguelen Island from the South Indian Ocean have been described by 24 sea-floor samples (Crosta et al., 2005). Generally, the distribution reveals a Permanently Open Ocean Zone (POOZ) signature where *Fragilariopsis*

\*Corresponding author. Tel.: +33 4 91 82 93 46; fax +33 4 91 82 19 91.

E-mail addresses: [leanne.armand@utas.edu.au](mailto:leanne.armand@utas.edu.au),  
[leanne.armand@acecrc.org.au](mailto:leanne.armand@acecrc.org.au) (L.K. Armand).

*kerguelensis*, *Thalassiosira lentiginosa* and *Thalassiothrix antarctica* dominate and a lack of samples occurs over Kerguelen Plateau. In this study we investigate the distribution of diatoms in the sediments both on and off the plateau to determine whether a signature of iron-fertilization or enhanced productivity is recorded given that an iron-induced “island mass effect” (Blain et al., 2001) was found to enhance the annual phytoplankton bloom in this region. Identifying the species behind the biological productivity induced by natural iron fertilization of Subantarctic Islands may be of use to the palaeontological record through the sediment archive. The hypothesis has been raised as to whether modern environments (Smetacek et al., 2004) or past events such as the Last Glacial Maximum (Abelmann et al., 2006), which enjoyed windier and dustier conditions, leave a record of iron fertilization in the sediments through a change in diatom community composition. A recent surface water study north of the Polar Front on the northeastern Kerguelen Plateau revealed differences in the abundance and species composition relative to iron availability, therefore suggesting iron-enriched diatom community separation in the surface waters over the northern region of the north Kerguelen Plateau (Blain et al., 2001). Similar evidence is provided by other surface water diatom distribution studies in the wake of Antarctic Islands (e.g., Holm-Hansen et al., 1997; Ward et al., 2005).

To identify iron-enriched effects on diatoms, new surface sediment samples were retrieved during the recent Kerguelen Plateau and Ocean Compared Study (KEOPS) mission (January–February, 2005) (Blain et al., 2007). Aside from the sediment distribution analysis, we also compare these results to overlying deep-water analyses in which we investigate diatom species composition, chlorophyll *a* and biogenic silica concentrations. We also compare the results to the surface abundance, dominance and fall out of diatom species overlying these sites (Cornet-Barthaux et al., 2007; Armand et al., 2008).

## 2. Regional setting

We schematically illustrate the position of our sediment sample sites in comparison to regional currents and water masses overlying the northern Kerguelen Plateau in Fig. 1, based on oceanographic studies (Park et al., 1991, 1998; Park and Gambérini, 1995, 1997; Charrassin et al., 2004) and work carried out during the KEOPS program (Park et al., 2008a, b; van Beek et al., 2008; Mongin et al., 2008). The entire Kerguelen Plateau extends from the Princess Elizabeth Trough (~63°S) to the Kerguelen Islands (49°S, 70°E). We refer to the plateau in this work broadly as the northeastern portion of the main plateau north of the Fawn Trough, delineated by the 2000-m bathymetric isoline (Fig. 1A). Plateau samples (A3, A3', B1, B5, C1 and C5) were no deeper than 562 m, the shallowest at 150 m near Heard Island. These samples were bathed in overlying waters principally of: Antarctic Surface Water (AASW), a

remnant 200-m, sub-surface winter water (WW), and Upper Central Deep Water (UCDW) (Fig. 1B). Considerable internal tide action occurs in this region (Park et al., 2008a), which is responsible for the re-suspension and source of iron and presumably other nutrients. This stimulates and sustains bloom conditions in the overlying surface waters (Blain et al., 2007). An additional iron source from around Heard Island has been hypothesized from radium isotopes and dissolved rare earth element observations (van Beek et al., 2008; Zhang et al., 2008). Station C11, off the plateau was located at a depth of 3350 m and was overlain by the same surface water structure of AASW, WW and UCDW, but also Lower Circumpolar Deep Water (LCDW) and AABW (Fig. 1B). Dezieau et al. (2000) indicated that in this deep-water region east of the Kerguelen Plateau, sediment drift deposits have accumulated up to 750 m in depth due to the northward and subsequent eastward route of AABW. This enhanced sea-floor deposition traps diatom frustules with an Antarctic origin along with those that contribute to the sediments from overlying surface waters.

## 3. Methods

Eight sediment stations were targeted during the KEOPS mission to correspond with time series stations (Table 1). Samples were collected by means of an Oktopus GmbH (Germany) multi-corer furnished with polycarbonate cylinders; 61 cm long by 9.5 cm in diameter (Viollier et al., 2005).

### 3.1. Surface sediments

Surface sediment samples (>4-mm surface material) were taken from seven of the eight stations; however, samples were only processed for five of these stations (Table 2, Fig. 1A). Sample C1, taken near Heard Island, contained coarse volcanic sands and was not processed, and A3' was a duplicate station of A3 and also not processed. Sediment samples were processed to remove organic and other material for qualitative assessment following the methodology described in Rathburn et al. (1997). Subsequent diatom counts followed Schrader and Gersonde (1978) and Laws (1983). A minimum of 400 diatom valves were counted at  $\times 1000$  magnification and identified to species or species group level. Taxonomy follows modern species concepts summarized in Hasle and Syvertsen (1997), and the specific diatom authorships are documented in Table 3. *Chaetoceros* *Hyalochaete* resting spores are poorly known to species level and were not observed within vegetative cells in the complimentary surface water study (Armand et al., 2008), and were grouped together. Relative abundances of the species categories were determined but did not include the presence of *Dactyliosolen antarcticus*, represented by girdle bands present in all sampled sediments, nor silicoflagellates.

Total absolute diatom abundance (ADA) followed the methodology in Armand (1997). The number of species

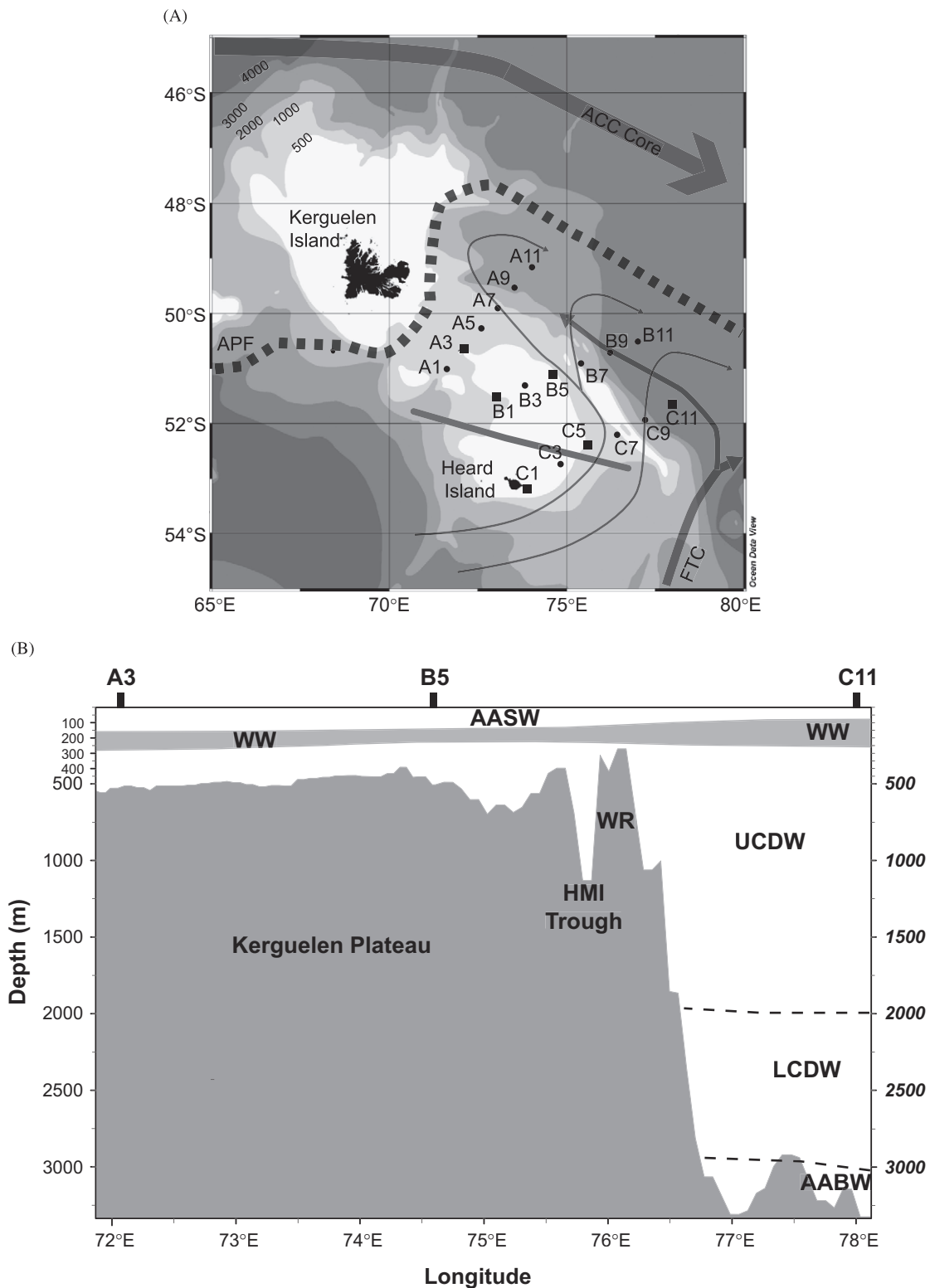


Fig. 1. Station locations and oceanographic features around the northeastern Kerguelen Plateau. (A) Station localities and major currents and fronts (modified from [Park et al. \(2008b\)](#)). (B) Schematic cross section of overlying water masses at stations A3, B5 and C11. Modified from [Park et al. \(2008a, b\)](#) and ([Mongin et al., 2008, Fig. 1](#)). ACC core—Antarctic Circumpolar Current Core, APF—Antarctic Polar Front, FTC—Fawn Trough Current, with northwestward-flowing branch, WW—remnant Antarctic winter water, AASW—Antarctic Surface Water, UCDW—Upper Central Deep Water, LCDW—Lower Central Deep Water, AABW—Antarctic Bottom Water, HMI Trough—Heard-McDonald Island Trough, and WR—Williams Ridge. Thin grey arrows represent geostrophic currents influenced by bottom topography over the plateau. Plotted using ODV ([Schlitzer, 2006](#)).

