Climate mediated size variability of diatom *Fragilariopsis kerguelensis* in the Southern Ocean

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A B S T R A C T

Fragilariopsis kerguelensis (O'Meara) Hustedt is the most abundant open ocean diatom species in Southern Ocean sediments and its average valve area has recently been used to infer glacial–interglacial paleoceanographic conditions. Studies from the Atlantic sector of the Southern Ocean demonstrated how larger average valve area of *F. kerguelensis* during the Last Glacial compared to the interglacial possibly relate to greater availability of iron (through wider sea ice coverage and higher eolian dust input). We present here data on average valve area of *F. kerguelensis* from three sediment cores covering the last ~42 cal ka BP from different zones of the Southern Ocean. Our records confirm previous results from the Atlantic sector, but highlight a different pattern from the Indian sector where the largest valves of *F. kerguelensis* are encountered during the Holocene. *Fragilariopsis kerguelensis* average valve area variations in the Antarctic Polar Front (APF) of the Atlantic sector and Subantarctic Front of the Indian sector are in phase with records of opal burial while this correlation does not hold for the APF of the Indian sector. Variations in circum-polar upwelling were suggested as the main controlling factor of opal production during the last 20,000 years. We here hypothesize that high nutrient input from the Antarctic Peninsula during the last deglaciation may have exerted a stronger control on *F. kerguelensis* average valve area and opal export in the Atlantic sector of the Southern Ocean than inferred changes in circum-polar upwelling.

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1. Introduction

Diatom distribution in the World Ocean is strongly related to silicic acid availability (Ragueneau et al., 2000) and, in turn, diatom production and remineralization modulate the cycling of silicon in the ocean (Nelson et al., 1995; Brzezinski and Nelson, 1996). In the Southern Ocean, opal burial, usually related to high preservation efficiency of diatoms in sediments underlying zones of high production, represents the main oceanic silicon sink (Anderson et al., 2009). However, little is known about species-specific silicon transport efficiency and its implication for high southern latitude palaeo records as only few studies have been carried out on diatom biometry (Cortese and Gersonde, 2007; Crosta, 2009; Cortese et al., 2012) and on diatom-mediated silicon export efficiency (Kemp et al., 2000, 2006).

Fragilariopsis kerguelensis (O'Meara) Hustedt is endemic to the Southern Ocean, and is one of the most abundant diatoms within the Permanent Open Ocean Zone (POOZ) (Hasle, 1969). Due to its excellent preservation potential (Smetacek et al., 2004), it also represents the most abundant species in the underlying surface sediments, where it contributes to the bulk of the diatom ooze belt (Zielinski and Gersonde, 1997). Its abundance in surface sediments is maximal within the range of 1–8 °C, under summer ice-free conditions (Crosta et al., 2005a). These specificities have been used to reconstruct past sea-surface temperature (SST) and sea-ice conditions in the Southern Ocean (Gersonde et al., 2005; Abelmann et al., 2006; Crosta et al., 2007, 2008).

Fragilariopsis kerguelensis apical length ranges between 8 μm and 90 μm in the phytoplankton (van der Spoel et al., 1973; Fenner et al., 1976; Assmy et al., 2006). Auxospore formation, maximal size of initial cells, gametangial cells and critical minimal size are probably mediated by environmental conditions such as light, temperatures and macro- and micro-nutrient content of surface waters (Assmy et al., 2006 and references therein). At the whole Southern Ocean scale, largest *F. kerguelensis* were found around

the Antarctic Polar Front both in the phytoplankton (van der Spoel et al., 1973) and in the underlying sediments (Cortese and Gersonde, 2007), probably in relation to initial high levels of macro- and micro-nutrients in surface waters and ecologically sustainable SST (Crosta et al., 2005a). However, co-limitation of iron and silicic acid over the course of the growing season dams primary productivity in the open ocean (Ragueneau et al., 2000). Changes in *F. kerguelensis* size and average valve area (FkergArea) in deep-sea sediment cores were recently used to infer changes in diatom productivity, physiology and environmental conditions. Cortese and Gersonde (2007) showed that FkergArea was larger during the Last Glacial (∼25 cal ka BP–18 cal ka BP) and decreased until present time except for a sharp peak during the deglacial period (∼16 cal ka BP–14 cal ka BP). The presence of large FkergArea during the Last Glacial and the deglaciation was attributed to high availability of iron (Cortese and Gersonde, 2007), in agreement with recent findings based on natural (Timmermans et al., 2008), *in situ* (Assmy et al., 2006) and laboratory (Timmermans and van der Wagt, 2010) experiments. The presence of larger FkergArea during the deglaciation may have resulted in the observed high deglacial biogenic silica burial in underlying sediments (Anderson et al., 2009). Similarly, larger FkergArea were found in the Subantarctic zone of the Atlantic sector of the Southern Ocean during the Last Glacial period and associated with higher dust-bearing iron and lower SST compared to the deglacial and the Holocene periods (Cortese et al., 2012). No deglacial peak in FkergArea was, however, recorded in the Subantarctic zone. In the Atlantic sector, larger FkergArea were found concomitant to low *F. kerguelensis* relative abundances in the Antarctic zone and to high *F. kerguelensis* relative abundances in the Subantarctic zone (Cortese et al., 2012), thus indicating no direct relationship between diatom size and productivity as previously suggested (Assmy et al., 2006). At the local scale, in the Antarctic coastal zone off Adélie Land, East Antarctica, where iron limitation is not as much of an issue as in the open ocean (Sambrotto et al., 2003; Vaillencourt et al., 2003) and nutrient availability was prominent during the entire Holocene period (Denis et al., 2009), larger *F. kerguelensis* average valve lengths concomitant to maximum relative and absolute abundances of *F. kerguelensis* were found during the warm Mid-Holocene Hypsithermal (7.7–3.8 cal ka BP) compared to the Early-Holocene cool period (8.8–7.7 cal ka BP) and Late-Holocene Neoglacial period (3.8–1 cal ka BP) (Crosta, 2009). These changes in *F. kerguelensis* average valve lengths in macro- and micro-nutrient rich environments during the whole growing season were attributed to changes in SST and sea ice presence, whereby SST during the colder Neoglacial period were out of the ecological range of *F. kerguelensis* (Crosta, 2009) and led to the formation of smaller auxospores and initial cells (Crosta, 2009). All these studies found, at times, contradictory lines of evidence and thus, demonstrate that site-specific variables strongly impact on a diatom community's average valve area. It is therefore essential to extend the use of fossil diatom biometry to a larger geographic array covering different oceanographic and climatic conditions.

