Glacial-interglacial variability in diatom abundance and valve size: Implications for Southern Ocean paleoceanography

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Abstract Antarctic sea ice extent along with Southern Ocean biological productivity varied considerably during glacial-interglacial periods, and both are known to have played a considerable role in regulating atmospheric CO₂ variations in the past. Here we present data on diatom absolute abundance (valves/g of sediment) and size over the past ~42 ka B.P. and how they link to glacial-interglacial changes in Antarctic sea ice extent, Southern Ocean frontal systems, and aeolian dust flux. Our records of sea ice and permanent open ocean zone diatom abundances suggest a shift in the Antarctic winter sea ice limit and Polar Front respectively up to the modern-day Polar Frontal Zone during marine isotopic stages (MIS) 2 and late MIS 3. In addition to glacial shifts in the Polar Front, diatom assemblages also recorded a plausible northward shifts in Polar Front during few intervals of MIS 1. Glacial periods north of the Polar Front in the Indian sector of the Southern Ocean were characterized by higher total diatom abundance, larger 

1. Introduction

The Southern Ocean acts as a connecting link between the Atlantic, Indian, and Pacific Oceans and is characterized by an array of oceanic frontal systems. Its Indian sector comprises three major fronts: the Subtropical Front (STF), Sub-Antarctic Front (SAF), and Antarctic Polar Front (APF) [Ori et al., 1995; Belkin and Gordon, 1996; Rintoul and England, 2002]. Unlike other sectors of the Southern Ocean, the presence of islands and ridges leads to a complex oceanography in this sector. The SAF, APF, and Southern Boundary of Antarctic Circumpolar Current form the Antarctic Circumpolar Current (ACC), which flows clockwise, mainly driven by the westerly wind system [Pollard et al., 2002]. The ACC is an influential component of the Southern Ocean, as it plays a dominant role in affecting biogeochemistry, hydrography, and sea ice distribution [Sigman and Boyle, 2000; Toggweiler et al., 2006].

Besides ACC, the sea ice surrounding Antarctica is also an important modulator of the Southern Hemisphere climate system. Sea ice is an impervious layer of the ocean surface and is bound to influence the air-sea exchange of gasses such as CO₂, O₂, N₂O, and dimethylsulfide [Delille et al., 2007]. Sea ice can also be an important sink for CO₂ through physical [Dieckmann et al., 2008], as well as biological, processes [Delille et al., 2007]. Most studies pertaining to past reconstruction of the Antarctic sea ice are restricted to the Last Glacial Maximum (LGM) [Climate: Long-Range Investigation, Mapping, and Prediction (CLIMAP), 1976, 1981; Cooke and Hays, 1982; Armand, 1997; Burkle and Mortlock, 1998; Crosta et al., 1998], with the exception of some studies from the Atlantic sector that cover pre-LGM times as well [Gersonde and Zielinski, 2000; Kunz-Pirrung et al., 2002]. Few studies [Crosta et al., 2004; Cortese and Gersonde, 2007; Shukla et al., 2013] have thrown light on the relation between diatom abundance and valve size and glacial-interglacial variation in Antarctic sea ice and frontal systems from the Indian sector of the Southern Ocean.

Under modern-day conditions, diatom valve accumulation rates reach maximum values in a zone between the APF and the maximum winter sea ice limit, a zone (opal belt) which is characterized by high silicate,
nitrate, and phosphate concentration and which represents a major sink for biogenic silica in the Southern Ocean [Zielinski and Gersonde, 1997; Esper et al., 2010]. During glacial periods, the northward shift in Antarctic winter sea ice extent and frontal systems (STF, SAF, and APF) is in phase with high biogenic opal fluxes and export production to the north of the modern-day APF in the Southern Ocean [Gersonde and Zielinski, 2000; Dezileau et al., 2003, De Deckker et al., 2012]. It is suspected that the northward expansion of this “opal belt,” a region characterized by high production and export of biogenic silica, might have resulted in the observed increase of biogenic opal fluxes during the glacial period [Anderson et al., 2002; Chase et al., 2003; Dezileau et al., 2003].

Despite the high concentrations of available nutrients in the Southern Ocean, phytoplankton are unable to fully utilize these nutrients because of iron limitation, brought about by low aeolian supply of lithogenic dust [Treguer and Jacques, 1992; Comiso et al., 1993; Martin, 1990; Martin et al., 1991]. The Southern Ocean is thus the largest high-nutrient low-chlorophyll region in the world ocean. The presence of islands represents an exception to this situation, as natural terrestrial iron input allows the development of large blooms. The Crozet Islands is one such system where natural iron fertilization fuels the diatom bloom specifically to the north of Crozet Island during austral summer [Salter et al., 2007; Seeyave et al., 2007]. Both chlorophyll $a$ and productivity were significantly higher to the north of Crozet Islands [Seeyave et al., 2007]. Given the presence of adequate macronutrient concentration and moderate mesozooplankton grazing pressure in the north of Crozet Islands [Fielding et al., 2007], the horizontal advection of dissolved Fe from the island promoted high productivity to the north of Crozet Island. The source for this can be from sediments on the shelf [Eiford et al., 2004], direct runoff, and leaching of soluble Fe from the suspended sediments while they are being laterally transported [Lam et al., 2006]. The natural Fe enrichment effect north of the Crozet Islands [Planquette et al., 2007] is stronger and sustained and occurs as a gradual accumulation of Fe over the winter period, when light limitation prevents phytoplankton growth and hence Fe uptake. Nevertheless, to invoke Fe controls on productivity requires appropriate current flows to deliver Fe to the north of Crozet Island. Current flows that transport Fe to the northern bloom area can be (1) anticyclonic meanders breaking off the SAF from north or west; (2) from anticyclonic flows around the island; and (3) wind-driven, northward Ekman flux across the plateau [Pollard et al., 2007]. The retentive circulation north of Crozet Islands, bounded by the SAF [Pollard et al., 2007; Venables et al., 2007], might allow Fe to accumulate in a constrained region, so that once light limitation is lifted, there is enough Fe to support a bloom [Seeyave et al., 2007].