Table 1  
KEOPS MUCO station details

Sample name	Date	Latitude (°S)	Longitude (°E)	Depth (m)
A3-MUCO-001	23/1/05	50°36.30	72°04.70	530
A3'-MUCO-008	12/2/05	50°37.63	72°04.93	527
B1-MUCO-004	2/2/05	51°29.47	73°00.29	362
B5-MUCO-003	1/2/05	51°05.85	74°35.80	545
C1-MUCO-006	9/2/05	53°11.35	75°51.05	150
C5-MUCO-005	7/2/05	52°24.66	75°35.67	562
C11-MUCO-002 (2)	28/1/05	51°38.80	77°58.90	3350

Table 2  
Summary of sediment and overlying deep-water layer analyses undertaken at each site

Sample name	Sediment		Water		
	Sample taken	Quantitative diatom assessment	Qualitative diatom assessment	BSi analyses	Chl- <i>a</i> analyses
A3	+	+	+	+	
A3'	+			+	
B1	+	+	+		
B5	+	+	+	+	+
C1	+				
C5	+	+		+	+
C11	+	+	+		+

observed in the sediments,  $S$ , were noted. To place the sediment assemblage diversity in the context of the abundances observed, we applied Shannon's diversity ( $H$ ) and evenness ( $E_H$ ) indices to the relative abundance data. Large values of  $H$  indicate greater diversity.  $E_H$  values closest to 1 indicate complete assemblage evenness.

### 3.2. Overlying deep-water layer diatom analyses

Four water samples were taken from the multi-corer for taxonomic assessment, biogenic silica and Chl-*a* concentrations (Table 2). No recovery of associated waters were made from stations B1 or C1 (Viollier et al., 2005). Overlying deep-water samples visibly containing a suspended marine fluff were siphoned off and between 0.05–1 L was retained for qualitative assessment. This material was gently agitated and sub-sampled into a 5-ml Utermöhl counting chamber. The samples were scanned at  $\times 40$  on a Nikon Eclipse TE200 inverted microscope for immediate on-board species composition and categorized as rare (1–2 individuals encountered), minor ( $<20$  individuals), common ( $>20$  individuals) or dominant (individuals present in all fields of view). We identify “dead cells” as those that we considered as empty frustules devoid of internal contents (such as chloroplasts) visible to the eye during microscopic examination.

### 3.3. Biogenic silica and Chlorophyll *a*

Particulate silica in the overlying deep water, including both biogenic and lithogenic silica, was sampled in

duplicate ( $2 \times 25$  ml) at three stations (Table 2). The samples were cascade filtered through 10- and 0.6- $\mu$ m filters. Each filter was stored in a Petri dish prior to analysis. Biogenic (BSi) and lithogenic silica (LSi) concentrations were then successively determined by a NaOH/HF digestion protocol modified from Brzezinski and Nelson (1995) as described in Mosseri et al. (2008). LSi results are not reported here. BSi concentration estimates were corrected for the inclusion of dissolved LSi during NaOH digestion by the measurement of aluminium by ICP-AES (Ragueneau et al., 2005). These corrections averaged  $21 \pm 12\%$ . Chl-*a* concentrations were determined fluorometrically after methanol pigment extraction (Raimbault et al., 1988, 2004).

## 4. Results

### 4.1. Diatom distribution in sediments

The ADAs were low (between  $13 \times 10^6$  and  $33 \times 10^6$  frustules  $g^{-1}$  dw) with the exception of the distinct elevated value at station A3 ( $105 \times 10^6$ ) near the Polar Front (Fig. 2A). The number of species observed in the sediments ranged narrowly between 27 at station B1 and 37 at station C5 (Table 4). Plateau stations, A3 and C5, presented the greatest assemblage diversity ( $H = 2.2$  and 2.1, respectively), while the off-plateau station, C11, had the lowest (1.7). Interestingly, station B1 with the lowest number of species observed revealed a greater diversity than stations B5 or C11 that recorded larger species numbers. In terms of evenness ( $E_H$ ) all stations had mid-ranging

Table 3  
KEOPS diatom results for sediment and overlying deep waters

Species	Max. RA (%) <sup>a</sup>	A3		B1		B5		C5		C11	
		Water (A)	Sediment	Water (NS)	Sediment	Water (C)	Sediment	Water (D)	Sediment	Water	Sediment (B)
<i>Actinocyclus curvatus</i> Janisch in A. Schmidt	0.5		0.5		0.2	r		r	0.2		
<i>Asteromphalus hookeri</i> Ehrenberg	0.4	m	0.2			r	0.2	m		r	0.4
<i>A. hyalinus</i> Karsten	0.2							r	0.2		
<i>A. parvulus</i> Karsten	0.8		0.2		0.2		0.8	r	0.2		0.4
<i>Azpeitia tabularis</i> (Grunow) Fryxell et Sims	1.3	r	0.5		0.8	c	0.8	r	0.4	m	1.3
<i>Chaetoceros atlanticus</i> Cleve	0.9						0.2	r/m	0.9		0.2
<i>Chaetoceros Hyalochaete</i> resting spores	17.7	c/d	17.7		16.8	m	5.7	c/d	7.5		4.9
<i>Chaetoceros</i> spp.								r			
<i>Coconeis</i> spp.	0.2						0.2				
<i>Coscinodiscus</i> spp.	0.8		0.5		0.8	m	0.2	r	0.4		0.2
<i>Corethron inerme</i> Karsten											
<i>Dactyliosolen antarcticus</i> Castracane		c (1)				c (1)		m (2)		c (1)	
<i>Eucampia antarctica</i> (Castracane) Mangin	7.6	m (3)	7.6		4.7	c	5.5	m	2.6	m	3.8
<i>E. ant</i> (terminal cells)	0.6		0.6				0.2				
<i>Fragilariopsis curta</i> (Van Heurck) Hustedt	0.4						0.2				0.4
<i>F. kerguelensis</i> (O'Meara) Hustedt	57.1	d	30.8		33.1	d	56.9	d (4)	44.9	d	57.1
<i>F. pseudonana</i> (Hasle) Hasle	0.4								0.4		0.2
<i>F. rhombica</i> (O'Meara) Hustedt	0.9		0.3				0.4		0.4		0.9
<i>F. ritscherii</i> Hustedt	0.2	r				m	0.2	r			
<i>F. separanda</i> Hustedt	1.5	r	0.3			m	0.6	r	0.4		1.5
<i>F. cf. sublineata</i> (Van Heurck) Heiden		r									
<i>Membraneis</i> spp.								r/m			
<i>Navicula directa</i> (Smith) Ralfs in Pritchard	1.1				0.6	r	0.4	m	1.1		
<i>N. sicula</i> (Castracane) Hustedt						r		r			
<i>Odontella weisflogii</i> Janisch ex Grunow in Van Heurck	0.6		0.6		0.4	r	0.4	r (5)	0.2	m	0.6
<i>Pleurosigma directum</i> Grunow in Van Heurck	0.4				0.4				0.4		
<i>Porosira glacialis</i> (Grunow) Jørgensen	0.2										0.2
<i>P. pseudodenticulata</i> (Hustedt) Jousé	0.2								0.2		
<i>Proboscicia alata</i> (Brightwell) Sundström	0.2							r	0.2		
<i>P. inermis</i> (Castracane) Jordan and Ligowski	0.4	r	0.3		0.2				0.4		
<i>P. truncata</i> (Karsten) Nöthig and Ligowski								r			
<i>Psammodictyon panduriforme</i> (W. Gregory) D.G. Mann						m		m			
<i>Pseudo-nitzschia lineola</i> (Cleve) Hasle	0.1							r	0.1		
<i>P-n. turgiduloides</i> Hasle (Hasle)	0.6		0.6		0.2				0.5		0.1
<i>P-n. hemii</i> Manguin								r/m			
<i>P-n.</i> spp.	0.1		0.1								
<i>Rhizosolenia antennata</i> (Ehrenberg) Brown f.	0.3	r	0.3		0.2	r		r	0.2		0.2
<i>semispina</i> Sundström											
<i>R. cf. crassa</i> Schrimper in Karsten						r				r	
<i>R. polydactyla</i> (Castracane) f. <i>polydactyla</i> Sundström	0.4						0.4				
<i>R. sima</i> f. <i>silicea</i> Sundström	0.2		0.2								
<i>R. simplex</i> Karsten								r			

Table 3 (continued)

Species	Max. RA (%) <sup>a</sup>	A3		B1		B5		C5		C11	
		Water (A)	Sediment	Water (NS)	Sediment	Water (C)	Sediment	Water (D)	Sediment	Water	Sediment (B)
<i>Rhizosolenia</i> spp.	0.3		0.3								
<i>Thalassionema nitzschoides</i> f. <i>capitulata</i> (Castracane)	0.4		0.2		0.2		0.2		0.2		0.4
Moreno-Ruiz											
<i>T. nitzschoides</i> f. <i>nitzschoides</i> (Grunow) Van	29.3	c	18.6		29.3	m	8.4	m	18.4		2.6
Heurck <sup>b</sup>											
<i>T. nitzschoides</i> f. <i>lanceolata</i> (Grunow) Pergallo et	1.3		1.3		0.6	m	0.2	m	1.3		0.6
Pergallo											
<i>T. nitzschoides</i> f. <i>parva</i> Heiden	0.5		0.5								0.2
<i>Thalassiosira antarctica</i> (veg.) Comber	0.6	m			0.6		0.4		0.4		
<i>T. antarctica</i> (resting) Comber	4.5		4.5		2.5	m	3.0	m	3.4		
<i>T. frenguelliopsis</i> Fryxell et Johansen	0.6		0.6		0.2		0.6				0.4
<i>T. gracilis</i> v. <i>gracilis</i> (Karsten) Hustedt	1.7	m	0.6		0.8	m	1.7		1.5	m	1.3
<i>T. gracilis</i> v. <i>expecta</i> (Van Landingham) Frxyell et	0.9		0.5		0.4		0.2	m	0.9		
Hasle											
<i>T. gravis</i> Cleve	0.5		0.5								
<i>T. latimarginata</i> Makarova	0.4		0.3			r	0.4		0.4		0.4
<i>T. lentiginosa</i> (Janisch) Fryxell	14.7	m	7.5		4.0	c	7.2	m	5.1	c	14.7
<i>T. oliverana</i> (O'Meara) Makarova et Nikolaev	1.1					r	0.8	r	0.6	c	1.1
<i>T. tumida</i> (Janisch) Hasle	0.6		0.6		0.6		0.2	r	0.2		0.2
<i>Thalassiosira</i> spp.	2.6	m (6)				m (6)		c (6)	2.6		
<i>Thalassiothrix antarctica</i> Schimper ex Karsten	4.2	d (7)	1.6		0.3	m (8)	1.2	r	1.3	c (9)	4.2
<i>Trachyneis aspera</i> (Ehrenberg) Cleve	0.8		0.2		0.2		0.8		0.4		
<i>Tropidoneis</i> group	0.4						0.2		0.4		0.2
Other centrics	0.9		0.8		0.8		0.6		0.9		0.9
Other pennates	0.2										0.2

r—rare; m—minor; c—common; and d—dominant.