We present here records of FkergArea from three sediment cores (two cores from south of the Antarctic Polar Front and one from the Subantarctic Front) from the Atlantic and Indian sectors of the Southern Ocean. These records are compared with a set of published ice core and marine records to assess the role of nutrient cycling and environmental conditions in the Southern Ocean on FkergArea. More precisely, we test whether variations in FkergArea over the last 42,000 years result from changes in iron availability (from different sources) and/or in environmental conditions (sea ice cover and SST), both processes have been climate mediated at this time scale.

2. Material and methods

We analyzed three sediment cores for *F. kerguelensis* average valve area variability (FkergArea), namely piston core TNO57-13-PC4 (53°2′S, 5°1′E, Antarctic Polar Front) from the Atlantic sector of the Southern Ocean (Fig. 1 – Atlantic APF), gravity core SO136-111 (56°40′S–160°14′E, Antarctic Polar Front) and piston core MD88-769 (46°04′S, 90°06′E, south of Subantarctic Front) from the Indian sector of the Southern Ocean (Fig. 1 – Indian APF and Indian SAF, respectively).

Stratigraphy for the Atlantic APF core is detailed in Shemesh et al. (2002), whereas age models for the Indian APF and SAF cores are detailed in Crosta et al. (2005b). Diatom analysis, sediment treatment and slide preparation followed the technique described in Rathburn et al. (1997). Diatom counts followed the procedures described by Schrader and Gersonde (1978) and Laws (1983). The absolute abundances, in number of frustules of *F. kerguelensis* per gram of dry sediment, were calculated using the equation detailed in Crosta et al. (2008). We use absolute abundances and FkergArea together (multiplying the average valve area and absolute abundances of this species) to assess the contribution of *F. kerguelensis* to biogenic silica accumulation, and thus provide a direct comparison with opal flux. This approach has never been applied to infer biogenic silica associated with fossil *F. kerguelensis* (hereafter noted FkergBSi) but is similar to the one used to reconstruct diatom biomass from diatom biovolume (Leblanc et al., 2012).

Valve area measurements of *F. kerguelensis* were performed at a time resolution of ∼0.5–2.25 cal ka BP ($n = 47$) for the Atlantic APF core (covering last ∼42 cal ka BP), 0.5–2 cal ka BP ($n = 52$) for the Indian APF core (last ∼40.5 cal ka BP) and 0.5–5.5 cal ka BP ($n = 27$) for the Indian SAF core (last ∼40 cal ka BP). One hundred specimens (only complete valves) of *F. kerguelensis* were measured in each sample along their apical length and transapical lengths. Measurements were performed manually by a single operator on the computer screen using the NIS Element BR software calibrated through a microscope using 1000× magnification (oil immersion objective). Standard error on the length and width measurements was around 0.2 μm similar to the standard error reported in Crosta (2009). The values of apical and transapical lengths were used for the valve area calculation following the equation below:

$$VA = AL * TL * 0.8$$

Where VA is the valve area in μm^2, AL is the apical length in μm and TL is the transapical length in μm. This equation is different than the one used in Cortese et al. (2012) and calculates more accurate valve area for long and narrow valves. Standard error on the valve area calculation was around 5%, based on the standard errors on AL and TL.

We described our down-core results and interpretations along three climatic periods namely glacial, deglacial and the Holocene covering the time periods ∼42–18 cal ka BP, ∼17–10 cal ka BP and ∼10–0 cal ka BP, respectively. Linear regression was used to describe the relationship between two datasets. The one-way ANOVA test was used to assess the (dis)similarities in the FkergArea, by testing paired populations across all three cores and among the climatic periods (Holocene, Deglacial, Glacial).

The data of *F. kerguelensis* biometry, abundances and FkergBSi for Atlantic APF (TNO57-13-PC4), Indian APF (SO136-111) and Indian SAF (MD88-769) cores are provided in Supplementary files A and B.

3. Results

In the Atlantic APF core, FkergArea was highest (∼280 μm^2) during the glacial and deglacial periods while lowest (∼240 μm^2)
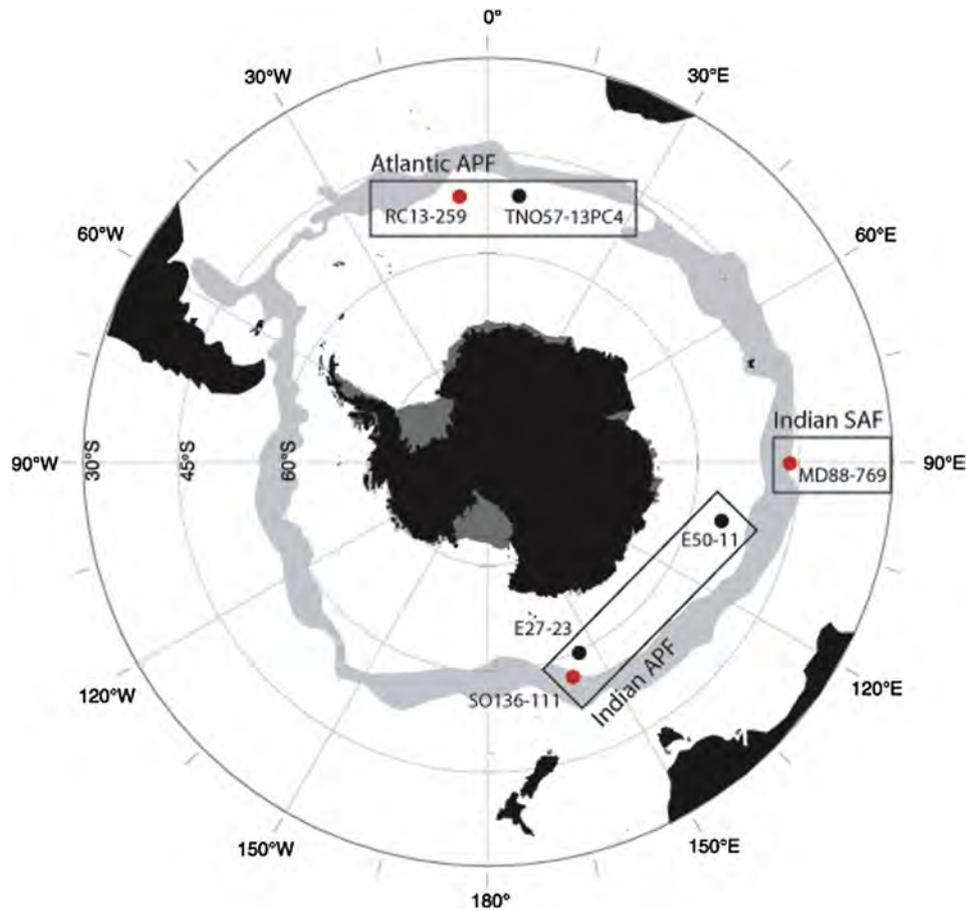
Fig. 1. Location of three cores (denoted with red circle) studied for size variability of *F. kerguelensis*, namely Atlantic APF: Core TNO57-13PC4, Indian APF: Core SO136-111 and Indian SAF: Core MD88-769. The black circles represent published records which were used for comparison (see text for details). Map modified after Gersonde et al. (2005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