Similar to natural Fe fertilization, the few artificial iron fertilization experiments conducted in the Southern Ocean by Boyd et al. [2000] resulted in an elevated phytoplankton biomass and rates of photosynthesis in surface waters causing large drawdown of CO$_2$ and macronutrients. The Southern Ocean Iron Release Experiment also led to a floristic shift that resulted in diatom-dominated blooms accounting for 75% of the primary production [Boyd et al., 2000].

The present study area is in close proximity of Crozet Island archipelago and could have been influenced by changes in terrestrial input during glacial-interglacial periods as a result of changing intensity of ACC. Similar studies by Manoj et al. [2012] have suggested that during glacial periods, erosion in shallow waters around the volcanic islands and ridges due to strengthened ACC could be an important mechanisms for enhanced terrigenous input to the core site. Likewise, an increase in iron input via upwelling and erosion of Kerguelen Plateau was considered to be a primary reason for greater biogenic opal fluxes to the north of the actual position of APF during MIS 2 relative to Holocene [Dezileau et al., 2003]. Apart from regional sources, the increase in iron-bearing dust from the Patagonian Desert during last glacial period played a vital role in relieving parts of the Southern Ocean from iron-limiting conditions [Petit et al., 1999]. On this account, during the last glacial period, the alleviation of iron deficit by the high dust input could have resulted in a greater uptake and utilization of carbon and nitrogen relative to silica in diatoms from the Polar Frontal Zone (PFZ) of the Indian sector of the Southern Ocean [Crosta et al., 2005]. This situation resulted in a greater concentration of unused silicic acid in the PFZ, thereby promoting silicic acid leakage and inducing shifts from nonsiliceous phytoplankton to diatoms in low-latitude upwelling systems [Crosta et al., 2005; Beucher et al., 2007].

In the Southern Ocean, F. kerguelensis displays strong spatial and temporal variability in size depending on iron availability, nutrient conditions, and sea surface temperature (SST) [Cortese and Gersonde, 2007; Crosta, 2009; Cortese et al., 2012; Shukla et al., 2013]. Larger F. kerguelensis were found in the proximity of the APF and are related to higher levels of macronutrients and micronutrients, along with physiologically viable
SST; thus, the valve area of this species may be useful in reconstructing past position and nutrient characteristics of the APF and the opal belt [Crosta et al., 2005; Cortese and Gersonde, 2007]. Size variability of *F. kerguelensis* during two artificial iron fertilization experiments in the Southern Ocean: EIFEX [Smetacek et al., 2005] and EisenEX [Smetacek, 2001] revealed larger valve sizes of *F. kerguelensis* in the fertilized patch, suggesting a possible relation between valve size and ambient surface water iron concentration [Cortese et al., 2012].

In this study we present diatom records for the past ~42,000 years from the Indian sector of the Southern Ocean and use them to improve our understanding of glacial-interglacial changes in diatom absolute abundance and valve sizes with respect to varying sea ice, frontal zones, aeolian dust, and terrestrial input.

2. Regional Setting

The core site is located at 43°42′S latitude and 45°04′E longitude to the north of Crozet Islands in the northern part of the Polar Frontal Zone (PFZ), which is presently a sea ice-free region (Figure 1). Oceanographic fronts and winter/summer sea ice extent allow the subdivision of the Southern Ocean into a series of latitudinal bands/zones. From south to north these are the following:

1. The sea ice zone (SIZ) [Treguer and Jacques, 1992] is bounded to the north by the summer sea ice extent and thus characterized by permanent sea ice coverage. The area between the winter and summer sea ice limit is referred to as seasonal SIZ (Figure 1).
2. The permanent open ocean zone (POOZ) is bounded by the APF to the north and the winter sea ice to the south.
3. The PFZ is bounded to the north by the SAF and to the south by the APF [Orsi et al., 1995; Belkin and Gordon, 1996].
4. The Sub-Antarctic Zone (SAZ) is the region located between the STF and SAF [Pollard et al., 2002] (Figure 1).

3. Materials and Methods

3.1. Chronology and Core Description

A marine sediment core (SK 200/22a) was retrieved from the Indian sector of the Southern Ocean using a piston corer from a water depth of 2370 m on board ORV Sagar Kanya. Chronology for SK 200/22a (Table 1)
was obtained using accelerator mass spectrometry (AMS) radiocarbon (14C) dating at selected intervals using the planktonic foraminifera *Globigerina bulloides* and/or *Neogloboquadrina pachyderma* [Manoj et al., 2013; Manoj and Thamban, 2015]. Visual examination of the core revealed that it consisted of alternating layers of calcareous white to grey sandy silt/clay up to the depth of 115 cm, followed by a dark greyish band dominated by silty clay between 130 and 148 cm and by light grey clay below this [Manoj et al., 2012].