<sup>a</sup>The maximum relative abundance of a species observed in the MUCO samples: (A) very broken valves-similar composition to sediment samples- only *Eucampia antarctica* chains still intact; (B) poor (heavily fragmented); (C) heavily fragmented, many aggregates of diatom detritus, 1 *Eucampia* doublet; and (D) heavily fragmented, many aggregates of diatom detritus. NS: not sampled, 1: disaggregated, 2: three complete cells observed, 3: rarely observed in chains of four cells, 4: intact cells and chains observed, 5: intact cells observed, 6: small cells < 10 µm, 7: incomplete specimens, 8: large fragments, cf—compares with, and 9: incomplete specimens, rare complete cells observed.

<sup>b</sup>—*Thalassionema nitzschoides* f. *nitzschoides*—this species includes both *T. nitz.* sensu stricto and the forma 1 described by Zielinski and Gersonde both authorships are: *Thalassionema nitzschoides* (Grunow 1862) Van Heurck 1896, *Thalassionema nitzschoides* forma 1 (sensu Zielinski et Gersonde 1997).



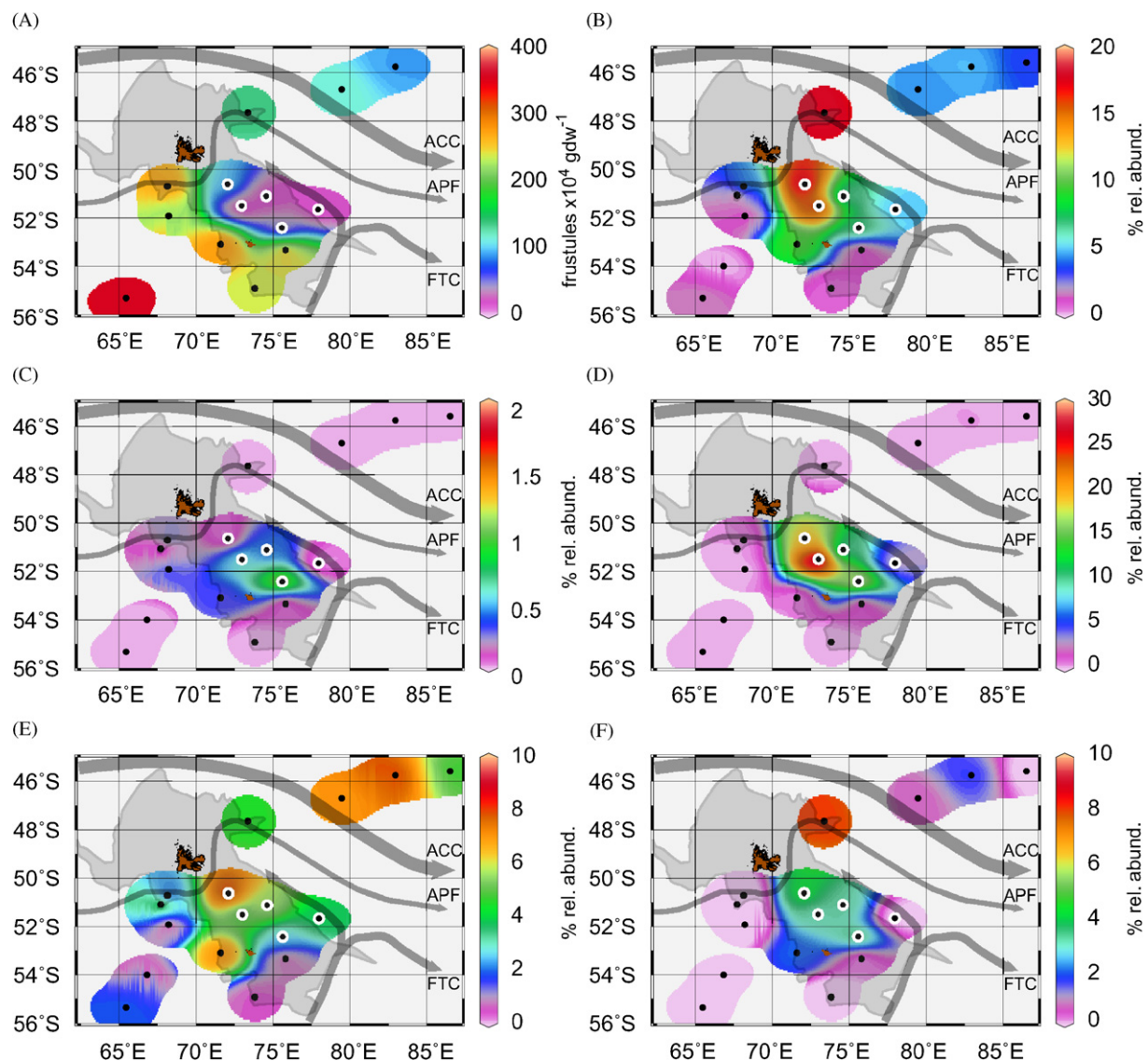


Fig. 2. Seafloor surface sediment distribution of major diatom species elevated around Kerguelen Plateau. (A) Absolute Diatom Abundance (ADA) in surface sediments. (B) *Chaetoceros Hyalochaete* resting spores, (C) *Navicula directa*, (D) *Thalassionema nitzschioides* f. *nitzschioides*, (E) *Eucampia antarctica*, and (F) *Thalassiosira antarctica*. White ringed points identify KEOPS samples; other points are from the Crosta et al. (1998) database (Table 5). The 2000-m depth contour delineates the northern Kerguelen Plateau. Abbreviations as in Fig. 1. Plotted using ODV (Schlitzer, 2006).

Table 4  
Diatom abundances and community description indices determined from sediment samples

Index	A3	B1	B5	C5	C11
ADA (frustules $\times 10^6 \text{ g m}^{-1} \text{ dw}$ )	105	13	20	32	21
No. species ( <i>S</i> )	34	27	34	37	30
Shannon's diversity ( <i>H</i> )	2.20	1.90	1.83	2.11	1.73
Shannon's evenness ( <i>E<sub>H</sub></i> )	0.63	0.58	0.52	0.59	0.51

values suggestive of a dominating contribution by one species over the remaining assemblage composition.

To place our samples in context, we compared them to nearby samples in the region (Crosta et al., 1998, Table 5) and examined the distributions of 11 species (Figs. 2B–F

and 3A–F). Most of these distributions show clear variations between the on-plateau and off-plateau stations. The on-plateau stations had elevated abundances of *C. Hyalochaete* resting spores (6–18%, Table 3, Fig. 2B) but included a lower though still important abundance of *F. kerguelensis* (30–57%, Table 3, Fig. 3A). The on-plateau stations also contained elevated abundances of *Navicula directa* (0.4–1.1%, Fig. 2C), *Thalassionema nitzschioides* f. *nitzschioides* (8.4–29.3%, Fig. 2D), *Eucampia antarctica* (3–8%, Fig. 2E), and the unique occurrence of *Thalassiosira antarctica* frustules (3–4.5%, Fig. 2F). Off-plateau station abundances were elevated for *T. lentiginosa* and *Thalassiothrix antarctica* (Table 3, Fig. 3B and D, respectively). Station B5 on the plateau had the closest community composition to that observed at C11.

Table 5

Sub-sample station locations from the Crosta et al. (1998) database, mapped in Figs. 2 and 3

Station name	Latitude (°S)	Longitude (°E)	Seafloor depth (m)
MDBX94-02	45°35'	86°31'	3205
KR88-02	45°45'	82°56'	3480
KR88-01	46°41'	79°29'	2925
RC11-98	47°39'	61°29'	4650
MD84-563	50°43'	68°09'	1720
MD80-304	51°04'	67°44'	1950
MD84-562	51°55'	68°14'	3553
MD84-561	53°05'	71°36'	1754
MD84-557	53°20'	75°48'	1080
MD80-301	54°00'	66°50'	3750
MD84-552	54°55'	73°50'	1780
RC8-46	55°20'	65°28'	2761

#### 4.2. Diatom distribution in overlying deep-water

A fluff layer was only observed clearly in the overlying deep-water layer from station A3 (~10 mm thick). In all five overlying deep-water samples *F. kerguelensis* was the most dominant or co-dominant species (Table 3). The species was observed as intact cells and chains. In sample C5 *C. Hyalochaete* resting spores were equally dominant with *F. kerguelensis*. At station A3 *T. nitzschioides* f. *nitzschioides*, *Thalassiothrix antarctica* (as fragments) and *C. Hyalochaete* resting spores were co-dominant with *F. kerguelensis* in the overlying deep-water assemblage that otherwise comprised 17 species.