during the Holocene period (Table 1, Fig. 2a). In the Indian APF core, FkergArea was conversely highest ($\sim$307 μm^2) during the Holocene period while lowest during the deglacial period ($\sim$261 μm^2) with an intermediate value ($\sim$276 μm^2) during the Last Glacial period (Table 1, Fig. 2b). In the Indian SAF core, FkergArea was highest ($\sim$298 μm^2) during the Last Glacial period while lowest ($\sim$266 μm^2) during the Holocene period with an intermediate value ($\sim$274 μm^2) during the deglacial period (Table 1, Fig. 2c).

Table 1
The following items are reported for each of the samples: samples analyzed, number of specimens measured, range of average apical length, range of average transapical length, range of average valve area and average valve area for Atlantic APF, Indian APF and Indian SAF for three climatic periods Holocene, deglacial and glacial. The above parameters are also listed from earlier studies (Cortese and Gersonde, 2007; Cortese et al., 2012) for comparison. ND represent no data.

Time periods	Studied cores and earlier studies	Samples analyzed	Specimens measured	Average apical axis range (μm)	Average transapical axis range (μm)	Average valve area range (μm^2)	Average valve area (μm^2)
Holocene	Atlantic APF	11	1100	32.07–38.46	8.18–9.22	222.90–289.52	250.64
	Indian APF	15	1500	36.58–45.54	8.87–9.54	269.01–353.45	307.16
	Indian SAF	3	300	35.03–37.60	8.40–9.01	245.46–276.43	266.08
	Cortese and Gersonde, 2007 Cortese et al., 2012	6	222	32.50–38.34	7.69–8.49	129.21–167.32	149.39
	Atlantic SAF (Core 1)	6	245	27.45–29.54	6.80–7.74	97.91–114.92	108
	Atlantic SAF (Core 2)	2	88	25.72–32.79	7.68–8.15	101.08–137.04	119.06
Deglacial	Atlantic APF	11	1100	35.67–38.89	8.66–9.23	256.51–297.74	279.64
	Indian APF	11	1100	32.92–44.23	8.82–9.42	228.86–343.43	260.58
	Indian SAF	5	500	35.44–37.19	8.74–9.45	263.22–286.36	274.38
	Cortese and Gersonde, 2007 Cortese et al., 2012	12	459	35.98–43.20	7.70–9.40	145.75–197.42	179.39
	Atlantic SAF (Core 1)	5	211	31.20–33.03	7.72–9.03	123.76–146.55	137.75
	Atlantic SAF (Core 2)	ND	ND	ND	ND	ND	ND
Glacial	Atlantic APF	25	2500	32.52–41.44	8.38–10.26	223.89–350.32	278.69
	Indian APF	26	2600	33.58–43.46	8.12–9.29	231.17–315.61	275.71
	Indian SAF	19	1900	36.27–39.77	9.34–9.84	286.06–318.29	298.33
	Cortese and Gersonde, 2007 Cortese et al., 2012	4	142	38.65–42.03	9.42–9.70	189.36–203.94	193.61
	Atlantic SAF (Core 1)	20	864	33.86–40.66	9.61–10.83	174.24–216.39	194.73
	Atlantic SAF (Core 2)	29	1269	33.72–41.42	9.97–10.91	173.44–223.85	199.82
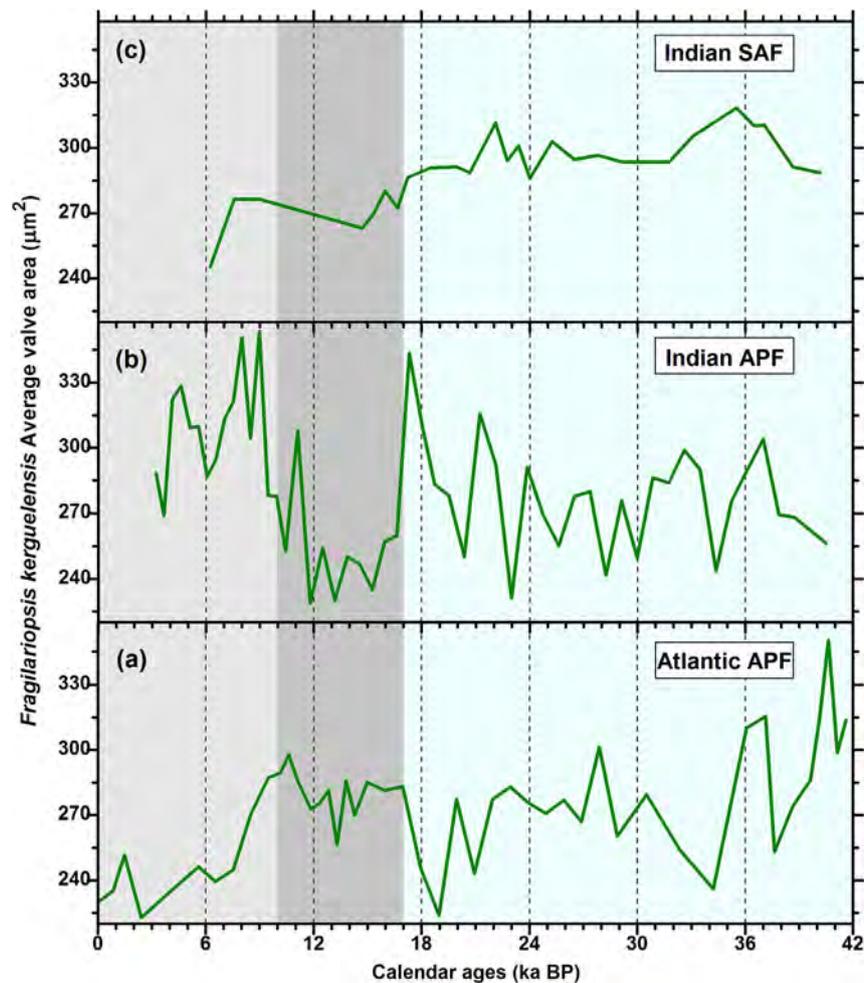
Fig. 2. *Fragilariopsis kerguelensis* average valve area (FkergArea) versus calendar ages for (a) Atlantic APF; (b) Indian APF; and (c) Indian SAF. Glacial, deglacial and the Holocene periods are highlighted with cyan, dark gray and light gray colors, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The results of one-way ANOVA tests for core to core comparisons of FkergArea are summarized in Table 2 (see Supplementary Table C for detailed dataset), and demonstrate that FkergArea were statistically different during the Holocene and glacial periods for all the three cores ($p > 0.05$). Similarly, FkergArea were statistically different during the glacial and deglacial periods for Indian APF and Indian SAF, and during the Holocene and deglacial periods for Atlantic APF and Indian APF ($p > 0.05$). Contrary to this, FkergArea were statistically similar during the Holocene and deglacial periods for Indian SAF, and during the glacial and