### 3.2. Diatom Analysis

Sediment processing and slide preparations for diatom analysis followed the techniques described by Batterby [1986] and Gersonde and Zielinski [2000], while diatom counts were performed according to Schrader and Gersonde [1978]. Normally, a minimum of 350–400 valves were counted in each sample at magnification of ×1000 using an inverted light microscope (Nikon Eclipse Ti-U). Taxonomic identification of diatoms followed Hasle and Syvertsen [1997], Scott and Thomas [2005], Round et al. [1990], and Cefarelli et al. [2010].

### 3.3. Diatom Groups

Southern Ocean diatoms having similar environmental preferences (in terms of sea ice and SSTs) were grouped on the basis of Q-mode factor analysis by Crosta et al. [1998]. In the present study, diatom assemblages were grouped into a permanent open ocean zone (POOZ) group (Figures 2c and 2d), a Sub-Antarctic Zone (SAZ) group (Figures 2e and 2f), and a sea ice group (Figures 2g–2j) (Table 2) following the study of Crosta et al. [1998].

### 3.4. Diatom Morphometry

Two diatom species, *Fragilariopsis kerguelensis* (pennate) and *Thalassiosira lentiginosa* (centric), were chosen for morphometric studies owing to their higher relative abundance throughout the core (Figures 2a and 2b). Length of apical axis of *F. kerguelensis* and radius of *T. lentiginosa* were measured manually using the nuclear inelastic scattering element imaging software connected to the Nikon Eclipse Ti-U inverted microscope. Sizes of these two diatoms were measured for every 2 cm depth interval up to 200 cm depth and there on every 5 cm interval up to 754 cm depth. Measurements were performed on 80 specimens each of *F. kerguelensis* and *T. lentiginosa* from a permanent slide for all selected depth intervals of the core.

### 3.5. Ice-Rafted Debris

The ice-rafted debris (IRD) in the core was studied by counting 300–400 grains in >125 μm size fraction under a binocular microscope. The methodology and distribution characteristics have been detailed by Manoj et al. [2012].

### 3.6. Statistical Analysis

One-way analysis of variance (ANOVA) was performed on the sizes of *F. kerguelensis* and *T. lentiginosa* between glacial and interglacial periods (by comparing MIS 1 and MIS 2–3). The ANOVA was performed to test whether the differences between the groups are statistically significant or not.
Figure 2. Diatom assemblages in the core SK 200/22a. (a) Apical length of *F. kerguelensis* and (b) radius of *T. lentiginosa*. POOZ diatoms: (c) *Fragilariopsis kerguelensis* and (d) *Thalassiosira lentiginosa*. SAZ diatoms: (e) *Azpeitia tabularis* and (f) *Hemidiscus cuneiformis*. Sea ice diatoms: (g) *Actinocyclus actinochilus*, (h) *Fragilariopsis ritscheri*, (i) *Fragilariopsis cylindrus*, and (j) *Fragilariopsis curta*. Scale = 10 µm.
4. Results

4.1. Temporal Variations in Diatom Groups

4.1.1. Sea Ice Diatom Group

The sea ice diatoms are exclusively found within the SIZ. This group is composed of six species, namely, *Fragilariopsis curta*, *Fragilariopsis cylindrus*, *Porosira glacialis*, *Actinocyclus actinochilus*, and *Fragilariopsis ritscheri*. The sea ice group is largely dominated by *F. curta* with 1–4.6% relative abundance of the total diatom assemblage during the LGM and the part of MIS 3. An increase in sea ice diatom abundance is evident at mid-MIS 3, and thereon, higher abundances were observed till the end of LGM (Figure 3a). Highest abundances of sea ice diatoms (~2.5–5%) were recorded between 38 and 20 ka B.P., followed by a decline during the last deglaciation and HS1 interval. No sea ice diatoms were observed during MIS 1 (Figure 3a).

4.1.2. Permanent Open Ocean Zone Diatom Group

POOZ diatoms are the dominant group throughout the core having relative abundances of 58–96%. The POOZ diatom group is mainly composed of eight species, namely, *Fragilariopsis kerguelensis*, *Thalassiosira lentiginosa*, *Thalassiosira gracilis*, *Thalassiothrix spp.*., *Thalassiosira oliverana*, *Fragilariopsis rhombica*, *Trichotoxon reinboldii*, and *Fragilariopsis separanda*. The dominant species in the group are *Fragilariopsis kerguelensis* (50–85%) and *Thalassiosira lentiginosa* (10–50%), while the remaining species accounts for less than 5% of the total assemblage. The relative abundance of POOZ diatoms varied from 80 to 96% between MIS 3 and MIS 2 and later on decreased sporadically starting from the last deglaciation and into the late MIS 1 (Figure 3b). The average relative abundances of POOZ diatoms during MIS 1 were the lowest (~78%) within the core. However, variation of POOZ diatoms within MIS 1 displayed higher abundance values (80–90%),

![Figure 3](figure3.png)

**Figure 3.** Variations in relative percentage (%) of diatom species or species groups from Sk 200/22a. (a) Sea ice diatom group (%), (b) permanent open ocean zone diatom group (%), and (c) Sub-Antarctic Zone diatom group (%).