Stations B5 and C5 on the plateau, revealed 25 and 34 species or species groupings, respectively (Table 3). Although

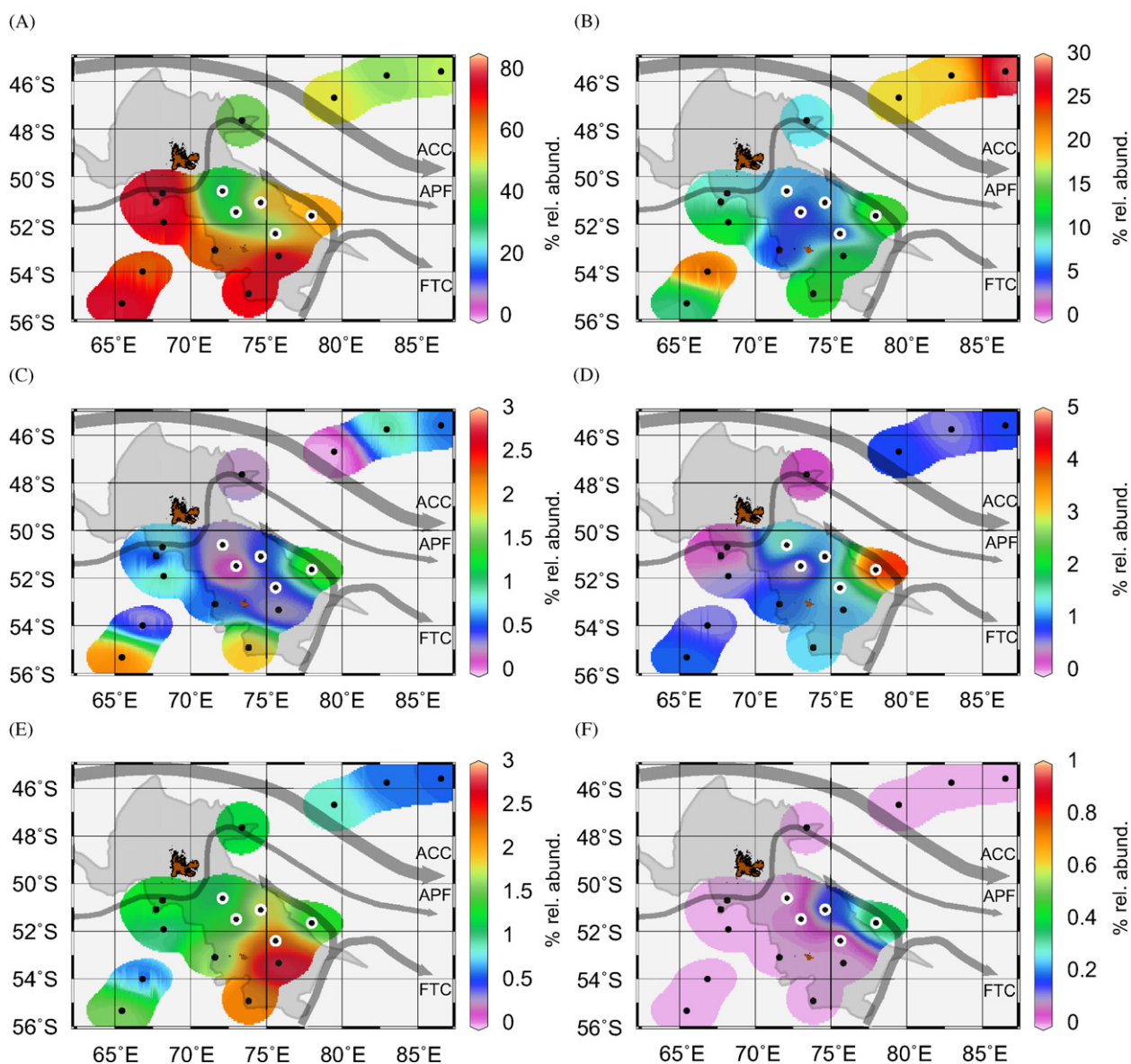


Fig. 3. Seafloor surface sediment distribution of major diatom species around Kerguelen Plateau. (A) *Fragilariopsis kerguelensis*, (B) *Thalassiosira lentiginosa*, (C) *Fragilariopsis separanda*, (D) *Thalassiothrix antarctica*, (E) *Thalassiosira gracilis*, and (F) *Fragilariopsis curta*. White ringed station points identify KEOPS samples; remaining points are from the Crosta et al. (1998) database (Table 5). The 2000-m depth contour delineates the Northern Kerguelen Plateau. Abbreviations as in Fig. 1. Plotted using ODV (Schlitzer, 2006).



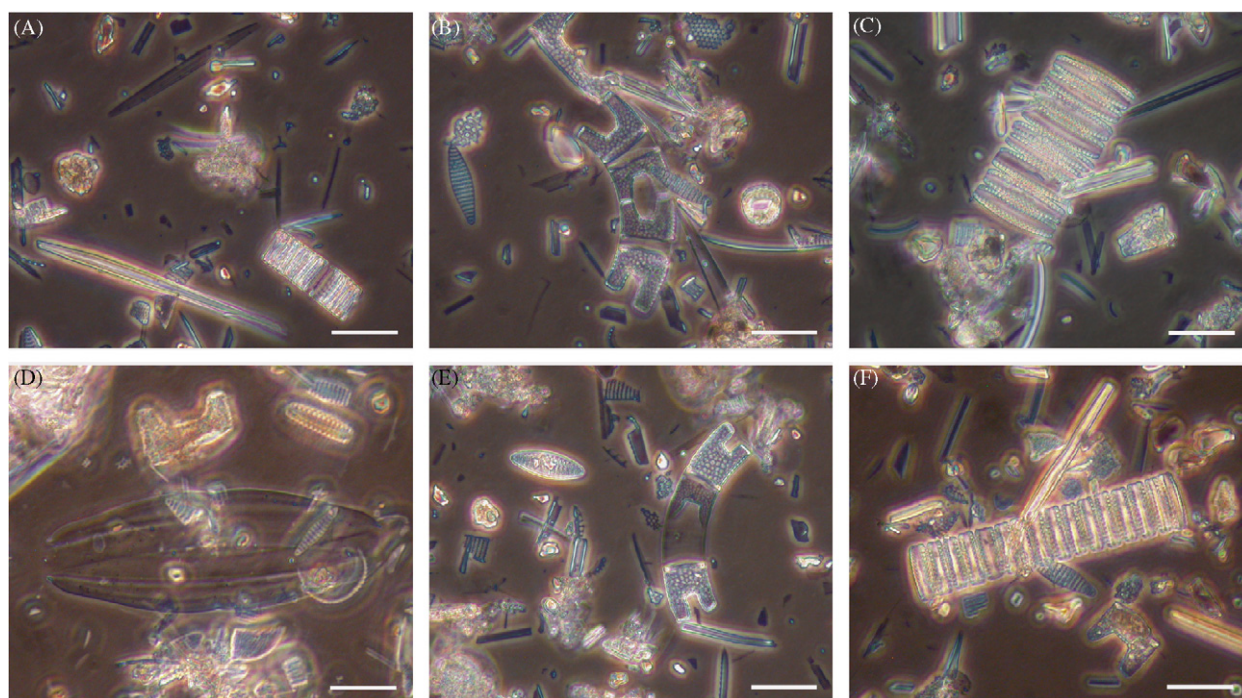


Fig. 4. Photomicrographs of chained and complete diatoms in overlying deep-water samples at Station C5. Chained and fragile diatom frustules preserved in the overlying deep-water samples are considered to be directly deposited by unknown mechanisms from the surface layers, whereas background diatom material is dominated by broken cells considered a product of zooplankton consumption and removed from the surface layer by faecal pellets. (A) Partial *Dactyliosolen antarcticus* frustule not disassociated into separate girdle bands. (B) Intact *Eucampia antarctica* v. *antarctica* chain with very fine girdle band elongation. (C) *Fragilariopsis kerguelensis* chain. (D) Intact and thinly silicified *Membraneis* spp. frustule. (E) *Eucampia antarctica* v. *antarctica* cell with one terminal ending “winter form” daughter cell in formation within the extended girdle bands. (F) Intact 16-cell chain of *Fragilariopsis kerguelensis*. Scale bar in all photos = 20  $\mu\text{m}$ .

all samples had the appearance of being fragmented and presumably consumed by zooplankton before their suspension above the sea-floor in these waters (referred to here as diatom detritus), there was some evidence that cells or chains arrived intact on the seafloor (including *C. Hyalochaete* resting spores that were observed as complete cells), especially at station C5 (*Dactyliosolen antarcticus*, *F. kerguelensis*, *Odontella weissflogii*, *Membraneis* spp.) and to a small degree at A3 (*E. antarctica*) (Fig. 4). The overlying deep-water assemblage from station B5 was heavily fragmented and to a certain degree aggregated. Microscopic examinations clearly indicate these cells are indeed devoid of chloroplasts.

Only 11 species were identified in the overlying deep-water off-plateau sample at station C11 (Table 3). This assemblage was dominated by *F. kerguelensis*, *T. lentiginosa*, *Thalassiosira oliverana*, dissociated *Dactyliosolen antarcticus* girdle bands, and predominantly fragmented *Thalassiothrix antarctica* frustules.

Chl-*a* concentrations from the overlying deep waters were high and ranged from 0.29 to 3.8  $\mu\text{g L}^{-1}$  (Table 6, Fig. 5). Plateau stations exhibited the range extremes, whereas the deep-water value at C11 was 1.05  $\mu\text{g L}^{-1}$ . Although we did not sample for Chl-*a* at station A3, the Chl-*a* concentrations were inverse to the perceived preservation of the diatom assemblages. For example, at

Table 6  
Overlying deep-water Chl-*a* and BSi values

Station	Mean Chl- <i>a</i> ( $\mu\text{g L}^{-1}$ ) <sup>a</sup>	Mean BSi ( $\mu\text{mol L}^{-1}$ ) <sup>b</sup>
A3		145 $\pm$ 23
A3'		160 $\pm$ 36
B1		
B5	3.8	181 $\pm$ 49
C5	0.3	230 $\pm$ 19
C11	1.0	

<sup>a</sup>Chl-*a* are from triplicates.