Table 2
Summary of ANOVA test conducted for average valve area of *F. kerguelensis* for three cores (Atlantic APF, Indian APF and Indian SAF) between cores and climatic periods. $<10^{-6}$ and $<10^{-3}$ represent statistically different valve areas ($p > 0.05$) whereas $>10^{-3}$ represent statistically similar valve areas ($p < 0.05$).

Atlantic APF through time	Atlantic APF Holocene	Atlantic APF deglacial	Atlantic APF glacial	**Indian APF through time**	Indian APF Holocene	Indian APF deglacial	Indian APF glacial	**Indian SAF through time**	Indian SAF Holocene	Indian SAF deglacial	Indian SAF glacial
Atlantic APF Holocene	–	$<10^{-6}$	$<10^{-6}$	Indian APF Holocene	–	$<10^{-6}$	$<10^{-6}$	Indian SAF Holocene	–	$>10^{-3}$	$<10^{-6}$
Atlantic APF deglacial		–	$>10^{-3}$	Indian APF deglacial		–	$<10^{-6}$	IndianSAF deglacial		–	$<10^{-6}$
Atlantic APF glacial			–	Indian APF glacial			–	Indian SAF glacial			–

Holocene between cores	Atlantic APF Holocene	Indian APF Holocene	Indian SAF Holocene	**Deglacial between cores**	Atlantic APF deglacial	Indian APF deglacial	Indian SAF deglacial	**Glacial between cores**	Atlantic APF glacial	Indian APF glacial	Indian SAF glacial
Atlantic APF Holocene	–	$<10^{-6}$	$<10^{-3}$	Atlantic APF deglacial	–	$<10^{-6}$	$>10^{-3}$	Atlantic APF glacial	–	$>10^{-3}$	$<10^{-6}$
Indian APF Holocene		–	$<10^{-6}$	Indian APF deglacial		–	$<10^{-3}$	Indian APF glacial		–	$<10^{-6}$
Indian SAF Holocene			–	Indian SAF deglacial			–	Indian SAF glacial			–

deglacial periods for Atlantic APF ($p < 0.05$), the significant finding of the study.

Additionally, one-way ANOVA test for comparisons of FkergArea across climatic periods demonstrate statistically different FkergArea ($p > 0.05$) during the Holocene period for all the three cores, during the deglacial period for Indian APF compared to Atlantic APF and Indian SAF, and during the glacial period for Indian SAF compared to Atlantic APF and Indian APF. Contrary to this, statistically similar FkergArea ($p < 0.05$) were found during the deglacial for Atlantic APF and Indian SAF, and during the glacial period of Atlantic APF and Indian APF.

In the Atlantic APF core, the absolute abundances of *F. kerguelensis* were highest during the deglacial period while lowest during the glacial period (Fig. 3a – black curve). The records of *F. kerguelensis* absolute abundances in the Indian APF core and in the Indian SAF core showed opposite patterns with an increasing trend from glacial to the Holocene period in the Indian APF core and a decreasing trend from glacial to the Holocene period in the Indian SAF core (Fig. 3b and c – black curves, respectively).

The inferred biogenic silica associated to *F. kerguelensis* burial (FkergBSi) mimics the records of the absolute abundances for all the three cores. Some offsets are, however, apparent during the Holocene period in the Atlantic APF core, the deglacial period in the Indian APF core and throughout the core in the Indian SAF core, indicating that *F. kerguelensis* absolute abundances in the sediment is not a precise measure of FkergBSi. FkergBSi variations can strongly modulate the BSi burial associated to a given diatom species. The main findings are greatest FkergBSi during the deglacial period for the Atlantic APF core (Fig. 3a – red curve), during the

Holocene period for the Indian APF core (Fig. 3b – red curve) and during the glacial period for Indian SAF core (Fig. 3c – red curve).

4. Discussion

Our data on *F. kerguelensis* average valve area (FkergArea), measured in three cores from different zones of the Southern Ocean allow us to test earlier proposed hypotheses on the control of *F. kerguelensis* size past changes, by addressing the following questions: (1) Is there a link between the FkergArea and the species productivity, tracked here through its absolute abundances? (2) How did environmental conditions impact on the FkergArea over the last 42 cal ka BP? (3) Were the processes controlling the FkergArea the same in both sectors/in all three zones, or were there regional differences?

