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Extensive phytoplankton blooms in the Atlantic sector of the glacial Southern Ocean

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[1] The sources and sinks of atmospheric carbon dioxide over glacial/interglacial cycles are under debate. Variation in productivity of the Antarctic Circumpolar Current (ACC) could potentially play a significant role, but current interpretations of sedimentary geochemical proxies suggest that glacial productivity was not higher than today. We present areal and down-core distribution patterns of previously overlooked diatom resting spores that indicate the occurrence of extensive phytoplankton blooms across the entire Atlantic sector of the ACC, particularly in the seasonal ice zone (SIZ), linked to higher iron input during the last glacial. Sea ice acts as an effective transporter of iron and enhances its bioavailability. The dominance of the deep living radiolarian *Cyladophora davisiana* in glacial SIZ sediments indicates that organic carbon export to mesopelagic depths was at least tenfold higher than today.

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1. Introduction

[2] Atmospheric CO_2 concentrations exhibit a repetitive pattern of gradual decline (to 180 ppm) and rapid increase (to 280 ppm) over the last four climate cycles that is correlated with temperature and dust deposition over Antarctica [*Petit et al.*, 1999]. Sources, sinks and regulatory mechanisms of the CO_2 are currently under debate and variation in productivity of the Antarctic Circumpolar Current (ACC) is suggested to play a significant role [*Sigman and Boyle*, 2000; *Watson et al.*, 2000]. The contemporary ACC is a weak CO_2 sink despite high nutrient levels because productivity is limited by iron availability [*Falkowski et al.*, 1998; *Boyd*, 2002; *Coale et al.*, 2004]. During glacial periods greater dust-borne iron input should have significantly enhanced productivity and CO_2 drawdown [*Martin*, 1990]. A recent compilation of marine productivity data of the last peak and middle glaciation suggest that iron fertilization could account for up to half of the observed CO_2 drawdown [*Kohfeld et al.*, 2005]. However, the biological and physical processes ruling the productivity and sequestration of carbon in the glacial ocean are not well understood. Information on glacial/interglacial variability and the magnitude of biological productivity and export of organic compounds derived from geochemical proxies is ambiguous because of the complexity of the system [*Sigman and Boyle*, 2000; *Anderson et al.*, 2002]. Current interpretations of these proxies tend to identify higher productivity in the zone north of the glacial winter sea ice edge (POOZ is permanent open ocean zone) but lower productivity in the seasonal ice zone (SIZ) [*Frank et al.*, 2000]. This scenario conflicts with ecological predictions based on current understanding of factors governing productivity of Antarctic phytoplankton and its impact on carbon drawdown [*Moore et al.*, 2000]. Here we present paleobiological proxies indicating higher productivity in the glacial SIZ compared to the Holocene in the Atlantic sector of the Southern Ocean.

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2. Material and Methods

[3] Diatom and radiolarian data are from surface sediments and last glacial sediment core sections collected during R/V *Polarstern* cruises in the Atlantic and Indian sectors of the Southern Ocean between 32° and 72°S (Figure 1). Surface sediment diatom data are from *Zielinski and Gersonde* [1997]. Last glacial (20–16 ka) diatom and *Cycladophora davisiana* data have been extracted from a large data set used to reconstruct last glacial sea surface temperatures and sea ice extent in the Southern Ocean [*Gersonde et al.*, 2003]. Additionally, last glacial *C. davisiana* data of *Hays et al.* [1976] were included in our mapping. Because of the scarcity or lack of biogenic carbonate, the age assignment of the samples used for the mapping of last glacial radiolarian and diatom abundances is based on a combination of the abundance fluctuation of the radiolarian *C. davisiana* and the diatom *Eucampia antarctica* with planktic and benthic oxygen isotope records and AMS ^{14}C measurements of organic carbon extracted from planktic foraminifers, or from the humic acid fraction in diatomaceous ooze samples [*Gersonde et al.*, 2003]. We further studied Core PS1768-8 located in the land-remote Antarctic zone (52°35.6′S, 4°28.5′E, Figure 1), which is 3° north of today's average winter ice edge but was seasonally ice covered during the glacial [*Gersonde et al.*, 2003, 2005]. The PS1768-8 diatom data are from *Zielinski et al.* [1998]. The age model of the