<sup>b</sup>BSi are from duplicates.

station C5 where Chl-*a* values were low, intact frustules and chains were observed in the overlying deep-water samples.

BSi concentrations in the overlying deep-waters of the three sampled stations were high ( $>100 \mu\text{mol L}^{-1}$ ) and ranged from 153 to 230  $\mu\text{mol L}^{-1}$  (Table 6, Fig. 5). Although variability was relatively large between the duplicates, we noted increasing total BSi concentrations from station A3 to station C5 over a west to east trajectory on the Kerguelen Plateau. From the size-fractionated data set of BSi, the large ( $>10 \mu\text{m}$ ) pool of BSi was reasonably dominant (51–65% of total BSi on average) at the three stations (Fig. 5). No sample was taken at station C11.

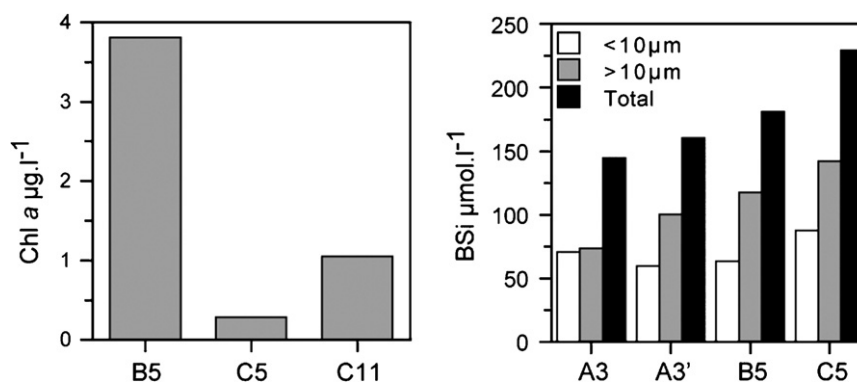


Fig. 5. Mean biogenic silica and Chl-*a* measurements in overlying deep-water at the sediment interface. BSi values divided into greater and less than 10-µm fraction contributions and also given as total BSi observed. A3' is the second sampling event 30 days later.

## 5. Discussion

### 5.1. Major species distributions

The mapped diatom distributions can be compared with the regional biogeography of Crosta et al. (2005) and reveal an “island mass effect” juxtaposed against the typical distributions of the open-ocean diatom ooze belt otherwise dominated almost exclusively by *F. kerguelensis*, *T. lentiginosa* and *Thalassiothrix* spp. Patches of abundance either on or off the Kerguelen Plateau are evident. The plateau appears as a “hot-spot”, exclusion zone or a tracer of currents around or over the northern plateau for several key species detailed below and illustrated in Figs. 2 and 3.

#### 5.1.1. Plateau related distributions

*Chaetoceros Hyalochaete* resting spores in sediment samples were particularly abundant to the north (Fig. 2B; 17% at A3), which agrees with deep-water layer dominance (Table 3) and surface water-column abundances at 100 m depth of dead vegetative cells and resting spores at station A3 (Armand et al., 2008). *Chaetoceros Hyalochaete* resting spores are normally reported as abundant, nearing complete domination, along the Antarctic coast although they occur throughout the Southern Ocean, with abundances up to 20% in the POOZ (Crosta et al., 1997; Armand et al., 2005). A clear signal of “abundant” *Chaetoceros* resting spores were observed south of the Polar Frontal Zone in the sediments and overlying fluffs of the southwest Indian Ocean (Riaux-Gobin et al., 2006). When our highest abundances observed in the most northerly situated plateau samples are placed in context with the Crosta et al. data set, it would appear that a northward plume extends along the northern Kerguelen Plateau. This region was sampled for sea-surface plankton by Blain et al. (2001), and elevated *Chaetoceros* spp., abundances were encountered from the plateau-break to the open-ocean stations. This genus was extremely dominant in abundance and biomass in the surface waters at Station A3 during the early demise of the bloom,

whereas higher numbers of viable resting spores were located at 150 m depth at Station C5 (Armand et al., 2008). Translocation studies of a related *Chaetoceros* species, *C. dictyota*, showed these species were enhanced when grown in the iron and silicic-acid-rich deep waters, which are considered the stimulant to the bloom on the plateau (Timmermans et al., 2008). We suspect that oceanographic currents bring these spores to the waters over the plateau, where resuspension and the availability of Si and Fe stimulate their reproduction and survival.

*Navicula directa* and *T. nitzschoides* f. *nitzschoides* show distinct elevations in their plateau distributions at stations C5 and B1, respectively (Fig. 2C and D). Surface-water-column observations of both living and dead *Navicula* spp., however, were highest at stations A3 and B5 (Armand et al., 2008). Other Kerguelen-related surface-water studies also indicate scarce occurrences of *Navicula* species on the plateau (Kopczyńska et al., 1986; Blain et al., 2001). An earlier summary of *Navicula directa* distribution (Armand, 1997, Fig. 3.21) noted the species rarely in the POOZ and in low percentages (0.4%) in the South Indian Ocean. Greatest abundances, up to 1.7%, were instead found along the Antarctic Peninsula. The species is considered benthic (Simonsen, 1974; Hasle and Syvertsen, 1997) and thus low abundances in the related surface-water studies in comparison to the sediment study are currently justified. Our on-plateau observations would strongly suggest that *Navicula* spp. are coastally defined and/or their preservation is enhanced in these shallower sediments.

Maximum abundances of 1–2% of *T. nitzschoides* f. *nitzschoides* were reported in the POOZ (Crosta et al., 2005) and up to 5% in the South Atlantic sector by Zielinski and Gersonde (1997, as their forma 1). Abundances of this species on-plateau (up to 29.3%, Table 3, Fig. 2D) greatly exceeded these values, whereas the abundance at the off-plateau station C11 (2.6%), were consistent with previously reported abundances. The elevated abundances of *T. nitzschoides* f. *nitzschoides* in the plateau sediments are at odds with the surface-water relative abundances of dead cells of less than 3% (Armand et al., 2008). Surface-water studies in the south Indian

Ocean have observed the species as a sub-dominant contributor with its distribution limited between the Subantarctic and Polar Fronts (Steyaert, 1973; Kopczyńska et al., 1986). Fiala et al. (1998) and Kopczyńska et al. (1998) found that *T. nitzschioides* remained secondary to *F. kerguelensis* abundances through subsequent summer bloom surveys at the HNLC Kerfix station west of our study region. The latter authors considered the abundances of *T. nitzschioides* (varieties were not identified) to be related to Polar Frontal conditions overlying the site and the possible intrusion from the Subantarctic waters to the north. The same Polar Frontal conditions prevail over the KEOPS study region on the plateau. The decreased depth over the plateau may have enhanced *T. nitzschioides* preservation in the sediments in contrast to its otherwise diluted signal observed at depth with other off-plateau HNLC stations.

*Eucampia antarctica* frustules in the KEOPS station sediments represent the open-ocean, spiralling chain variety *E. antarctica* var. *antarctica* (varieties described in Fryxell and Prasad, 1990; surface water column observations in Armand et al., 2008). Although a clear sea-floor distribution pattern with respect to the two varieties of *E. antarctica* has yet to be documented (Armand, 1997; Armand et al., 2005), our current samples of *E. antarctica* v. *antarctica* in comparison with the abundances of the Crosta et al. (1998) database identified abundances increasing to the north of the plateau (A3, 7.6%) and into the Subantarctic Zone (Fig. 2E). In the overlying deep-water sample taken at A3 infrequent doublet chains were observed as the only intact cells making it to the sea floor. The accumulation of dead cells (within chains or as empty single cells and half frustules) in the surface water-column at station A3 were observed to increase with depth and over time, these observations were noted when the single-celled *E. antarctica* community domination commenced over the site (Armand et al., 2008). We hypothesize that *E. antarctica* frustules recorded in the sediments to the northeast were focused by the action of the major southeast trending water currents and related to otherwise bloom conditions on the plateau as observed at Station A3. The implications of this focusing are to hinder selection of appropriate proxy samples for the determination of palaeo SST records on cores taken in this region or for the addition of sea-floor sediments into a palaeo database that should have a regional, rather than whole, Southern Ocean scope. To the south of the plateau *E. antarctica* abundances were at trace levels. Only towards the modern winter sea-ice edge are *E. antarctica* abundances in the Crosta et al. database re-elevated, presumably by the appearance of the sea-ice related variety (not shown here; see Armand et al., 2005).

*Thalassiosira antarctica*, as heavily silicified resting stages, also revealed an “island effect” distribution. The distribution corroborates an elevated abundance previously observed, but considered aberrant data directly northeast of Kerguelen (Fig. 2F, Armand et al., 2005).

Curiously, no *T. antarctica* cells were encountered in any KEOPS surface-water sample (Armand et al., 2008) and equally no other regional study has identified this species in surface-water or sediment trap samples. The species source around Kerguelen is unknown, yet the species is known from the Antarctic coastline (Hasle and Heimdal, 1968). We do not believe that our specimens are members of the morphometrically close, but rare, species *Thalassiosira scotia* Fryxell and Hoban; a species reported only from South Georgia and in association with the high-chlorophyll shelf waters (Johansen et al., 1985; Priddle et al., 1986). There is potential to study the three populations recognized to understand their genetic speciation and thus their ecological relationship to productive coastal regions. The fact that our specimens occur mainly as the solid resting cell would imply that nutrient or environmental stress plays a significant role in export out of the surface water column and entrainment in the sediments.

#### 5.1.2. Plateau diminished distributions

The distribution of *F. kerguelensis* (Fig. 3A), demarcates the on-plateau stations from the high abundances in the south eastern Atlantic sector versus those in the southern Indian sector (which lie predominately in the Subantarctic Zone; see Crosta et al., 2005, Fig. 2). Sediment abundances of *F. kerguelensis* from the KEOPS plateau samples mostly fell in the range of 30–45%, which were lower than the circumpolar abundances expected for the POOZ. The C11 and B5 samples exhibited abundances >50% as is normally encountered. The abundance of dead *F. kerguelensis* cells in surface-column waters at C11 was also consistent with the dominance of this species in the sediments (Armand et al., 2008). The dominant abundance of *F. kerguelensis* at each station directly affected the derived evenness value,  $E_H$  (Table 4). The lowest  $E_H$  values at C11 and B5 were representative of the ~57% domination of this species in both assemblages. Whereas, the  $E_H$  value for A3, where *F. kerguelensis* dominance was contained to a mild ~30%, was observed as slightly higher. Evenness values for plateau located stations can be viewed as interplay between the dominances of *F. kerguelensis*, *T. nitzschioides* f. *nitzschioides* and *C. Hyalochaete* resting spores (Table 3).