4.1. Fragilariopsis kerguelensis average valve area and productivity

The average valve size of a diatom community is generally dependent on diatom productivity, as vegetative multiplication leads to size reduction and greater abundances (Drebes, 1977; Round et al., 1990; Mann, 1993). Conversely, sexual reproduction leads to size restoration (Edlund and Stoermer, 1997). This relationship between diatom size and productivity is looser in sediments where a discrete sample (1 cm slice here) represents tens/hundreds of years and, subsequently, tens/hundreds of seasonal blooms, each having its own dynamics. Additional processes such as grazing, dissolution, transport and winnowing may further alter the initial signal. Despite these limitations we believe that, if
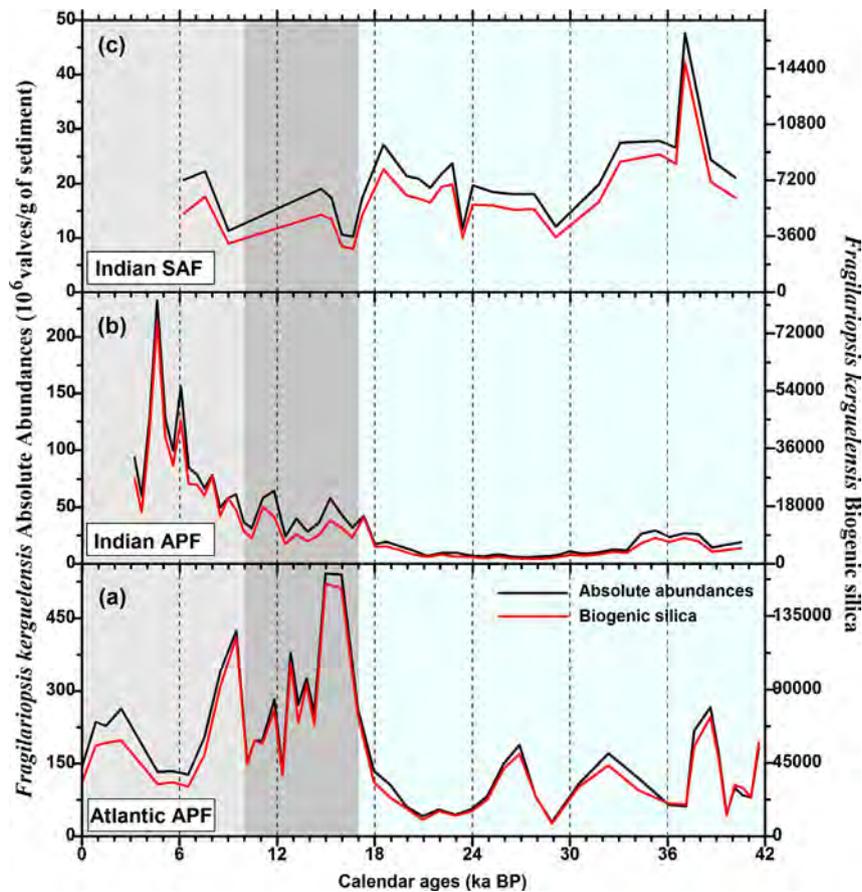
Fig. 3. Down-core records of *Fragilariopsis kerguelensis* absolute abundances (black curves) and inferred biogenic silica associated to *Fragilariopsis kerguelensis* burial (FkergBSi) (red curves) for (a) Atlantic APF (b) Indian APF and (c) Indian SAF. Glacial, deglacial and the Holocene periods are highlighted with cyan, dark gray and light gray colors, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

FkergArea variations were solely controlled by productivity, one should expect an anti-correlation between absolute abundances and FkergArea during the past 42 cal ka BP. The absence of significant anti-correlation between absolute abundances and FkergArea in all three cores (during the three periods or during the whole 42 cal ka BP), suggest that additional processes controlled FkergArea variations in the different sectors/zones of the Southern Ocean.

4.2. F. kerguelensis average valve area and environmental conditions (SST and sea ice)

The occurrences of statistically similar FkergArea for the Last Glacial period in the two APF cores, while statistically different for deglacial and the Holocene periods (Fig. 2, Table 2), suggest a strong regional difference between the Atlantic and Indian sectors, which is also expressed in *F. kerguelensis* absolute abundances (Fig. 3a and b − black curves, respectively). Such regional differences since the Last Glacial Maximum (LGM) may result from local processes superimposed on global change.

We compared our data on FkergArea to published estimates of February sea-surface temperature (SST) and sea ice cover for each of the three cores (Hodell et al., 2001; Shemesh et al., 2002; Crosta et al., 2005b). The records of SST and sea ice cover follow a glacial−interglacial pattern with (1) low SST and extended sea ice cover during the Last Glacial, (2) initiation of deglaciation and sea ice retreat at 20−18 cal ka BP, (3) warm early Holocene and (4) cool mid-to-late Holocene (Fig. 4b).

Crosta (2009) showed that SST and sea ice cover have an important impact on *F. kerguelensis* and *Fragilariopsis curta* average valve lengths in the coastal sea ice zone, where both species are at their lower and upper ecological range, respectively. We do not expect such a large control of SST on FkergArea variation in the open ocean cores at least for the Atlantic and Indian APF where glacial−interglacial SST variations (SST range 2−7 °C) fall within the ecological range of *F. kerguelensis* (Fig. 4b, left and middle panels) (Armand et al., 2005; Crosta, 2009). Indeed, in the two cores, variations in FkergArea do not visually mirror changes in SST (Fig. 4a and b, left and middle panels). Conversely, for the Indian SAF core, SST changes may have influenced FkergArea as SST were within *F. kerguelensis* ecological range during the Last Glacial while slightly out of the ecological range during the deglacial and the Holocene periods (Fig. 4a and b, right panel). Larger FkergArea during more favorable conditions may result from the formation of larger auxospores thanks to optimized silicic acid uptake at peak ecological conditions (Edlund and Stoermer, 1997; Chepurnov et al., 2004).

Changes in sea ice cover have the potential to affect FkergArea by two opposite processes. A broader sea ice extent is known to have dampened production of open ocean diatoms and silica burial south of the modern Polar Front during glacial time (Burckle, 1984; Burckle and Cirilli, 1987). Conversely, sea ice melting during spring-summer is known to increase macro- and micro-nutrient input to the surface ocean (Lannuzel et al., 2007, 2008, 2010) thus stimulating diatom production (Sigmon et al., 2002) which, in turn, usually results in greater abundances of large size diatoms as previously suggested (Cortese and Gersonde, 2007; Crosta, 2009).