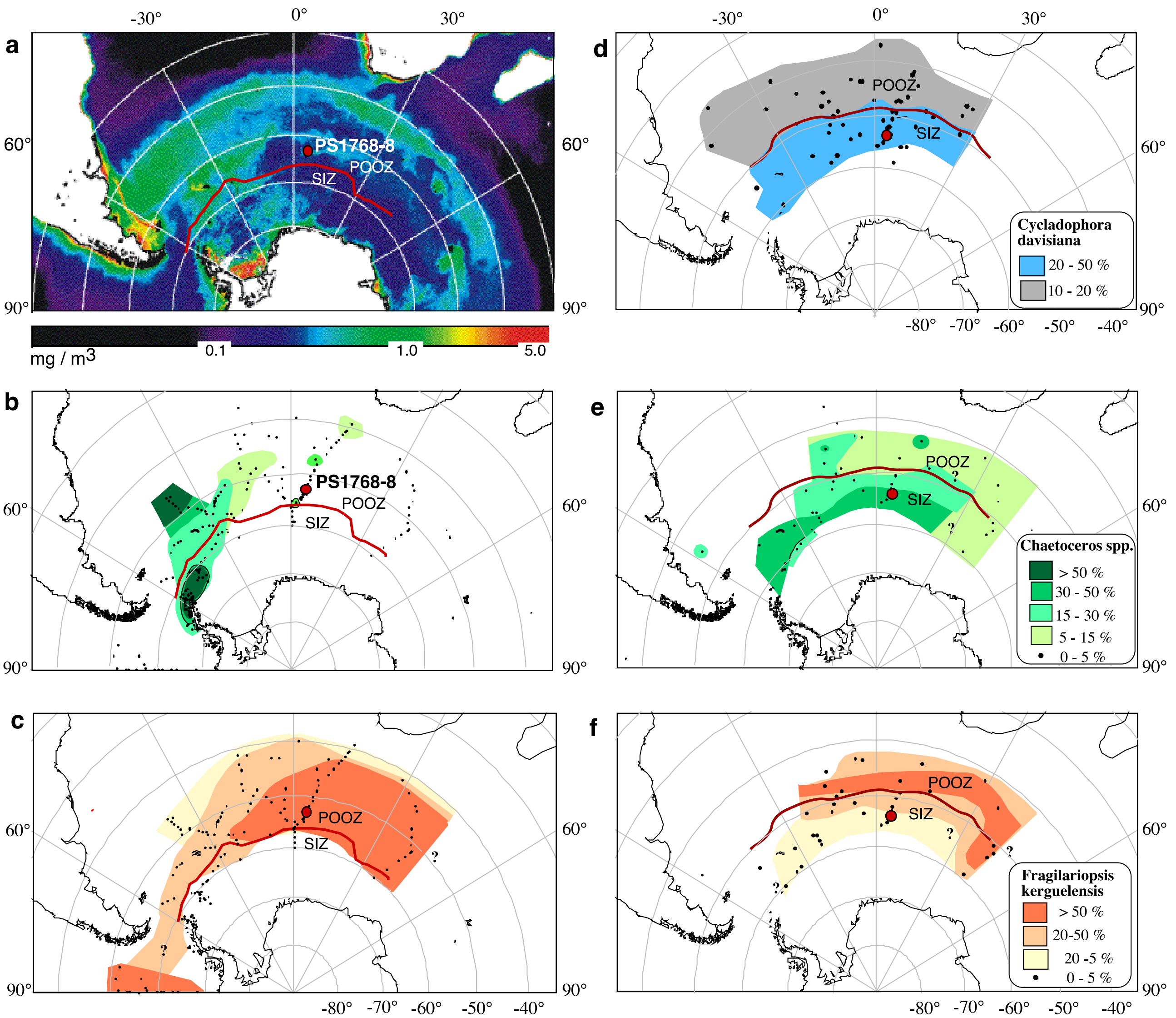


Figure 1. (a) Southern Ocean chlorophyll composite (November 1997 to March 2002) from Sea-viewing Wide Field-of-view Sensor. (b) Percentages of *Chaetoceros* spores in diatom assemblages in surface sediments. (c) Percentages of *Fragilariopsis kerguelensis* in diatom assemblages in surface sediments. (d) Percentages of *C. davisiana* in last glacial radiolarian assemblages from 33 R/V *Polarstern* cores and additional data sets [*Hays et al.*, 1976]. (e) Percentages of *Chaetoceros* spores in last glacial diatom assemblages. (f) *Fragilariopsis kerguelensis* in last glacial diatom assemblages. Only values $>10^7$ diatom valves g^{-1} dry sediment were considered, which excludes areas of strong BSi dissolution such as the Weddell Gyre. The red line indicates the extent of the respective average winter sea ice cover [*Gersonde et al.*, 2005], and the red dot indicates the site of Core PS1768-8 presented in Figure 3. The seasonal ice zone (SIZ) and permanent open ocean zone (POOZ) are also indicated.

core as well as factors for conversion to vertical rain rates (VRR) and supplementary geochemical data are from *Frank et al.* [1996, 2000], and $\delta^{13}C$ data are from G. Fischer (personal communication, 2004). Geochemical sediment composition was determined on freeze-dried and ground subsamples. Total organic carbon (TOC) was measured on Leco Carbon Determinator (CS-125) after removal of carbonate (TIC) with hydrochloric acid. Surface sediment samples were taken with a box corer (BC) or multiple corer (MC). Generally the top 0.5 cm of the sediment surface was removed from two MC tubes (diameter: 6 cm) or from 405 cm^2 area of the BC. Quantitative sample preparation for light microscopy of the sediment samples was done following standard procedures [*Abelmann et al.*, 1999; *Gersonde and Zielinski*, 2000].

3. Significance of the Biological Proxies

[4] The productive regions in the Atlantic sector of the modern Southern Ocean south of 45°S (Figure 1a), reflected

in chlorophyll concentrations >1 mg m^{-3}, are restricted to the continental margins with oceanward extensions off the Patagonian shelf and along the Antarctic Peninsula plume. High export production of particulate organic carbon (40–60 g C m^{-2} yr^{-1}) [*Falkowski et al.*, 1998; *Schlitzer*, 2002] is characteristic for these regions that are subject to iron input via dust and extensive contact with landmasses [*Martin*, 1990; *Mahowald et al.*, 1999; *Elrod et al.*, 2004; *Jickells et al.*, 2005]. In contrast, the land-remote ACC, east of about 15°W and in the eastern Pacific sector, has lower chlorophyll concentrations (<0.2 mg Chl m^{-3}), hence lower productivity and also export [*Schlitzer*, 2002].