*Thalassiosira lentiginosa* mirrored the distribution of *F. kerguelensis* in the POOZ where its maximum abundance in the sediments remained around 30%. Abundances on the plateau fell below 8% (Fig. 3B) analogous to previously observed distributions well north of the Polar Frontal Zone or along the Antarctic coastline (Crosta et al., 2005, Fig. 8). Only the C11 sample with 14% relative abundance remained representative of the general regional distribution pattern previously identified in the Crosta et al. database. Sediment trap studies at the nearby KERFIX time series station indicated the species presence fluctuated monthly although some summer increases have been observed in the POOZ environment (Kopczyńska et al., 1998; Pichon et al., unpublished data). The complimentary



surface waters study verified increased abundances of *T. lentiginosa* off the plateau (Armand et al., 2008).

*Fragilariopsis separanda* (Fig. 3C) was largely absent from the plateau and increased abundance at the deeper seafloor location to 2%. *Fragilariopsis separanda* has been confined southward of the Polar Front (Zielinski and Gersonde, 1997) although occurrences within the Subantarctic Zone have been reported in the sediments and surface waters (Kopczyńska et al., 1986; Armand et al., 2005, 2008). The combined *F. separanda*/*rhombrica* group enumerated in the surface water column revealed highest abundances off-plateau at Station C11, suggesting the group's presence diminishes over the plateau due to unfavourable environmental conditions and increased dissolution effects on other taxa increasing their presence. Interestingly, *F. rhombica*, a virtual mirror image of *F. separanda* but with finer areolation on the valve face, was retained in the surface sediments of the plateau (not shown here) and may represent an indication of the nutrient-rich/bloom conditions on-plateau.

#### 5.1.3. Current influenced distributions

The abundance of *Thalassiothrix antarctica* (Fig. 3D) in the sediments was consistent with previous seafloor sediment distributions (Crosta et al., 2005, Fig. 10). Values remained under 2% on the plateau and surrounding POOZ, with the exception of the 4% relative abundance noted at station C11. This peak in abundance is the highest value documented in this region (Table 3) and the Crosta database. The elevated deposition may be related to focusing by deep water sourced from the Australian Antarctic Basin more so than the Fawn Trough current given that no other sediment sample in this region shows high abundances. Fig. 3D also hints at a reduction of this species presence along the Polar Front. Surface-water samples revealed very low abundances of *Thalassiothrix antarctica* (Armand et al., 2008) comparing starkly with the deep-water occurrences observed in this sediment study (Table 3). This observation may be in part a methodological artefact, as we suspected and Kopczyńska et al. (1986) found, that the species was more common when net hauls were used for sampling.

*Thalassiosira gracilis* abundances were reasonably constant (~1.5%) and elevated over the Kerguelen Plateau region, but point to a minor abundance peak south of the plateau culminating at station C5 (2.4%) (Fig. 3E). Abundances of *T. gracilis* in the POOZ sediments ranged from 1% to 5% (Crosta et al., 2005), although in the Indian sector of the South Ocean abundances increased towards the location of the maximum winter sea-ice extent. This observation corresponds well with earlier French investigations in the south Indian Ocean (Jacques et al., 1979; Sournia et al., 1979; Kopczyńska et al., 1986, 1998; Fiala et al., 1998; Pichon et al., unpublished data) where *T. gracilis* was found to be dominant in southerly located sample sites and of low, sporadic representation in POOZ sediment traps. In the surface-water samples *T. gracilis*

abundances were generally absent in the northern plateau stations, and approximately equivalent at stations C1, C5 and C11 (max. 1%, Armand et al., 2008), yet in the overlying deep-water samples the species remained a minor component at most stations (Table 3). The slight incursion of elevated abundances on the southern perimeter of the plateau may be relative to the incursion of cooler Antarctic surface waters observed by Charrassin et al. (2004), or more likely the northeastward traverse of the Fawn Trough current from the Enderby Basin crossing the northeastern Kerguelen Plateau around and onto the plateau via the HMI Trough (see Park et al., 2008b, for nomenclature), which permits a stronger preservation signal in the sediments (Fig. 1A, Mongin et al., 2008; van Beek et al., 2008; Zhang et al., 2008; Park et al., 2008b).

The rare occurrences of *Fragilariopsis curta* in the sediments from stations C11 and B5 are considered allochthonous (Fig. 3F) as their normal sedimentary signature is tightly linked to the Antarctic coast bounded to the north by the maximum sea-ice edge (Armand et al., 2005). Additionally, *F. curta*'s preferred habitat has been linked to sea-ice cover (Garrison, 1991). Sedimentary traces of excursions from this Antarctic coastal region have been attributed to iceberg pathways in the Atlantic Ocean (DeFelice and Wise, 1981; Zielinski and Gersonde, 1997) and bottom-water transport in the Southeast Indian Ocean (Abbott, 1973). We consider the traces of *F. curta* most likely related to deep-water transportation via AABW along the eastern margin of the Kerguelen Plateau.

#### 5.2. Overlying deep-water layer signatures and sources

Only 10 species observed in the overlying deep-water samples did not occur in the sediment samples (Table 3). Shannon's diversity index ( $H$ ) suggested a weak influence of dissolution with depth on the assemblage  $H$  values revealed in Table 4, in as much as diversity was lowest at station C11. Evenness ( $E_H$ ), the number of species and the ADA did not appear to be related to the preservation of an assemblage at depth. The dominance of a certain number of species in both regions, notably *F. kerguelensis*, remained a bias in the observations as revealed by the  $E_H$ . The ubiquitous dominance of *F. kerguelensis* in the Indian Ocean with respect to the Kerguelen region and across the Polar Front has been remarked by several studies (Jacques et al., 1979; Kopczyńska et al., 1986; Blain et al., 2001; Pichon et al., unpublished data).

Our Chl-*a* observations on the plateau from the overlying deep water samples did not correspond with observations made later in the season (April–May) on the northwestern Kerguelen Plateau (Riaux-Gobin et al., 1997). A Chl-*a* reading from their overlying deep-water sample at station 2 was  $0.086 \mu\text{g L}^{-1}$ . This value was over 3 times lower than the minimum value we observed in similar samples on the Kerguelen Plateau (Table 6). Our overlying deep-water, diatom observations showed variable Chl-*a* concentrations with fragmented material having higher

Chl-*a* concentrations than intact samples (Stations C5 and B1).

The thick fluff layers in deep (>3000 m depth) POOZ locations west of Kerguelen Plateau, considered the result of a rapid sedimentation event with high pigment content (up to  $13 \mu\text{g L}^{-1}$ ; Riaux-Gobin et al., 1997), were not observed in our C11 sample east of Kerguelen Plateau. There was no discernable overlying fluff layer there but the overlying deep water did contain a Chl-*a* signature of  $1 \mu\text{g L}^{-1}$ . We were unable to provide a conclusive relationship between diatom observations and Chl-*a* content due to our lack of adequate data coverage.

Deep-water BSi concentrations did not directly reflect surface-water concentrations with lowest deep-water BSi observed at the bloom site A3. The spread of concentration values increased slightly from station A3 to C5 where reduced diatom fragmentation in the deep-water sample was noted. Such variation of BSi concentrations in the overlying deep water could reflect differential dissolution processes down through the water column where diatom remains are either exported intact (e.g., by direct bloom fall-out) or fragmented (e.g., via transit in the zooplankton gut). The degree of species-specific silicification and the resulting rapidity of sedimentation are also likely to play a large role in the concentration of BSi in the water column. As our BSi data represent the first such observations in the overlying deep-water layer to our knowledge, we are not aware of the range or circumstances for such large BSi elevations in the overlying deep waters. There is potential for the use of BSi in overlying deep waters to be used as an indicator of recently deposited diatoms or detrital matter in combination with diatom analysis; however, the variable dissolution related to variations in frustule silicification complicate such a relationship.

The direct effects of dissolution on frustules in the overlying deep waters was not assessed since the majority of material observed was diatom detritus, considered the undigested matter of zooplankton. Ebersbach and Trull (2008) observed that the majority of exported material (>100  $\mu\text{m}$ ) over stations A3 and C5 at the end of the bloom period was composed of large faecal pellet aggregations containing diatom detritus, which decreased in particle size and flux with depth. Our overlying deep-water observations of diatom detritus already in a heavily fragmented state at both A3 and C5 are consistent with these observations.

### 5.3. Species composition and iron related productivity tracers

Our observations on and eastward of the Kerguelen Plateau are consistent with the use of *C. Hyalochaete* resting spores as indicators of high-carbon, low-silica exporting blooms and conversely for the use of *F. kerguelensis* for low-productivity, low-carbon, high-silica exporting conditions (Smetacek et al., 2004; Abelman et al., 2006). We observed elevations of *C. Hyalochaete* resting spore abundances,

increased surface POC export (Savoye et al., 2008) and a low depth-integrated  $\rho\text{Si}:\rho\text{NO}_3$  uptake ratio of 1–2 (Mosseri et al., 2008) in certain sections of the plateau, most notably A3. In contrast *F. kerguelensis* abundances and POC export were lower off the plateau (station C11), and depth-integrated  $\rho\text{Si}:\rho\text{NO}_3$  uptake ratios were 3–7 times greater. However, not all regions on the plateau show large POC export, nor is any single plateau station dominated by *C. Hyalochaete* resting spores in the sediments.