The presence of sea ice at the location of the Atlantic and Indian APF cores during the Last Glacial period (Fig. 4b, left and middle panels) might be responsible for relatively large FkergArea through seasonal iron limitation alleviation (Hoffmann et al., 2008). This idea was reported earlier by Cortese and Gersonde (2007) because sea ice is thought to act as an effective transporter of iron and enhances its bioavailability (Abelmann et al., 2006). Our results revealed statistically similar FkergArea in the two APF cores during the Last Glacial, even if these two locations are far apart. Sea ice

retreat throughout the deglacial was relatively similar in both sectors of the Southern Ocean and by 18 cal ka BP, the locations of both cores were ice-free. However, FkergArea responded differently during the deglacial in the two sectors whereby FkergArea was found to have increased in the Atlantic APF (Fig. 4a, left panel) and decreased sharply in the Indian APF (Fig. 4a, middle panel). This discordance persisted through the Holocene period as well, when the Atlantic APF experienced smallest FkergArea while the Indian APF recorded the largest FkergArea.

In the Indian SAF core, the larger FkergArea during the Last Glacial period is unlikely to have been directly influenced by changes in sea ice cover, which was restricted to the POOZ and Antarctic zone, However, this location may have been affected by nutrient-rich cold water in summer as a result of sea ice melt.

Our observations suggest that sea ice seasonal melting no longer played a role in the FkergArea since 18 cal ka BP in the Antarctic zone. Other processes are, therefore, needed to explain the different evolution of FkergArea in the different sectors since 18 cal ka BP.

### 4.3. Fragilariopsis kerguelensis average valve area and nutrient cycling

Reconciliation of FkergArea with previously published isotopic composition of diatom-bound intrinsic organic matter $\delta^{15}N_{diat}$ (Shemesh et al., 2002; Crosta et al., 2005b) and silicon stable isotopes $\delta^{30}Si$ (De La Rocha et al., 1998; Brzezinski et al., 2002; Beucher et al., 2007) in different zones of the Southern Ocean allowed us to investigate how nutrient cycling could have modulated the FkergArea during glacial−interglacial periods.

Down-core records of $\delta^{15}N_{diat}$ and $\delta^{30}Si$ are strongly anti-correlated in all three zones (Fig. 4c) suggesting an inverse relationship of nitrate and silicic acid relative utilization during the past 42 cal ka BP, as a result of changes in the physiological response of diatoms to variable iron supply (Brzezinski et al., 2002, 2003) through eolian dust (Andersen et al., 1998; Mahowald et al., 1999) and/or circumpolar upwelling (Anderson et al., 2009).

Higher $\delta^{15}N_{diat}$ and lower $\delta^{30}Si$ during the Last Glacial have been interpreted to result from greater availability of iron through increased dust input, as recorded in Antarctic ice cores (Petit et al., 1999). Such greater iron stocks in surface waters of the glacial ocean have been previously invoked to explain the large FkergArea in the Antarctic and Subantarctic zones of the Atlantic sector of the Southern Ocean (Cortese and Gersonde, 2007; Cortese et al., 2012). Our data demonstrate large FkergArea between 40 and 18 cal ka BP in the Indian APF and Indian SAF cores (Fig. 4a, middle and right panels) similarly suggesting high iron stocks in the Antarctic and Subantarctic zones of the Indian sector of the Southern Ocean during glacial time. Glacial iron enrichment in the Indian Ocean may result from greater eolian dust deposition (Andersen et al., 1998) and enhanced sediment remobilization from the Kerguelen Plateau (Dézileau et al., 2000, 2003; Blain et al., 2007).

Both geochemical and FkergArea records disagree regionally since ∼18 cal ka BP, when the eolian dust flux abruptly dropped (Fig. 4e). In the Indian SAF core, the $\delta^{15}N_{diat}$ has decreased continuously since the Last Glacial, while the $\delta^{30}Si$ has increased continuously (Fig. 4c, right panel) suggesting increasing iron limitation until the mid-Holocene, which could be attributed to a slowing down of the Antarctic Circumpolar Current (ACC) and a southward shift of the Polar Front Zone (PFZ). The response is reflected in the continuous reduction of FkergArea (Fig. 4a, right panel).