[5] Resting spores of small-celled species of the ubiquitous diatom genus *Chaetoceros* (*C. curvisetus*, *C. debilis*, *C. socialis*, *C. neglectus*, *C. simplex*) mirror the productive zones in the underlying sediments, whereas those in the regions of low productivity are dominated by the much larger, vegetative frustules of the pennate diatom *Fragilariopsis kerguelensis* with overlap only in the region where the two zones merge (Figures 1b and 1c). Resistance to dissolution is the only property common to *Chaetoceros* spores and *F. kerguelensis* as the two taxa represent very different ecological and hence biogeochemical regimes which are outlined next.

[6] Much of the new production in iron-rich areas is mediated by episodic phytoplankton blooms dominated by fast growing, weakly silicified diatom genera, including spore-forming species of *Chaetoceros*, (subgenus *Hyalochaetae*) that buildup biomass till nitrate exhaustion [*Smetacek*, 1985]. Their molar silicon:nitrogen demand is about 1 and their thin vegetative frustules dissolve rapidly after death. A well-studied, highly productive area where *Chaetoceros* dominates the diatom assemblages is the Bransfield Strait region, which is characterized by primary production rates of about 1600 mg C m^2 d^{-1} during the austral spring. Highest organic carbon fluxes (144 mg C m^2 d^{-1}) here are strongly coupled with high *Chaetoceros* abundances (60 to 80%) [*Gersonde and Wefer*, 1987; *Wefer et al.*, 1988; *Abelmann and Gersonde*, 1991; *Leventer*, 1991]. The percentage of vegetative cells converted into spores varies and increases following nutrient exhaustion, which also induces mass sinking of the bloom [*Smetacek*, 1985; *Leventer*, 1991]. In the bloom aftermath, vegetative cells, spores and phytodetritus clump into rapidly sinking aggregates [*Smetacek*, 1999] that gather as fluffy layers on the seafloor, even at abyssal depths [*Beaulieu*, 2002]. These blooms are the major component of the biological carbon pump, which sequesters carbon in the ocean interior [*Smetacek*, 1999; *Smetacek et al.*, 2004]. The small, thick-walled, grazer-resistant *Chaetoceros* spores represent an effective survival strategy ensuring substantial presence in virtually all diatom blooms [*McQuoid and Hobson*, 1996]. Because *Chaetoceros* spores preserve better than the thin-walled cells of vegetative *Chaetoceros* and other diatoms, they often dominate the sedimentary diatom assemblages underlying productive regions, e.g., open ocean areas such as the temperate and polar North Atlantic [*Schrader and Koc Karpuz*, 1990] and land near Southern Ocean regions [*Crosta et al.*, 1997; *Zielinski and Gersonde*, 1997] (Figure 1). These are regions of major organic carbon export but of lower biogenic silica deposition [*Lisitzin*, 1985; *Falkowski et al.*, 1998]. Hence the spores are robust indicators of presence or absence of high-carbon, low-silica exporting phytoplankton blooms.

[7] In contrast, *F. kerguelensis* is a prominent member of the sparse, large-celled, heavily silicified diatom assemblage (Si:N ratios 2–6) characteristic of the iron-limited ACC [*Smetacek*, 1999]. *Fragilariopsis kerguelensis* reaches peak abundance in the permanent open ocean zone (POOZ) of the ACC south of the Polar Front [*Zielinski and Gersonde*, 1997; *Smetacek et al.*, 2004; *Fischer et al.*, 2002]. Its distribution to the north appears constrained by low silica concentrations and to the south by the SIZ [*Zielinski and Gersonde*, 1997]. The thick, strong frustules of *F. kerguelensis* are suggested to have evolved as protection against grazing, ensuring long-term persistence in the surface layer [*Hamm et al.*, 2003]. They preserve very well in the sediments and contribute the bulk of siliceous ooze accumulating under the ACC. Indeed the highest biogenic silica accumulation rates coincide with highest *F. kerguelensis* densities in surface sediments [*Zielinski and Gersonde*, 1997]. Since these regions underlie the least productive areas (Figure 1), it follows that the rate of opal accumulation in the sediments is not a proxy for productivity of the surface water but is actually quite the opposite, largely because of the ecological properties of this species. *Fragilariopsis kerguelensis* responds to artificial and natural (from melting icebergs) iron input by increasing biomass [*Bathmann et al.*, 1997; *Boyd*, 2002] but, although little is known about its fate, there is no doubt that empty frustules reach greater depths than the plasma. Hence *F. kerguelensis* is an indicator of low-carbon, high-silica exporting regimes [*Smetacek et al.*, 2004].