The question as to whether the observed diatom communities were representative of HNLC and iron-replete bloom conditions, in comparison with the two indicator species described above, is not necessarily clear-cut. From our accompanying short-term study of the surface-water diatom distribution it is evident that the diatom bloom over the Kerguelen Plateau (at repeat station A3) was dominated in abundance by *C. Hyalochaete* species (e.g., *C. socialis*) but later evolved into a more monospecific *E. antarctica* v. *antarctica* community during the demise of the bloom (Armand et al., 2008). In the open ocean (repeat station C11) the surface water community remained constant over the survey period, representing a classic open-ocean assemblage dominated by *Fragilariopsis pseudonana* and *F. kerguelensis*.

Our sediment study nonetheless revealed a few surprises: *F. kerguelensis* did occur in greater abundances than *C. Hyalochaete* resting spores and enormous abundances of *T. nitzschoides* f. *nitzschoides* (stations A3 and B5). The latter species is conversely considered by Smetacek et al. (2004) as an “iron-deficient” indicator species. To use our island-affected distributions as a means of identifying indicator species of higher productivity events in the Southern Ocean during past climatic events confuses the issue of iron source, productivity sustained and oceanographic processes related to the otherwise unique distributions. In this case, understanding the modern sea-ice melt bloom production with respect to sea-ice related species and their ecology will be far more useful in identifying the increase in productivity response hypothesized in the sea-ice zone during glacial periods (Abelman et al., 2006) than that observed around Subantarctic islands. In consequence, the chemical source, bioavailability and enhancement processes behind such blooms (i.e. release of deposited atmospheric sourced iron from the sea-ice or increase of iron supply from the UCDW, Blain et al., 2008) will be more poignant to the goals of identifying palaeo-productivity in the Southern Ocean.

The ecology of diatom species in all regions is still very poorly understood. The role of diatom survival through resting spores and stages is important to at least three species (*C. Hyalochaete* species, *E. antarctica* and *T. antarctica*) and this is evident over the plateau from the sediment record, and for *C. Hyalochaete* species from the water column. The influence of oceanographic circulation patterns both as intrusions on the plateau and as tides across the plateau (Charrassin et al., 2004; van Beek et al., 2008; Zhang et al., 2008; Park et al., 2008a, b) may play a



role in the resuspension of *C. Hyalochaete* resting spores into the surface waters and their success in achieving bloom proportions northwestward of Kerguelen. The overlying deep-water at the sediment interface on the western Kerguelen Plateau proved positive to inoculum revival tests within 10 days for *C. Hyalochaete* species (Riaux-Gobin et al., 1997; Pinturier-Geiss et al., 2001). Thus *Chaetoceros* species can take advantage of constant vertical exchange with the surface waters. Tidal influence was reported as an important factor by Boden (1988) when assessing the influence of the “island mass effect” on the appearance of a *Chaetoceros radicans* bloom on the Prince Edward Archipelago. Other Antarctic island studies (e.g., Elephant Island: Helbling et al., 1995; South Georgia: Ward et al., 2005; Ward et al., 2006) all identify mesoscale island-related features and frontal systems playing an important role in the distribution of phytoplankton taxa, whether it be the introduction of Subantarctic taxa or introduction of nutrients to surface waters in the wake of the island. The ecological advantage of survival through resting spores or forms that are resuspended into favourable surface-water conditions is equally important in understanding the bloom dynamics in the wake of these islands.

## 6. Conclusions

An “island mass effect” on diatom sedimentary compositions was observed over the plateau in comparison to HNLC open-ocean locations. This difference was just perceivable in generalized values provided by the ADA, total species number, diversity and evenness indices; which we consider the result of *F. kerguelensis*’ dominance and the dissolution of lightly silicified taxa as a function of depth. It was more clearly delineated in the unique appearance of *T. antarctica* combined with elevated “hot spot” abundances of *T. nitzschioides* f. *nitzschioides*, *E. antarctica*, *Navicula directa* and *C. Hyalochaete* resting spores. In addition the open-ocean samples had elevated abundances of *F. kerguelensis*, *T. lentiginosa* and *Thalassiothrix antarctica*. The observation of overlying deep-water samples emphasized the dominance of *F. kerguelensis* remains. Most overlying deep-water samples revealed fragmented to dispersed aggregates of diatom detritus; however, complete chains and cells of heavily silicified taxa were sporadically encountered, with the best preservation at plateau station C5. Plateau stations had a greater number of species preserved compared to the C11 off-plateau. The preliminary study of BSi and Chl-*a* concentrations in the overlying deep waters revealed extremely high BSi values and highly variable Chl-*a* that appeared un-related to the species preservation observed.

A role for current transport was indicated by the appearance and heightened abundances of cooler water or Antarctic sea-ice-influenced taxa on the plateau (*T. gracilis*, *T. antarctica*) and in the off-plateau stations (*F. curta* and *Thalassiothrix antarctica*). Our understanding

of current movement towards and on to the plateau is still immature, regardless of the tantalizing advances of Park et al. (2008a), Charrassin et al. (2004), Zhang et al. (2008) and van Beek et al. (2008) with their incursions of Antarctic-sourced water over the plateau. The AABW focusing of diatoms in deep waters skirting the Kerguelen Plateau identified by Dezileau et al. (2000) could only be decoded by the allochthonous contribution of *F. curta* and the largest reported abundance of *Thalassiothrix antarctica* in the current sea-floor database. We hypothesize that *E. antarctica* abundances elevated in the northeast sediments of the Indian Ocean are most likely sourced from bloom events on the plateau and focused by deep-water currents.

The use of *C. Hyalochaete* resting spores as a proxy for high-carbon, low-silica exporting blooms may not be applicable in this Subantarctic island situation, in as much that our observations found these spores in association with two heavily silicified species (*F. kerguelensis* and *T. nitzschioides* f. *nitzschioides*) considered indicative of the opposite condition in the Kerguelen bloom region. It is evident that evaluating palaeo-productivity hypotheses based on the signals of a few major diatom species requires careful consideration with respect to their proxy basis.

## Acknowledgements

We thank our PI Prof. S. Blain, the Captain and crew of the *RV Marion Dufresne II* and scientific participants of the KEOPS mission both at sea and on land. We particularly thank Eric Viollier and Bruno Bombled for their assistance with sampling. LA is a recipient of a European Union FTP6 Marie Curie Fellowship and funding from this program supported her work in this research. LA, BQ, JM and NG’s work is supported by the Centre National de la Recherche Scientifique (CNRS), Institut National des Sciences de L’Univers (INSU) and l’Institut Paul Émile Victor (IPEV). XC’s participation is funded by Centre National de la Recherche Scientifique (CNRS), Programme national d’Etude de la Dynamique du Climat (PNEDC) and Missions Scientifiques des Terres Australes et Antarctiques Françaises (IPEV-TAAF). Mme. V. Cornet-Barthaux (COM-LOB) assisted with photomicroscopy. The two anonymous referees and special volume editor T. Trull provided thoughtful remarks that improved the manuscript.

## References

- Abbott Jr., W.H., 1973. Vertical and lateral patterns of diatomaceous ooze found between Australia and Antarctica. Ph.D., Department of Geology, University of South Carolina.
- 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, 002006.
- Armand, L.K., 1997. The use of diatom transfer functions in estimating sea-surface temperature and sea-ice in cores from the southeast Indian Ocean. Ph.D., Australian National University, Canberra.