<table>
<thead>
<tr>
<th>Table 2. Summary of Diatom Groups From the Core SK 200/22a</th>
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<tr>
<td><strong>POOZ Diatom Group</strong></td>
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<tr>
<td><em>Fragilariopsis kerguelensis</em></td>
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<tr>
<td><em>Thalassiosira lentiginosa</em></td>
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<td><em>Thalassiosira gracilis</em></td>
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<td><em>Thalassiothrix spp.</em></td>
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<tr>
<td><em>Thalassiosira oliverana</em></td>
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<tr>
<td><em>Fragilariopsis rhombica</em></td>
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<tr>
<td><em>Trichotoxon reinboldii</em></td>
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<td><em>Fragilariopsis separanda</em></td>
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grey bands) between ~13.4–12.5 ka B.P., 11–9.7 ka B.P., and 8.7–7.3 ka B.P., followed by a decreasing trend up to ~4.1 ka B.P. (Figure 4a). During the late MIS 1 (4.1–2.1 ka B.P.), an increase in the POOZ diatom abundance was observed, where the values peaked up to ~85%. The average abundances were higher, varying between 88.4% and 85.1% during MIS 3 and early MIS 2, respectively. In general, the POOZ diatoms were more abundant during glacial period relative to interglacial period.

4.1.3. Sub-Antarctic Zone Diatom Group
This diatom group is composed of four species/species group Azpeitia tabularis group, Thalassiosira oestrupii, and Thalassionema nitzschioides var. lanceolata. Amongst SAZ diatoms, the Azpeitia tabularis group is dominant throughout the core. Variation of relative abundances of the SAZ group displayed an increasing trend toward the end of the last deglaciation (19%), and relatively lower abundances, varying between 1 and 10%, were observed during LGM and MIS 1 (Figure 3c). Similarly, average abundances of this group were higher during the last deglaciation (10.56%), and comparatively lower average abundance of SAZ diatoms was observed during MIS 3 (6%), early MIS 2 (6%), and MIS 1 (5%).

4.2. Variations in Total Diatom Concentration for the Last 42,000 Years
Diatom abundance varied considerably from late MIS 3 to MIS 1. In MIS 3, diatom abundance escalated from 1–4 × 10^8 valves/g in early MIS 3 (~42–38 ka B.P.) up to 5 × 10^8 valves/g in late MIS 3 (Figure 4a). Highest abundance of diatoms (6.7 × 10^8 valves/g) was found during LGM, which was succeeded by an abrupt decrease in abundance toward 0.98 × 10^8 valves/g during the last deglaciation. Within MIS 1, an increase in diatom abundance from 8.7 × 10^7 to 4.5 × 10^8 valves/g was seen from ~11.5 to 8.7 ka B.P. (early Holocene), which preceded the highest diatom abundance (~4.6–5.5 × 10^8 valves/g), found between ~4 and 2.1 ka B.P. (late Holocene) (Figure 4a). Relatively lower diatom concentration (1–2 × 10^8 valves/g) was found during mid-Holocene (8.3–4.3 ka B.P.) (Figure 4a). For the last ~42 ka B.P., the variation in absolute abundances of F. kerguelensis and T. lentiginosa largely imitates the diatom absolute abundance trend, suggesting the dominance of these species in total diatom assemblages (Figure 4). Within MIS 1, higher values of diatom absolute abundance between 12.8 and 8.7 ka B.P. (early MIS 1) are consistent with the increased abundance of POOZ diatoms during these intervals. However, the distinct high value peaks in diatom absolute abundance at ~4 and 2.1 ka B.P. are not completely in phase with POOZ diatom peaks (at 3 and 2.1 ka B.P.), but both records display an increasing trend during the late Holocene intervals, wherein the increase in POOZ diatoms lags the diatom absolute abundance (Figure 4a).

4.3. Glacial-Interglacial Variation in Diatom Valve Sizes
Higher values (>44 μm) of F. kerguelensis apical length were observed from the mid-MIS 3 up to the late part of the LGM (Figure 4c). These higher values during glacial period were followed by an abrupt decrease during the HS1 interval and thereon displayed lower values (<44 μm) during MIS 1. The F. kerguelensis
abundance record closely followed the apical length data, displaying increased abundance during the period (glacial) of larger valve sizes (Figure 4c). Similarly, abundance and size (radius) records of *T. lentiginosa* displayed higher values during the glacial period (late MIS 3 up to LGM) (Figure 4b). A positive size-abundance relation in *F. kerguelensis* and *T. lentiginosa* was observed for the last ~42 ka (Figure 5).