[8] The radiolarian *Cycladophora davisiana* is a dominant member of the radiolarian assemblage in glacial sediments of high-latitude oceans but is scarce throughout its range in the Holocene [*Hays et al.*, 1976]. *Cycladophora davisiana* predominates today only in the Sea of Okhotsk (SOk), regarded as "a modern analogue of climatic and oceanographic conditions" favorable to this species [*Morley and Hays*, 1983]. The SOk is characterized by a seasonal sea ice cover and is highly productive. Estimates of SOk primary production range between 220 g C m^{-2} yr^{-1} [*Sorokin and Sorokin*, 1999] and 450 g C m^{-2} yr^{-1} [*Shuntov*, 2001]. Diatoms, which are important primary producers in the modern SOk are dominated by *Chaetoceros* spores in surface sediments (up to 70%) [*Shiga and Koizumi*, 2000]. *Cycladophora davisiana* is most abundant in the cold (1°–2°C), ventilated SOk Intermediate Water (SOIW) between 200–600 m, generated by brine discharge from sea ice formation on the shelf [*Nimmergut and Abelmann*, 2002; *Abelmann and Nimmergut*, 2005]. The major source of organic carbon to the SOIW stems from the pulse of phytodetritus following the spring bloom that develops in the surface meltwater layer and is terminated by nutrient exhaustion. [*Sorokin and Sorokin*, 1999]. In contrast to other similar highly productive areas (e.g., Bering Sea), the summer biomass in the SOk is dominantly mesopelagic (67%), whereas the summer biomass in the Bering Sea (with similar primary production and biomass as in the SOk but very low *C. davisiana* values) is dominantly epipelagic