- Armand, L.K., Crosta, X., Romero, O., Pichon, J.-J., 2005. The biogeography of major diatom taxa in Southern Ocean sediments. 1: ice-related species. *Palaeogeography, Palaeoclimatology, Palaeoecology* 223 (1–2), 93–126.
- Armand, L.K., Cornet-Barthau, V., Mosseri, J. and Quéguiner, B., 2008. 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].
- Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Martin-Jézéquel, V., Le Fèvre, J., Mayzaud, P., Marty, J.-C., Razouls, S., 2001. A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep-Sea Research I* 48, 163–187.
- Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, C., Carlotti, F., Christaki, U., Corbière, A., Durand, I., Ebersbach, F., Fuda, J.-L., Garcia, N., Gerringa, L., Griffiths, B., Guigue, C., Guillermin, C., Jacquet, S., Jeandel, C., Laan, P., Lefèvre, D., Lomonaco, C., Malits, A., Mosseri, J., Obernosterer, I., Park, Y.-H., Picheral, M., Pondaven, P., Remeny, T., Sandroni, V., Sarthou, G., Savoye, N., Scouarnec, L., Souhaut, M., Thuiller, D., Timmermans, K., Trull, T., Uitz, J., van-Beek, P., Veldhuis, M., Vincent, D., Viollier, E., Vong, L., Wagener, T., 2007. Impacts of natural iron fertilization on the Southern Ocean. *Nature* 446, 1070–1074.
- Blain, S., Sarthou, G., Laan, P., 2008. Distribution of dissolved iron during the natural iron fertilization experiment KEOPS (Kerguelen Plateau, Southern Ocean). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.028].
- Boden, B.P., 1988. Observations of the island mass effect in the Prince Edward Archipelago. *Polar Biology* 9, 61–68.
- Brzezinski, M.A., Nelson, D.M., 1995. The annual silica cycle in the Sargasso Sea near Bermuda. *Deep-Sea Research I* 42, 1215–1237.
- Charrassin, J.-B., Park, Y.-H., Le Majo, Y.L., Bost, C.-A., 2004. Fine resolution 3D temperature fields off Kerguelen from instrumented penguins. *Deep-Sea Research I* 51 (12), 2091–2103.
- Cornet-Barthaux, V., Armand, L., Quéguiner, B., 2007. Biovolume and biomass measurements of key Southern Ocean diatoms. *Aquatic Microbial Ecology* 48, 295–308.
- Crosta, X., Pichon, J.-J., Labracherie, M., 1997. Distribution of *Chaetoceros* resting spores in modern peri-Antarctic sediments. *Marine Micropaleontology* 29, 283–299.
- Crosta, X., Pichon, J.-J., Burckle, L.H., 1998. Application of modern analog technique to marine Antarctic diatoms: reconstruction of maximum sea-ice extent at the Last Glacial Maximum. *Paleoceanography* 13 (3), 286–297.
- Crosta, X., Romero, O., Armand, L.K., Pichon, J.-J., 2005. The biogeography of major diatom taxa in Southern Ocean sediments. 2: open-ocean related species. *Palaeogeography, Palaeoclimatology, Palaeoecology* 223 (1–2), 66–92.
- DeFolice, D.R., Wise, S.W.J., 1981. Surface lithofacies, biofacies and diatom diversity patterns as models for delineation of climatic change in the southeast Atlantic Ocean. *Marine Micropaleontology* 6, 29–70.
- Dezileau, L., Bareille, G., Reyss, J.L., Lemoine, F., 2000. Evidence for strong sediment redistribution by bottom currents along the Southeast Indian Ridge. *Deep-Sea Research I* 47, 1899–1936.
- Ebersbach, F., Trull, T., 2008. Sinking particle properties determined from image analysis of polyacrylamide gels deployed in drifting sediment traps during KEOPS: implications for ecosystem controls on carbon export in an area of persistent natural iron inputs in the Southern Ocean. *Limnology and Oceanography* 53, 212–224.
- Fiala, M., Kopczyńska, E.E., Jeandel, C., Oriol, L., Vétion, G., 1998. Seasonal and interannual variability of size-fractionated phytoplankton biomass and community structure at station Kerfix, off Kerguelen Islands, Antarctica. *Journal of Plankton Research* 20 (7), 1341–1356.
- Fryxell, G.A., Prasad, A.K.S.K., 1990. *Eucampia antarctica* var. *recta* (Mangin) stat. nov. (Biddulphiaceae, Bacillariophyceae): life stages at the Weddell Sea ice edge. *Phycologia* 29 (1), 27–38.
- Garrison, D.L., 1991. Antarctic sea ice biota. *American Zoologist* 31, 17–33.
- Hasle, G.R., Heimdal, B.R., 1968. Morphology and distribution of the marine centric diatom *Thalassiosira antarctica* Comber. *Journal of the Royal Microscopical Society* 88 (3), 357–369.
- Hasle, G.R., Syvertsen, E.E., 1997. Marine diatoms. In: Tomas, C.R. (Ed.), *Identifying Marine Phytoplankton*. Academic Press, New York, pp. 5–361.
- Helbling, E.W., Villafane, V.E., Holm-Hansen, O., 1995. Variability of phytoplankton distribution and primary production around Elephant Island, Antarctica, during 1990–1993. *Polar Biology* 15, 233–246.
- Holm-Hansen, O., Hewes, C.D., Villafane, V.E., Helbling, E.W., Silva, N., Amos, T., 1997. Distribution of phytoplankton and nutrients in relation to different water masses in the area around Elephant Island, Antarctica. *Polar Biology* 18, 145–153.
- Jacques, G., Descolas-Gros, C., Grall, J.-R., Sournia, A., 1979. Distribution du phytoplancton dans la partie Antarctique de l'Océan Indien en fin d'été. *Internationale Revue der Gesamten Hydrobiologie* 64 (5), 609–628.
- Johansen, J.R., Doucette, G.J., Fryxell, G.A., 1985. The genus *Thalassiosira* (Bacillariophyceae): morphology of heterovalve resting spores of *T. scotia*. *American Journal of Botany* 72 (12), 1861–1870.
- Kopczyńska, E.E., Weber, L.H., El-Sayed, S.Z., 1986. Phytoplankton species composition and abundance in the Indian Sector of the Antarctic Ocean. *Polar Biology* 6, 161–169.
- Kopczyńska, E.E., Fiala, M., Jeandel, C., 1998. Annual and interannual variability in phytoplankton at a permanent station off Kerguelen Islands, Southern Ocean. *Polar Biology* 20, 342–351.
- Laws, R.A., 1983. Preparing strewn slides for quantitative microscopical analysis: a test using calibrated microspheres. *Micropaleontology* 29 (1), 60–65.
- Mongin, M., Molina, E., Trull, T.W., 2008. Seasonality and scale of the Kerguelen Plateau phytoplankton bloom: a remote sensing and modeling analysis of 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. and Cornet-Barthau, V., 2008. Impact of iron on silicon utilization by diatoms in the Southern Ocean: a case study 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].
- Park, Y.-H., Gambérini, L., 1995. Large-scale circulation and its variability in the south Indian Ocean from TOPEX/POSEIDON altimetry. *Journal of Geophysical Research* 100 (C12), 24911–24924, 24929.
- Park, Y.-H., Gambérini, L., 1997. Cross-frontal exchange of Antarctic Bottom Water in Crozet Basin. *Deep-Sea Research II* 44 (5), 963–986.
- Park, Y.-H., Gambérini, L., Charriaud, E., 1991. Frontal structure and transport of the Antarctic Circumpolar Current in the South Indian Ocean sector, 40–80°E. *Marine Chemistry* 35, 45–62.
- Park, Y.-H., Charriaud, E., Fieux, M., 1998. Thermohaline structure of the Antarctic surface water/winter water in the Indian sector of the Southern Ocean. *Journal of Marine Systems* 17, 5–23.
- 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].
- Pinturier-Geiss, L., Laureillard, J., Riaux-Gobin, C., Fillaux, J., Saliot, A., 2001. Lipids and pigments in deep-sea surface sediments and interfacial particles from the Western Crozet Basin. *Marine Chemistry* 75, 249–266.
- Priddle, J., Heywood, R.B., Theriot, E., 1986. Some environmental factors influencing phytoplankton in the Southern Ocean around South Georgia. *Polar Biology* 5, 65–79.
- Ragueneau, O., Savoye, N., Del Amo, Y., Cotten, J., Tardiveau, B., Leynaert, A., 2005. A new method for the measurement of biogenic silica in suspended matter of coastal waters: using Si:Al ratios to

- correct for the mineral interference. *Continental Shelf Research* 25, 697–710.
- Raimbault, P., Rodier, M., Taupier-Letage, I., 1988. Size fraction of phytoplankton in the Ligurian Sea and the Algerian basin (Mediterranean Sea): size fraction versus total concentration. *Marine Microbial Food Webs* 3, 1–7.
- Raimbault, P., Lantoine, F., Neveux, J., 2004. Dosage rapide de la chlorophylle *a* et des phaeopigments par fluorimétrie après extraction au méthanol. Comparaison avec la méthode classique d'extraction à acétone. *Océanis* 30 (2), 189–205.
- Rathburn, A.E., Pichon, J.-J., Ayress, M.A., DeDecker, P., 1997. Microfossil and stable-isotope evidence for changes in Late Holocene paleoproductivity and paleoceanographic conditions in the Prydz Bay region of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 131, 485–510.
- Riaux-Gobin, C., Hargraves, P.E., Neveux, J., Oriol, L., Vétion, G., 1997. Microphyte pigments and resting spores at the water–sediment interface in the Subantarctic deep sea (Indian sector of the Southern Ocean). *Deep-Sea Research Part II* 44 (5), 1033–1051.
- Riaux-Gobin, C., Fortugne, M., Jensen, K.G., Bentaleb, I., Cauwet, G., Chrétiennot-Dinet, M.-J., Poisson, A., 2006. Surficial deep-sea sediments across the Polar Frontal system (Southern Ocean, Indian sector): particulate carbon content and microphyte signatures. *Marine Geology* 230, 147–159.
- Savoye, N., Trull, T.W., Jacquet, S.H.M., Navez, J., Dehairs, F., 2008. <sup>234</sup>Th-based export fluxes during a natural iron fertilization experiment in the Southern Ocean (KEOPS). *Deep-Sea Research II*, this issue [doi:10.1016/j.dsr2.2007.12.036].
- Schlitzer, R., 2006. Ocean Data View <<http://odv.awi.de>>.
- Schrader, H.J., Gersonde, R., 1978. Diatoms and silicoflagellates. In: Zachariasse, W.J., Riedel, W.R., Sanfilippo, A., Schmidt, R.R., Brolsma, M.J., Schrader, H.J., Gersonde, R., Drooger, M.M., Broekman, J.A. (Eds.), *Micropaleontological Counting Methods and Techniques—An Exercise on an Eight Metres Section of the Lower Pliocene of Capo Rossello, Sicily*. Utrecht Micropaleontological Bulletin, pp. 129–176.
- Simonsen, R., 1974. The diatom plankton of the Indian Ocean Expedition of R/V *Meteor* 1964–1965. “Meteor” *Forsch.-Ergebnisse Reihe D*(19), 1–107.
- Smetacek, V.S., Assmy, P., Henjes, J., 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. *Antarctic Science* 16 (4), 541–558.
- Sournia, A., Grall, J.-R., Jacques, G., 1979. Diatomées et Dinoflagelles planctoniques d’une coupe meridienne dans le sud de L’Océan Indien (campagne Antipod I du *Marion DuFresne*, mars 1977) (Plankton diatoms and dinoflagellates along a Meridian transect in the Southern Indian Ocean (Cruise Antipod I of the R/V “*Marion DuFresne*,” March 1977). *Botanica Marina* XXII, 183–198.
- Steyaert, J., 1973. Distribution of plankton diatoms along an African–Antarctic transect. *Investigaciones Pesqueras* 37 (2), 295–328.
- 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.dsr2.2007.12.032].
- Van Beek, P., Bourquin, M., Reyss, J.L., Souhault, M., Charette, M. and 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].
- Viollier, E., Bombled, B., Sangiardi, P., Scouarnec, L., 2005. Biogeochemistry of Kerguelen Plateau Sediments. KEOPS Cruise Report MD145/KEOPS. Report no. OCE/2005/01. IPEV, Brest.
- Ward, P., Shreeve, R., Whitehouse, M., Korb, B., Atkinson, A., Meredith, M., Pond, D., Watkins, J., Goss, C., Cunningham, N., 2005. Phyto- and zooplankton community structure and production around South Georgia (Southern Ocean) during Summer 2001/02. *Deep-Sea Research Part I: Oceanographic Research Papers* 52 (3), 421–441.
- Ward, P., Shreeve, R., Atkinson, A., Korb, B., Whitehouse, M., Thorpe, S., Pond, D., Cunningham, N., 2006. Plankton community structure and variability in the Scotia Sea: austral summer 2003. *Marine Ecology Progress Series* 309, 75–91.
- 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].
- Zielinski, U., Gersonde, R., 1997. Diatom distribution in Southern Ocean surface sediments (Atlantic sector): implications for paleoenvironmental reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 129, 213–250.