Within MIS 1, higher values of *T. lentiginosa* abundance and radius were observed between 12.8 and 8.7 ka B.P. (early MIS 1) with distinct high value peaks at ~4 and 2.1 ka B.P. (Figure 4b). Variation of *F. kerguelensis* absolute abundance and apical length showed higher values between 12 and 8.3 ka B.P. (early Holocene) and late Holocene (4–2.1 ka B.P.) (Figure 4c). Comparison of P00Z diatom records with that of *F. kerguelensis* and *T. lentiginosa* sizes and abundance revealed some inconsistencies throughout the MIS 1. However, higher values of *F. kerguelensis* and *T. lentiginosa* sizes and abundance during early Holocene are still comparable with the increased abundance of P00Z diatoms between 11 and 7.3 ka B.P. Moreover, P00Z diatoms display a decreasing trend from 7.3 to 4.1 ka B.P., during which abundances and sizes of *F. kerguelensis* and *T. lentiginosa* were lower. An increase in the P00Z diatoms and *F. kerguelensis* size/abundance records is observed from ~4.3 to 2.1 ka B.P., whereas the increase in *T. lentiginosa* size/abundance during this interval leads the P00Z diatoms records by ~0.3–0.8 ka B.P.

There is a remarkable agreement between the size variability observed in *F. kerguelensis* and *T. lentiginosa*, as the average size curves shown in Figures 4b and 4c have a very similar variability pattern. The average length of *F. kerguelensis* during glacial period is 45 μm, while for MIS 1 interglacial it is 37 μm, (Table 3). Similarly, *T. lentiginosa* has an average radius of 26 μm during glacial period and 23 μm for MIS 1 (Table 3). In general, these two diatom species have substantially larger valves during glacial period as compared to interglacial period. This is also evident from the box and whisker plot (Figure 6) displaying larger *F. kerguelensis* apical length and *T. lentiginosa* radius during MIS 2 and MIS 3 compared to interglacial stage (MIS 1). Additionally, during MIS 2 *F. kerguelensis* and *T. lentiginosa* have a large size range of 15 μm (37.2 to 51.5 μm) and 8 μm (22.2 to 30 μm), respectively, indicating major variability in diatom sizes during this period (Figure 6).

### Table 3. Results of One-Way ANOVA Test Conducted for *F. kerguelensis* Apical Axis Length and *T. lentiginosa* Radius

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<tr>
<th>Groups</th>
<th>Average</th>
<th>F</th>
<th>P Value</th>
<th>F Crit</th>
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<tr>
<td></td>
<td>Glacial-Interglacial Comparison of <em>F. kerguelensis</em> Apical Length</td>
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<tr>
<td>MIS 1</td>
<td>37.01992</td>
<td>173.5767</td>
<td>1.0085E–24</td>
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<tr>
<td>MIS 2–3</td>
<td>45.15462</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Glacial-Interglacial Comparison of <em>T. lentiginosa</em> Radius</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>MIS 1</td>
<td>23.0464</td>
<td>88.40412</td>
<td>7.37E–16</td>
<td>3.925</td>
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<tr>
<td>MIS 2–3</td>
<td>25.96749</td>
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Figure 5. Correlation between *F. kerguelensis* average apical length and absolute abundance and *T. lentiginosa* average radius and absolute abundance.
The results of one-way ANOVA for *F. kerguelensis* lengths reveal that *F. kerguelensis* apical lengths were significantly different between glacial (MIS 2 + MIS 3) and interglacial period (MIS 1) \((P < 0.05)\) (Table 3). Similarly, a statistical difference \((P < 0.05)\) in *T. lentiginosa* radii was observed between glacial and interglacial periods (Table 3).

5. Discussion

5.1. Evidence for Glacial-Interglacial Migration of Fronts and Sea Ice Extent

The present study reveals higher abundance of sea ice zone diatom at the core site SK 200/22a during LGM and late MIS 3 (Figures 7b and 8h), probably due to the northward shift of Antarctic winter sea ice extent into...
the modern PFZ (Figure 9b). Contrastingly, reduced sea ice diatom abundance during the modern condition (interglacial period) and last deglaciation at the core site suggests retreating winter sea ice extent (Figures 9a and 9c). Our sea ice diatom records are consistent with the sea ice extent reconstruction by Crosta et al. [2004] from the eastern Indian sector of the Southern Ocean (Figures 7a and 7b), supporting a northward shift in the winter sea ice limit during glacial periods. Our hypothesis of an expanded winter sea ice limit (up to the modern-day PFZ) during LGM is in agreement with earlier studies on LGM sea ice reconstruction [CLIMAP, 1976, 1981; Cooke and Hays, 1982; Crosta et al., 1998; Gersonde et al., 2003, 2005]. The closest match of our data was with the results of the recent circum-Antarctic compilation [Gersonde et al., 2005], suggesting a nearly 10° latitudinal shift in winter sea ice limit to the north of the modern APF during LGM in the western Indian sector of the Southern Ocean (including the core site).

The IRD record was also studied in conjunction with the sea ice diatoms to understand the glacial-interglacial variability of the Antarctic sea ice extent and ice rafting events (Figures 7b and 7c). IRD deposition, which is related to increased production of icebergs and/or increased survival of icebergs and sea ice in the region [Manoj et al., 2013], was significantly high during the last deglaciation and occasionally during late MIS 3 (Figure 7c). During the LGM, sea ice extent in the Southern Ocean seems to have significantly expanded and the subsequent early deglacial warming leads to the increased sea ice melting and ice rafting, depositing

Figure 8. Glacial-interglacial variation of (a) diatom absolute abundance (valves/g), (b) SAZ diatoms, (c) POOZ diatoms, (d) European Project for Ice Coring in Antarctica Dome C dust flux [Lambert et al., 2008], (e) Fe mass accumulation rate [Martinez-Garcia et al., 2011], (f) F. kerguelensis average apical axis length (μm), (g) T. lentiginosa average radius (μm), (h) sea ice diatom group (%), and (i) global sea level relative to present [Bintanja et al., 2005].
the IRD to the core site [Manoj et al., 2013]. However, during early MIS 3 and MIS 1 there was a decline in IRD concentration, consistent with sea ice diatom records, suggesting a decreased sea ice extent during those times (Figure 7c).