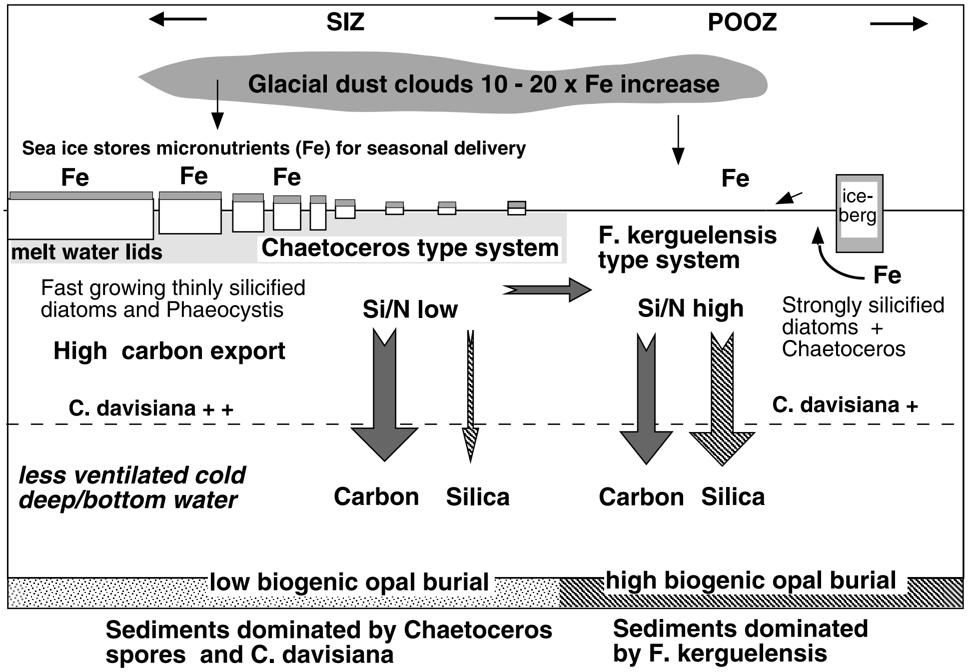


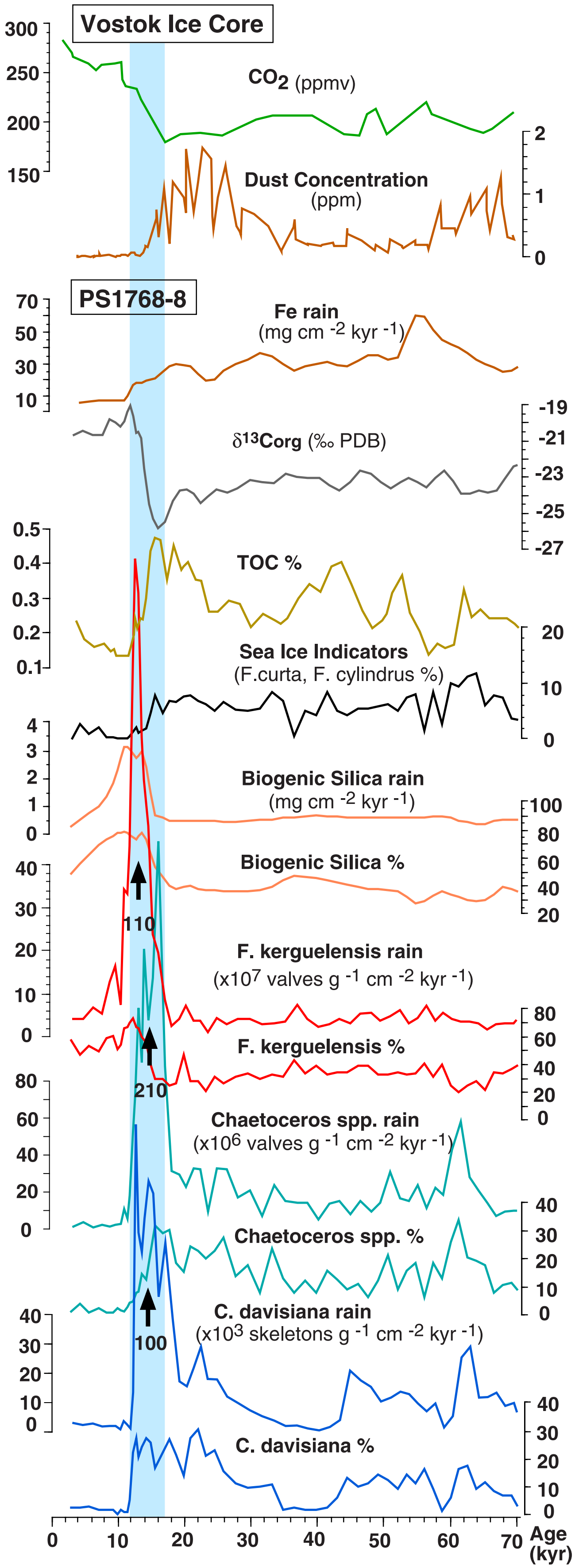
Figure 2. Schematic illustration of the last glacial productivity regimes in the Atlantic sector of the Southern Ocean. In the seasonal ice zone (SIZ), dust deposition and storage on sea ice increases bioavailability of iron that is delivered during spring melting into shallow meltwater lenses providing optimal growth conditions for the *Chaetoceros*-type productivity system composed of fast growing thinly silicified diatoms (e.g., *Chaetoceros* vegetative cells) and nonsiliceous phytoplankton (*Phaeocystis*). This system utilizes more nitrate than silicate. High carbon export efficiency into the cold, less ventilated deep/bottom water is indicated by *C. davisiana* feeding on sinking phytodetritus. *Chaetoceros* resting spores are formed and exported to the seafloor at the end of the productivity season. This leads to high accumulation of *Chaetoceros* spores and *C. davisiana* but low biogenic silica in the sediment record. In the permanent open ocean zone (POOZ), bioavailability of iron is presumably lower than in the SIZ, supplied by upwelling, dust, and melting icebergs, leading to the *Fragilariopsis kerguelensis*–type system dominated by strongly silicified diatoms that export mainly biogenic silica to the sediments. Part of the glacial diatom assemblage is also composed of *Chaetoceros* spores (Figure 1e). This suggests that iron fertilization has also affected the productivity regime in the glacial POOZ resulting in higher carbon export than in the modern system.

(62%) [*Hays and Morley*, 2003]. *Hays and Morley* [2003] estimated an annual mesopelagic faunal consumption of 248 g C m^{-2} yr^{-1}. They concluded that, using the highest estimates for primary production, the export efficiency in the SOk is at least 55% but probably higher. Accordingly, the combination of two factors, the occurrence of a cold and ventilated intermediate/deep water mass and the high export of phytodetritus, is responsible for the high abundances of *C. davisiana* in the SOk; thus the species is an indicator of high carbon export to a cold mesopelagic layer [*Abelmann and Nimmergut*, 2005].

4. Last Glacial Productivity and Export Scenario

[9] Winter sea ice cover in the glacial Atlantic sector was 100% more extensive than present and the ACC cold-water realm south of the Subantarctic Front (SAF) was displaced equatorward by more than 5° of latitude [*Gersonde et al.*, 2005]. *Fragilariopsis kerguelensis* distribution in glacial sediments mirrors this northward shift in hydrographical regime. This is accompanied by a northward displacement of the zone of maximum biogenic opal burial [*Frank et al.*, 2000; *Gersonde et al.*, 2003] while glacial *Chaetoceros* spore distribution is very different, as spores were present in every sample examined, with highest abundances in the SIZ and extending eastward to about 30°E (Figures 1e and 1f). This is robust evidence for the occurrence of episodic carbon-sinking blooms across the Atlantic ACC although their magnitude and frequency will have varied regionally.

[10] The highest bloom frequency can be expected in the SIZ because of its optimal growth conditions: melting sea ice releases snow-settled dust, accumulated over many months, together with algal cells and resting spores into shallow, nutrient-rich, meltwater lenses at the time of maximum solar insolation (Figure 2). Indeed, given the tenfold higher dust input during glacials [*Mahowald et al.*, 1999; *Watson et al.*, 2000] and the enhanced bioavailability of its iron content due to conditioning within snow [*Edwards and Sedwick*, 2001], it is difficult to explain why SIZ blooms will not have been much more extensive



than today. Such blooms are a regular feature of the SIZ along the Peninsula plume and the land near Ross Sea where spore producing *Chaetoceros* species, as also colonies of the haptophyte flagellate *Phaeocystis*, are prominent to dominant [*Hart*, 1942; *Smith et al.*, 1996; *Smetacek et al.*, 2004]. The association between these genera is close because *Phaeocystis* colony formation commonly occurs on *Chaetoceros* spines [*Smetacek et al.*, 2004]. These genera also contribute to open ocean blooms in the northern North Atlantic, the only high-latitude ocean, which, because it is fertilized by African dust [*Mahowald et al.*, 1999], experiences an annual phytoplankton bloom terminated by nutrient exhaustion [*Falkowski et al.*, 1998].