In the Indian APF core, the $\delta^{15}N_{diat}$ has decreased continuously since the Last Glacial while the $\delta^{30}Si$ increased abruptly at 20 cal ka BP (Fig. 4c, middle panel). These records are interpreted as indicating lower relative utilization of nitrate and greater
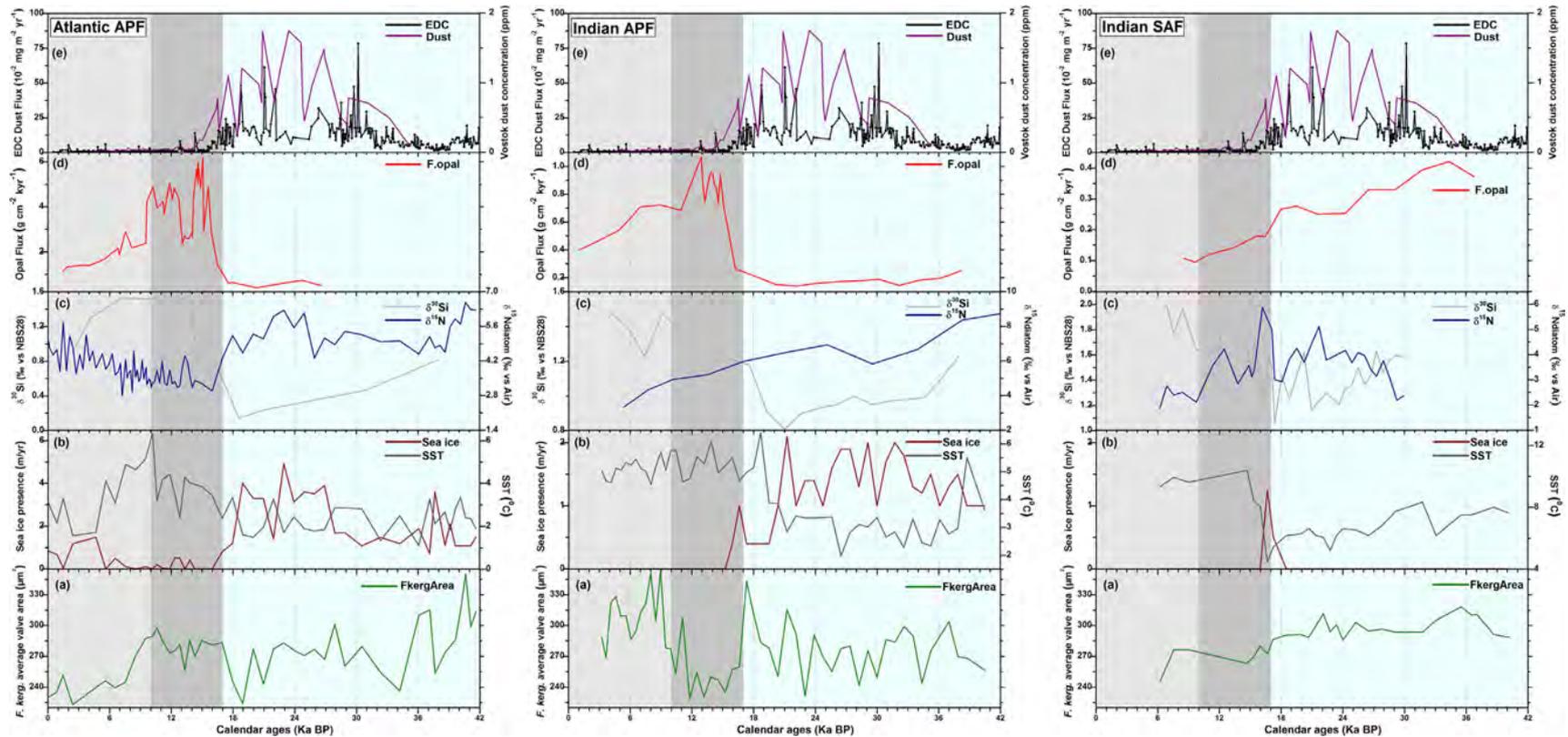
Fig. 4. Down-core records of average valve area of *F. kerguelensis* (a), Sea ice presence (b — brown curve), February Sea-surface temperature (b — dark gray curve), $\delta^{30}Si$ (c — light gray curve), $\delta^{15}N_{diat}$ (c — blue curve), Opal Flux (d — red curve), Fe flux (e — black curve) and dust concentration (e — purple curve). For Atlantic APF, sea ice presence, $\delta^{15}N_{diat}$, Feb SST data from Shemesh et al. (2002), $\delta^{30}Si$ data from (Brzezinski et al., 2002) and Opal Flux data from Anderson et al. (2009) are also shown. For Indian APF, sea ice presence, $\delta^{15}N_{diat}$ and Feb SST data are from Crosta et al. (2005b), $\delta^{30}Si$ data from De La Rocha et al. (1998) and Opal Flux data from Anderson et al. (2009). For Indian SAF, sea ice presence, $\delta^{15}N_{diat}$, Feb SST data are from Crosta et al. (2005b), $\delta^{30}Si$ data from Beucher et al. (2007) and Opal Flux data from Dézileau et al. (2003). Fe flux data from Lambert et al. (2008) and dust concentration data from Vostok Ice Core (Petit et al., 1999) on independent time scales. Glacial, deglacial and Holocene periods are highlighted with cyan, dark gray and light gray colors, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

utilization of silicic acid since the LGM (Beucher et al., 2007). As Indian APF core is too far away from the Kerguelen Islands to be significantly influenced by sediment resuspension-controlled iron fertilization (Blain et al., 2007), we conclude that iron limitation has been prevalent since 20 cal ka BP, as a result of the strong reduction in eolian dust input (Fig. 4e, middle panel). Iron limitation is reflected in the FkergArea during the deglacial period, where smallest FkergArea are found during the 17–10 cal ka BP period (Fig. 4a, middle panel) when δ^{30}Si increased, demonstrating a shift in diatom physiology toward greater Si/N uptake (Brzezinski et al., 2002, 2003). Large FkergArea are recorded again (since 10 cal ka BP), an indication of higher nutrient stocks during the Holocene. Today, most of the macro- and micro-nutrients of Antarctic surface waters come from the Southern Ocean upwelling by vertical diffusion, a process that is especially efficient in the PFZ where strong mixing exists. Indian APF core is located at the Polar Front and our results thus suggest that the iron source since 10 cal ka BP in the southeastern Indian sector of the Southern Ocean was through the circumpolar upwelling.

In the Atlantic APF core, δ^{15}N$_{diat}$ values decreased from Last Glacial period until ~16 cal ka BP when they started increasing again throughout the deglacial and Holocene (Fig. 4c, left panel). δ^{30}Si values increased abruptly at ~18 cal ka BP to reach highest values between 14 and 6 cal ka BP, when they started decreasing again (Fig. 4c, left panel). This pattern should again indicate iron limitation, increasing Si/N uptake, as a result of low eolian dust fluxes to the Southern Ocean since 18 cal ka BP. However, at this location FkergArea were statistically identical during the deglacial period and the Last Glacial (Table 2), possibly indicating another source of macro- and micro-nutrients to support high productivity (Anderson et al., 2009) and large diatoms (Fig. 4a, left panel). This source was attributed to the Southern Ocean circum-polar upwelling (Anderson et al., 2009) and may have affected the Indian sector as well. However, we found statistically different FkergArea during the deglacial period in the Atlantic APF core and in the Indian APF cores (Table 2), two cores located close to the modern position of the Polar Front. This may indicate that oceanographic conditions and nutrient stocks were different in both the sectors since the LGM. To account for large FkergArea during the 17–10 cal ka BP period in the Atlantic APF core, we here propose that the west Atlantic sector of the Southern Ocean was receiving high amounts of macro- and micro-nutrients from the Antarctic Peninsula during the deglacial period. Several lines of evidence support this proposition. Recent studies have provided compelling evidence of lateral transport of dissolved iron in the Atlantic sector from the continental shelves of the Antarctic Peninsula (de Jong et al., 2012). The concentration of dissolved iron was shown to decrease exponentially with increasing distance from the Antarctic Peninsula and the western Weddell Sea. Furthermore, in the western Atlantic sector of the Southern Ocean, horizontal advection of dissolved iron was found to dominate over vertical diffusion, whereas the atmospheric contribution was found to be significant in the eastern Atlantic sector. Such large fluxes explain the high iron utilization by phytoplankton in modern surface waters of the Atlantic sector of the Southern Ocean compared to the Indian sector, where vertical diffusion is the most important source of nutrients (Boyd et al., 2012). Horizontal advection of macro- and micro-nutrients may have been much greater in the past, especially during periods of deglaciation. Indeed, δ^{18}O$_{Si}$ values from the Atlantic APF core indicate the presence of meltwater peaks at ~14 and 11 cal ka BP, thus suggesting upper water column stratification during the deglacial period (Shemesh et al., 2002), which is at odds with increased vertical diffusion (Anderson et al., 2009). The meltwater peaks were related to iceberg discharge, and the origin of these iceberg surges during the deglaciation was from the Antarctic