Higher abundance of POOZ diatoms during the MIS 3 and LGM (Figure 7d) hints at a possible extension of POOZ into the modern PFZ (near to/north of the core site) (Figure 9b). This strengthens the argument that the expansion of winter sea ice limit in the Southern Ocean was accompanied by a northward shift of the APF during glacial periods in the Indian sector. Similarly, earlier studies [Dezileau et al., 2003; Gersonde et al., 2005; Manoj et al., 2013] have reported a 5–10° northward shift of APF in the Indian sector of the Southern Ocean during LGM, supporting the proposed glacial expansion of POOZ. The lower abundance of POOZ diatoms during MIS 1 (Figure 7d) is possibly an indication of southward shifts in POOZ along with APF. However, higher POOZ diatom abundance during 11–9.7 ka B.P., 8.7–7.3 ka B.P., and 3–2.1 ka B.P. interval argues for a northward shift of APF possibly up to ~45°S, 50–45°S, and ~45°S, respectively (Figure 4a). These assumptions are mostly consistent with the studies of Katsuki et al. [2012] from the Indian sector of the Southern Ocean revealing the northward shift of APF up to ~45°S (10 ka B.P.), ~47°S (7 ka B.P.), and ~45°S (3 ka B.P.) during Holocene. The northward shifts and retreats of APF during the Holocene are of shorter duration and not comparable to the glacial shifts in the fronts.

Sub-Antarctic Zone diatoms mark the proximity of STF and SAF: An increase in their abundance at the core site, currently located under the modern-day PFZ, during the last deglaciation (Figures 7d and 7e), is probably an indication of southward shift in SAF, thereby expanding the SAZ into the modern-day PFZ during these times (Figure 9c). The southward expansion of the SAZ is additionally supported by decreasing POOZ conditions at the core site during the last deglaciation as indicated by decreases in abundance of POOZ diatoms. Lower abundances of SAZ diatoms during MIS 1, LGM, and MIS 3 (Figure 7e) could be a result of a more northerly position of the SAZ as compared to the last deglaciation. A recent study [Gersonde et al., 2005] has suggested that in the western Indian sector of the Southern Ocean including the core site, there could have been a northward expansion of SAZ during LGM, primarily due to northward shift of STF, with no major changes in SAF position. These details are well discussed by Romero et al. [2015] suggesting that the STF is at its northernmost position during early and middle stages of full glacial and it starts to shift southward rightly before glacial terminations, allowing increased leakage through Indian Ocean surface flow. The average abundances of SAZ diatoms are almost similar during MIS 1 and LGM, thereby recording no major southward shifts in SAZ and SAF during these periods.

**Figure 9.** Schematic diagram showing the glacial-interglacial shifts in sea ice extent and frontal system in the Indian sector of Southern Ocean.
5.2. Enhanced Diatom Productivity During Glacial Period

The variation of diatom absolute abundance for the last ~42 ka B.P. is largely comparable to the total organic carbon and opal records [Manoj, 2014], suggesting a significant increase in diatom productivity during the LGM and late MIS 3 specifically. The highest diatom abundance during LGM is also consistent with high export production [Kumar et al., 1995; Martinez-Garcia et al., 2011] and opal productivity [Dezileau et al., 2003], supporting the notion that the Southern Ocean north of the APF was characterized by an increase in biological productivity as opposed to the Antarctic zone. The increased diatom abundance during LGM and late MIS 3 is correlatable with higher dust flux recorded in the EDC ice core from Antarctica [Lambert et al., 2008] and Fe mass accumulation rate (MAR) in the ODP site 1090 sediment core from the Atlantic sector of the Southern Ocean [Martinez-Garcia et al., 2011] (Figures 8a, 8d, and 8e). The high abundance of diatoms specifically during LGM and late MIS 3 is believed to have promoted an increase in NO\textsubscript{3}:Si(OH)\textsubscript{4} and CO\textsubscript{2aq}:Si (OH)\textsubscript{4} uptake ratio and C\textsubscript{org}:BSi and N\textsubscript{org}:BSi storage ratio by diatoms in response to iron fertilization in the Indian sector of the Southern Ocean [Crosta et al., 2005; Beucher et al., 2007]. The only mismatch between diatom abundance, dust, and Fe MAR was observed during MIS 1, for reasons which will be discussed later in this section. The locations for which reference data are available (EDS dust flux and ODP site 1090 Fe MAR) are far apart from the core site and may thus not necessarily capture all the intricacies and variability at the core site. Hence, the role of iron-bearing dust on total diatom abundance at our core site is still questionable despite the similar variability pattern between EDC dust flux, Fe MAR (ODP site 1090), and diatom abundance records.