[11] The counterpart of *F. kerguelensis* in modern North Pacific sediments is the morphologically similar *Denticulopsis seminae*, but glacial sediments are more similar to those of the modern North Atlantic where *Chaetoceros* spore abundance is 40–60% [*Sancetta*, 1992]. Strong evidence that iron addition stimulates growth of carbon-sinking blooms in the iron-limited North Pacific comes from a recent in situ iron fertilization experiment, which induced a massive bloom (24 mg Chl m^{-3}) dominated (>90% of biomass) by one of the cosmopolitan spore producing *Chaetoceros* species (*C. debilis*) [*Tsuda et al.*, 2003]. The experiment had to be terminated just as nitrate exhaustion was reached and it is most likely that a significant portion of the bloom subsequently settled out of the surface layer as living cells and spores. We conclude that the glacial productivity scenario can be visualized as a northward displacement of today's silica-sinking POOZ and an eastward extension of the modern carbon-sinking Patagonian and Antarctic Peninsula plumes across the entire Atlantic sector. The areal extent of the zone with *Chaetoceros* spore concentrations between 5% and 50% is equivalent to 14 million km^2 during the glacial, compared to 4 million km^2 today (Figures 1b and 1e).

[12] Support for this scenario is provided by the close similarity between distribution patterns of *Chaetoceros* spores and the radiolarian *Cycladophora davisiana* (Figures 1d and 1e) and also sheds light on the export behavior of the glacial Southern Ocean, assuming that the present-day conditions in the SOk are analogous to those that existed in the last glacial Southern Ocean. In the SOk a much larger proportion of zooplankton biomass is located below the mixed layer and extends well into the mesopelagic zone inhabited by *C. davisiana* [*Nimmergut and Abelmann*, 2002; *Hays and Morley*, 2003; *Abelmann and Nimmergut*, 2005]. It is not known why the vertical distri-

Figure 3. Percentages and vertical rain rates (VRR) of *Chaetoceros* spores, *F. kerguelensis*, *C. davisiana*, diatom sea ice indicators, and total organic carbon (TOC) as well as $\delta^{13}C_{org}$ (G. Fischer, personal communication 2003), iron, and biogenic silica [*Frank et al.*, 2000] for the past 70,000 years from Core PS1768-8 in comparison with dust concentration and CO_2 measured in the Vostok ice core [*Petit et al.*, 1999]. Abundances greater than 3% of the diatom sea ice species *Fragilariopsis curta* and *Fragilariopsis cylindrus* indicate the presence of seasonal sea ice cover [*Gersonde et al.*, 2005].

bution of zooplankton differs so much from the pattern characteristic of all other deep basins but it certainly indicates that the food supply to subsurface layers in the SOk is substantially greater than elsewhere.

[13] Assuming that the size of the *C. davisiana* stock is a function of the food supply, a quantitative estimate of glacial carbon flux can be made by comparison with the SOk. The glacial *C. davisiana* accumulation rates in Core PS1768-8 are about an order of magnitude higher ($10-20 \times 10^4$ specimens cm^{-2} kyr^{-1}) than those in surface sediments of the SOk ($20-80 \times 10^3$ specimens cm^{-2} kyr^{-1}), whereas the vertical rain rates are in the same range ($30-90 \times 10^3$ specimens cm^{-2} kyr^{-1}) (Figure 3) [*Abelmann and Nimmergut*, 2005]. This suggests an organic carbon export in the glacial SIZ that was at least as high as in the SOk today. Comparing the annual mesopelagic faunal consumption in the SOk estimated at 248 g C m^{-2} yr^{-1} [*Hays and Morley*, 2003] with the present-day export flux south of 30°S averaged from modeling results of 27.6 g C m^{-2} yr^{-1} [*Schlitzer*, 2002] and with ^{230}Th-corrected sediment trap data at 700 m depth from the present Antarctic Polar Front of 7.2 g C m^{-2} yr^{-1} [*Rutgers van der Loeff et al.*, 2002], we estimate that the glacial organic carbon export in the SIZ of the Atlantic sector of the Southern Ocean was at least tenfold higher than today.

5. Last Glacial/Interglacial Transition

[14] The transition period from the glacial maximum to the Holocene is marked by sharp peaks in *Chaetoceros* spore and *F. kerguelensis* rain rates that rise steeply and simultaneously around 16–17 ka (Figure 3). *Chaetoceros* spores increase tenfold together with *C. davisiana* that increases fivefold from the glacial average over a period of 3 kyr to decline abruptly to negligible values typical for the Holocene by 13 ka. *Fragilariopsis kerguelensis* rain rates increase twentyfold and peak 3 kyr later than *Chaetoceros* spores, following retreat of the ice cover, to decline to Holocene values that are slightly higher than the glacial average. Biogenic silica (BSi) rain rates largely mirror those of *F. kerguelensis* (Figure 3).