Peninsula (Labeyrie et al., 1986; Kanfoush et al., 2000; Nielsen et al., 2007). This meltwater lid in the Atlantic sector during the deglacial period was suggested to have resulted in greater abundances of diatoms due to increased iron input (Bianchi and Gersonde, 2004; Abelmann et al., 2006). We here thus hypothesize that high nutrient input from the Antarctic Peninsula to the Atlantic sector during the last deglaciation may have been a more important control on FkergArea than the inferred changes in circum-polar upwelling. Our argument is in agreement with previous findings (Hendry et al., 2011). Equally, our hypothesis also offers an explanation for the lower FkergArea during the Holocene compared to the Last Glacial and deglaciation, which may have resulted from decreased lateral advection from the now deglaciated Antarctic Peninsula and a sluggish ACC (Dézileau et al., 2000). This is further supported by the present location of the Atlantic APF core which is ~3° of latitude south of the Polar Front and few degrees of latitude north of the mean winter sea ice edge where FkergArea are smaller than in the PFZ (Cortese and Gersonde, 2007).

4.4. Fragilariopsis kerguelensis average valve area and biogenic silica

The biogenic silica due to F. kerguelensis burial (FkergBSi) is here estimated through the FkergArea and the absolute abundance of the species in down-core sediments, in the same way diatom biomass is inferred from diatom biovolume and carbon content (Leblanc et al., 2012).

FkergBSi burial is in phase with opal fluxes in the Atlantic APF and Indian SAF cores (Figs. 3a,c and 4d, left and right panels), whereas a phase opposition is apparent for the Indian APF core (Figs. 3b and 4d, middle panel). These results indicate that the diatom F. kerguelensis was the main biogenic silica carrier to the sea-floor in the Atlantic APF and in the Subantarctic zone of the Indian sector of the Southern Ocean during the last 42 cal ka BP, in the absence of Thalassiothrix antarctica mats (Grigorov et al., 2002). Conversely, because both FkergArea and FkergBSi are out of phase with the buried opal fluxes, we suggest that F. kerguelensis was not the main biogenic silica carrier to the sea-floor in the Indian APF zone. Other heavily silicified diatom species, such as Thalassiosira lentiginosa (Janisch) Fryxell, therefore, may have been responsible for the opal fluxes preserved in the Indian APF. Thalassiosira lentiginosa is indeed the second most abundant diatom species in both the Atlantic and Indian APF cores, accounting for 10–30% of the diatom assemblages and presenting a substantial abundance pattern like F. kerguelensis (Crosta et al., 2004). It is also possible that inter-sector differences in F. kerguelensis silicification existed due to different macro- and micro-nutrient stocks, whereby F. kerguelensis valves were less silicified in the Indian sector than in the Atlantic sector of the Southern Ocean, as observed today for different oceanic regions (Baines et al., 2010). The development of new techniques to determine diatom ornamentation and quantify diatom silicification in deep-sea sediment cores is therefore needed to refine our understanding of diatom palaeo-physiology and their role in past nutrient cycles.

5. Conclusions

Measurements of FkergArea from three sediment cores from different zones of the Southern Ocean (Core TNO57-13-PC4 from the Atlantic APF; Core SO136-111 from the Indian APF and Core MD88-769 from the Indian SAF) covering the last ~42 cal ka BP reveal how climatic conditions and nutrient cycling, forced by climatic changes, could have driven FkergArea variations due to changing environmental conditions from Last Glacial to interglacial. The greater FkergArea during the Last Glacial period strongly

suggests a control on valve size by the greater availability of iron under the windier conditions of the Last Glacial period. During the deglacial period, smaller FkergArea was found in the Indian APF and Indian SAF cores, whereas larger FkergArea was found in the Atlantic APF core. The main oceanographic difference between the two sectors of the Southern Ocean during the last deglaciation was the presence of iceberg surges and associated lateral transport of micro- and macro-nutrients in the Atlantic APF. The other two cores from the Indian sector were too far from this iron source. We here hypothesize that high nutrient input in the Atlantic APF from the Antarctic Peninsula during the last deglaciation was a more important control on FkergArea and diatom physiology than the inferred increase in circum-polar upwelling. During the Holocene period, smaller FkergArea was found in the Atlantic APF and Indian SAF cores due to iron limitation, whereas the occurrence of larger FkergArea in the Indian APF core suggests availability of high nutrient stocks, especially iron through circum-polar upwelling.

Several lines of development would improve the interpretations depicted above. A sea-floor mapping of FkergArea for the Indian sector of the Southern Ocean, to be compared to existing database for the Atlantic sector of the Southern Ocean (Cortese and Gersonde, 2007), would provide important insight on the modern relationship between FkergArea and environmental conditions. FkergArea down-core records from the Pacific sector of the Southern Ocean, which is remote from iron-bearing eolian dust, would document whether the Atlantic sector is a particular basin in the Southern Ocean due to the vicinity of the Antarctic Peninsula and the entrance zone of the North Atlantic Deep Water. Technical developments to measure biogenic silica contained in the diatom valves and measurements of other highly silicified diatom species would help refining the role of each species in biogenic silica and organic carbon to the sea-floor and, hence, on atmospheric CO_2.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2013.03.005.

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