POOZ diatom relative abundances and diatom absolute abundances are coupled during MIS 2, late MIS 3 (~35 ka B.P.), and partially during MIS 1 (Figures 8a and 8c). This implies that during MIS 2 and late MIS 3, the expansion of the POOZ to the present core site could have provided nutrient-replete conditions and probably stimulated diatom abundance during these periods. This assumption is also supported by the increase in sea ice extent during glacial periods, as evident from the sea ice diatom records, again suggesting a northward displacement of the modern-day nutrient-replete Antarctic zone into the study area during the glacial periods. The greater supply of nutrients from Antarctic zone to the north of APF during glacial period could also reflect the lower nutrient utilization (or unused nutrients) in Antarctic zone [Anderson et al., 2014].

The situation seems to be different during last deglaciation, when a retreat of POOZ conditions to the south of the core site and southward shift of SAZ (toward the core site) could have led to the warming and stratification of upper water column; this is well reflected in the absolute abundance record, displaying lower values. The synchronicity between the timings of changing SAZ diatoms, POOZ diatom, sea ice diatoms, and diatom absolute abundance records (Figures 8a–8c and 8h) argues for the possible control of shifting SAZ, POOZ, and APF on diatom productivity in the past.

As the study area is close to Crozet Island, the lowered sea level during glacial periods [Bintanja et al., 2005] (Figure 8i) might have exposed large portions of the continental shelf around these islands, resulting in increased shelf to slope lithogenic material (and associated micronutrients) transport [Romero et al., 2012]. In addition, stronger glacial winds, and northward shifts in both the westerly wind system [Moreno et al., 1999] and ACC [Dezileau et al., 2000], might have stimulated wind-induced shallow water erosion around these oceanic islands. These processes would have fuelled higher Fe and micronutrient input to the core site during glacial period [Dezileau et al., 2003; Mazaud et al., 2007, 2010; Manoj et al., 2012], thus promoting the rise in diatom abundance.

Within MIS 1, the increasing trend in diatom absolute abundance (few intervals) despite the extremely low values in EDC dust flux and ODP site 1090 Fe MAR (Figures 8a, 8d, and 8e) suggests the presence of an alternate mechanism which might have brought macronutrients/micronutrients to the study area. The rise in diatom abundance around early and late Holocene is believed to be governed by local processes rather than aeolian dust deposition. During the early and the late Holocene, there are evidences of possible northward shift of APF (as discussed in section 5.1); this opens up the possibility of expanding POOZ to the present core site, thereby favoring the rise in diatom concentration. Under present conditions, the waters north of Crozet Islands are enriched with iron-rich sediment derived from water circulating at the shallower depths of Crozet Islands [Pollard et al., 2007; Venables et al., 2007]. This natural iron fertilization is known to fuel the annual phytoplankton bloom dominated by diatoms in the region [Seeyave et al., 2007] and could possibly offer a mechanism for the enhanced diatom abundance during the late MIS 1.
5.3. Diatom Valve Size Variation During Last Glacial-Interglacial Cycle

The valve size variation for the past ~45 ka B.P. revealed how average valve sizes of *F. kerguelensis* and *T. lentiginosa* are positively correlated to their respective abundance, wherein larger valve sizes are observed when the abundance of these species is higher (during LGM and mid-MIS 3). Under the modern conditions, with similar sedimentary distribution, *F. kerguelensis* and *T. lentiginosa* tend to decrease in abundance to the south of the maximum winter sea ice limit (lower ecological limit) and to the northern PFZ (upper ecological limit) [Crosta et al., 2005]. The positive size-abundance relationship is related to the fact that the core site is located today at the upper ecological limit for *F. kerguelensis* and *T. lentiginosa*. In the northern region of PFZ, more adequate environmental conditions during cooler glacial period for *F. kerguelensis* and *T. lentiginosa* probably allowed the restoration of initial cells and overall larger average size. Recent studies by Cortese et al. [2012] have revealed a positive response of *F. kerguelensis* valve area to the aeolian dust input in the Atlantic sector of the Southern Ocean over the past several glacial terminations. Likewise, larger diatom sizes from our study are associated with increased EDC dust flux and ODP site1090 Fe MAR during late MIS 3 and LGM and followed by a decreasing trend from the last deglaciation to MIS 1 (Figures 8d–8g), probably suggesting a control of Fe-bearing dust on diatom sizes. However, the linkages between Fe-bearing dust and diatom sizes from the Southern Ocean still remain hypothetical and need further studies; moreover, other factors such as changing SSTs and nutrient conditions may also have a control on diatom sizes [Cortese et al., 2012]. Furthermore, during alleviation of iron limitation (MIS 2) an increase in carbon and nitrogen uptake leads to enriched values of δ¹³C and δ¹⁵N in diatoms from PFZ [Hutchins and Bruland, 1998; Beucher et al., 2007; Crosta et al., 2005]; this also possibly explains the larger sizes of *F. kerguelensis* and *T. lentiginosa* during glacial periods. Significantly, there is a similarity in the variation of *F. kerguelensis* and *T. lentiginosa* abundance and size with total organic carbon and opal records [Manoj, 2014] for the last 42 ka. This suggests that *F. kerguelensis* and *T. lentiginosa* were the main carriers of biogenic silica and organic carbon to the seabed in the northern PFZ of the Indian sector of the Southern Ocean. So considering our size/abundance records and the estimates of diatom bound δ¹³C, δ¹⁵N, and δ³⁰Si from SAF core MD88-769 from the Indian sector [Beucher et al., 2007; Crosta et al., 2005], we can infer that increased size and abundance of *F. kerguelensis* and *T. lentiginosa* are associated with greater uptake of NO₃⁻ and organic carbon relative to Si(OH)₄ during glacial period.