[15] The substantial increases in carbon and silica export during the transition to the Holocene in this area are not accompanied by increasing iron rain rates and are hence likely to have been triggered by enhanced nutrient input to the surface layer associated with a major shift in deep circulation which disrupted the fairly stable, stratified conditions prevailing throughout the preceding 50 kyr in the deep ACC [*Spero and Lea*, 2002]. This fundamental change in ocean ventilation in the glacial SIZ is accompanied by steeply increasing atmospheric CO_2 levels and negative organic carbon isotope signatures obtained from Core PS1768-8 (Figure 3) suggesting that outgassing occurred despite greater carbon export rates because of high nutrient and CO_2 loads in upwelling water exceeding the phytoplankton export. The δ^{13}C minimum event at the termination occurred synchronously in low- and high-latitude areas initiated by the reorganization of thermohaline circulation and North Atlantic Deep Water production [*Spero and Lea*, 2002]. It follows that nutrient concentrations were replete in the SIZ during the termination but substantially lower during the preceding 50 kyr.

6. Discussion

[16] The current debate on glacial ACC productivity seeks to reconcile contradictory information derived from various proxies and models [*Sigman and Boyle*, 2000; *Anderson et al.*, 2002]. The glacial ecological scenario documented by previously overlooked *Chaetoceros* spores can help to resolve the issue by differentiating two types of productivity regimes: high-carbon, low-silica and high-silica exporting zones in the SIZ and POOZ, respectively (Figures 1d–1f). The former regime sequesters C, N and P in the deep water column (Si:N < 1, depending on the contribution of *Phaeocystis*, which lacks Si, to phytoplankton biomass) but buries organic carbon only under reducing conditions, whereas the latter sequesters Si in deep water (Si:N > 3) but also buries a substantial amount as opal [*Fischer et al.*, 2002]. However, iron fertilization via dust, upwelling and icebergs enhanced productivity and carbon export in the glacial POOZ. This is indicated by increased numbers of *Chaetoceros* spores and *C. davisiana* in these sediments (Figures 1b, 1d, and 1e) in comparison to Holocene values as well as by other productivity proxies such as authigenic uranium [*Kumar et al.*, 1995; *Frank et al.*, 2000; *Chase et al.*, 2001; *Anderson et al.*, 2002].

[17] The significantly enhanced organic carbon export in the glacial SIZ suggested by our paleobiological proxies contradicts conclusions reached by previous studies [*Kumar et al.*, 1995; *Francois et al.*, 1997; *Frank et al.*, 2000]. Although glacial SIZ productivity was assumed to be low in these studies, the authors of a recent global ocean compilation of available paleoproductivity results postulate that glacial ocean biology contributed up to half of the observed atmospheric CO_2 reduction [*Kohfeld et al.*, 2005]. However, the assumption of low productivity and export in the glacial SIZ primarily relies on the observation of low biogenic opal accumulation [*Frank et al.*, 2000; *Francois et al.*, 1997], because proxies such as biogenic barium, authigenic uranium, ^{10}Be, and organic carbon, exhibit a locally varying and partly inconsistent pattern in this area. On their own, some of the latter geochemical proxies may be interpreted as indicative of higher biogenic export during the glacial than during the Holocene, but it cannot be excluded that these signals may be biased by diagenetic and chemical processes (e.g., related with changes in oxygen content of bottom and pore waters) during and after deposition [*Kumar et al.*, 1995; *Frank et al.*, 2000; *Anderson et al.*, 2002]. In Core PS1768-8, Ba_{bio} remobilization during the last glacial caused by reducing suboxic conditions can be traced by the simultaneous deposition of authigenic uranium [*Frank et al.*, 2000], a relationship described earlier by *McManus et al.* [1999]. Enrichment of authigenic uranium and ^{10}Be in glacial SIZ sediments has been explained by sediment focusing and scavenging of detrital particles (e.g., Fe) so far, but can be also interpreted as indicative of higher export of organic matter [*Kumar et al.*, 1995; *Francois et al.*, 1997; *Frank et al.*, 2000]. The latter interpretation is consistent with our results, which show that silica and carbon fluxes

are decoupled and that high glacial carbon fluxes are accompanied by low silica fluxes (Figure 3). Thus our biological proxies provide further evidence that changes in opal flux cannot be directly translated into changes in the export of organic carbon, as has been concluded from other investigations [*Kumar et al.*, 1995; *Francois et al.*, 1997].

[18] It should be pointed out that Core PS1768-8 is located in the Holocene POOZ, but at the outer edge of the glacial SIZ (Figure 1) hence likely to be influenced by meandering of the front. Thus the rain rates of both *Chaetoceros* spores and *F. kerguelensis* are high but a negative correlation is not apparent (Figure 3). We speculate that the core site was subject to multiyear, local oscillations in the extent and magnitude of winter sea ice, with high *F. kerguelensis* rain rates in the ice-free periods and *Chaetoceros* spores in the ice-covered ones. Such short-term oscillations cannot be resolved in the bioturbated cores of the ACC.