The glacial-interglacial variations in *F. kerguelensis* length and *T. lentiginosa* radius follow closely the pattern observed in the abundances of POOZ and sea ice diatoms, (Figures 8c and 8f–8h), suggesting an affinity of larger *F. kerguelensis* and *T. lentiginosa* sizes for cooler SSTs and higher nutrient availability as a result of a northward shift of the APF. Our results are similar to those presented in Cortese et al. [2012] revealing an inverse correlation between valve size of *F. kerguelensis* and SST for past several glacial terminations. In coastal Antarctica, longer *F. kerguelensis* valves during warm as opposed to cool intervals were linked to improved environmental conditions (during warm intervals) that moved this species away from its lower ecological limit in terms of sea ice and SST [Crosta, 2009]. Likewise, we speculate that in the Indian Ocean sector of the Southern Ocean north of the APF, relatively smaller valve sizes during MIS1 are due to the conditions (mainly SST) close to/beyond the upper ecological limit of the species, as also suggested by Shukla et al. [2013]. Within MIS 1, northward position of APF during few intervals of early and late Holocene may have relieved *F. kerguelensis* from warmer SSTs; hence, minor increase in *F. kerguelensis* apical length was observed.

The length of *F. kerguelensis* at our core site is longer than that found in any other sector of the Southern Ocean, a result which is consistent with Shukla et al. [2013]. Similarly, larger valve sizes of *F. kerguelensis* from surface sediment studies were reported in the West Indian Ocean sector of the Southern Ocean, close to the present study area [Cortese and Gersonde, 2007]. The longer apical length of *F. kerguelensis* in the present study compared to other sectors of the Southern Ocean [Shukla et al., 2013] is probably due to the following: (1) the proximity of the core site to the Crozet Island, where natural and continuous iron fertilization occurs through the “island mass effect” phenomenon [Planquette et al., 2007], and (2) an increase in the intensity of the ACC during glacial periods, which might in turn have increased the island mass effect, thereby fuelling the increase in *F. kerguelensis* apical length.

In the present study the positive response of *T. lentiginosa* to aeolian dust/Fe input is at odds with previous studies on *T. oceanica*, which shows a limited dependency on iron availability [Strzepek and Harrison, 2004; Peers and Price, 2006]. *T. oceanica* is an open ocean species of the genus *Thalassiosira* and has its iron-requiring electron transport...
protein replaced with equivalent ones that need copper instead [Strzepek and Harrison, 2004; Peers and Price, 2006], thereby reducing its iron requirement. Moreover, centric and pennate diatoms have different iron-storing ability and iron-acquiring system in the open ocean, where the Fe supply is usually more sporadic in nature [Jickells et al., 2005; Kustka et al., 2007; Allen et al., 2008]. Nevertheless, detailed study on T. lentiginosa (especially in open ocean settings away from continental iron sources) is imperative to ascertain the response of centric diatoms to iron supply or their affinity for other micronutrients.

6. Conclusions

Based on a diatom record obtained from the Indian sector of the Southern Ocean, we have qualitatively reconstructed the glacial-interglacial variation of Antarctic sea ice extent and frontal systems at site SK 200/22a. Further, we also analyzed the influence of glacial-interglacial changes in environmental variables on diatom abundance and size variation. The results can be summarized as follows:

1. During the LGM and late MIS 3, the present-day ice-free PFZ of the Indian sector of the Southern Ocean was seasonally influenced by winter sea ice. Subsequently, during MIS 1 there was a retreat of the winter sea ice limit to the south of the modern-day PFZ.

2. The relative abundance of POOZ diatom groups also recorded this northward shift of the APF during the glacial period and parts of MIS 1. No major shift in the position of the SAF was recorded during glacial period compared to the present interglacial. Contrarily, during the last deglaciation, a possible southward shift of SAF was recorded, wherein it was positioned close to/south of the present study area.

3. The present core site was characterized by higher diatom productivity during glacial periods (LGM and late MIS 3). This is largely a result of a northward expansion of the circum-Antarctic upwelling belt and/or opal belt, providing nutrient-replete conditions at the core site. Additionally, enhanced glacial terrigenous input from the nearby Crozet islands, as a result of stronger glacial flow of the ACC, probably contributed micronutrients and macronutrients to the study area, thus further promoting an increase in diatom abundance.

4. The valve size variability of two diatom species (F. kerguelensis and T. lentiginosa) from the PFZ (core SK 200/22a) over the last 42 ka B.P. revealed a close association of larger diatom sizes for cooler SSTs (glacial period) and higher nutrient availability (due to the northward shift of the APF) during LGM and late MIS 3. During MIS 1, an increase in SST, along with the southernmost position of the APF (most parts of the MIS 1), could have played a vital role in lowering diatom sizes. The proximity of the core site to the Crozet Islands is speculated to be the reason for the larger diatom sizes in the present study as compared to available results from other sectors of the Southern Ocean. For the past 42 ka, highly silified diatoms such as F. kerguelensis and T. lentiginosa possibly contributed in transporting biogenic silica and organic carbon to the seabed, in the northern PFZ of the Indian sector of the Southern Ocean.

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