[19] Information on the nutrient status of the last glacial Southern Ocean is scanty [*Francois et al.*, 1997; *Elderfield and Rickaby*, 2000; *Rosenthal et al.*, 2000; *Brzezinski et al.*, 2002]. Lower glacial phosphorus utilization in the SIZ reconstructed from the Cd/Ca ratio of planktic foraminifera, is based on a temperature difference between the last glacial and today of about 4°C [*Elderfield and Rickaby*, 2000]. This does not conform with recently established paleotemperature estimates in the SIZ of the Atlantic sector. These indicate that the difference between glacial temperatures and those of today range between only 0.5°–1°C [*Gersonde et al.*, 2003, 2005], which would balance the inferred glacial increase in P utilization. Furthermore, a productivity regime dominated by *Phaeocystis* and weakly silicified diatoms, as suggested in this study for the glacial SIZ, would contribute to lower P utilization because *Phaeocystis* has higher N:P ratios [*Arrigo et al.*, 1999]. This flagellate can dominate blooms both in deep and shallow mixed layers [*Smith and Asper*, 2001; *Smetacek et al.*, 2004].

[20] Interestingly, the fairly uniform glacial $\delta^{13}C_{org}$ values of −24 to −26 ‰ recorded in Core PS1768-8 are in the same range as those of surface sediments in the productive Peninsula plume [*Fischer*, 1991] and shift to uniform values of −21 to −19 ‰ in the Holocene during the *F. kerguelensis* transition peak. The underlying reasons for this pattern are not understood but this ratio seems to be influenced more by fractionation processes in the surface layer, e.g., smaller cells take up less ^{13}C than larger cells [*Fischer*, 1991; *Rosenthal et al.*, 2000], than by the degree of utilization of dissolved inorganic carbon. A reduction in cell size from 20 to 5 μm would decrease δ^{13} C by up to 15 ‰ [*Lourey et al.*, 2004]. *Fischer* [1991] reports $\delta^{13}C$ measurements on assemblages dominated by small pennate diatoms (*Fragilariopsis curta and F. cylindrus*) released from melting sea ice in the northwestern Weddell Sea ranging around −28 ‰. Since the more negative $\delta^{13}C_{org}$ values of the glacial and termination are related to higher total organic carbon percentage (TOC%) and higher *Chaetoceros* spore rain rates (Figure 3) it is reasonable to assume that these are due to the carbon locked in the spores and in other small diatoms.

[21] Indications that the nutrient status in the glacial SIZ differed from today comes from bulk $\delta^{15}N$ and diatom $\delta^{30}Si$ measurements that suggest lower silicic acid utilization relative to nitrate [*Francois et al.*, 1997; *DeLaRocha et al.*, 1998; *Brzezinski et al.*, 2002]. The "silica leakage" hypothesis developed from these measurements maintains that increased deposition of iron-enriched dust resulted in nitrate but not silicic acid depletion which was subsequently exported from the Southern Ocean [*Brzezinski et al.*, 2002; *Matsumoto et al.*, 2002]. This is in agreement with our data indicating a productivity system in the glacial SIZ governed by thinly silicified diatoms and nonsiliceous primary producers such as *Phaeocystis* with low Si:N demand. However, it remains unclear to what extent the excess silicic acid was removed by *F. kerguelensis* production in the glacial POOZ.

[22] The fact that substantial iron rain rates continued for 2 kyr after dust concentrations in the Vostok ice core reached their Holocene low needs explanation (Figure 3). We suggest that sea level rise during this period led to breakup of extensive glacial ice shelves resulting in episodic, large-scale melting of icebergs along the ACC that would release their dust loads accumulated over the preceding several kiloyears to the surface water. Such an iceberg fertilization event in the land-remote ACC, signaled by high surface iron concentrations and accompanied by extensive phytoplankton blooms, has been reported [*Smetacek et al.*, 1997]. Alternatively, iron input could have been affected by enhanced upwelling of deep water with higher iron concentrations than in the current ocean [*Latimer and Filippelli*, 2001]. Elucidation and quantification of the sequence of events during the termination will require closer examination of cores from other sites in the ACC and a better understanding of the ecology of spore-forming *Chaetoceros* in relation to other diatom species.

7. Conclusion

[23] The widespread and consistently high accumulation rates of *Chaetoceros* spores and *C. davisiana* throughout the last glacial are compelling evidence for substantially higher productivity and organic carbon export into substantially colder, saltier [*Adkins et al.*, 2002] and less ventilated [*Sikes et al.*, 2000] than present deep waters in the Atlantic sector. The occurrence of less ventilated glacial Southern Ocean deep waters is also assumed from modeling results of the Atlantic Ocean that point to a stratified deep ocean maintained by density differences of northern and southern glacial deep waters [*Toggweiler*, 1999; *Gildor et al.*, 2002]. Enhanced productivity and carbon export in the glacial SIZ is related to more extensive glacial sea ice cover, which increased bioavailability of dust-borne iron. We suggest that CO_2 drawdown in the glacial SIZ was substantially higher than today because of the combination of at least three factors: (1) high iron availability, (2) sea ice cover during winter [*Stephens and Keeling*, 2000], and (3) deep ocean stratification [*Toggweiler*, 1999; *Gildor et al.* 2002].

[24] A recent review of glacial productivity based on geochemical interpretations of available proxies concludes

with two (competing) scenarios [*Anderson et al.*, 2002]. Our findings, based on ecological interpretation of overlooked paleoecological proxies, support both scenarios: a glacial high-carbon, low-silica-exporting SIZ and high-silica-exporting POOZ. A model linking ACC productivity in the Atlantic sector to iron input via Patagonian dust, parameterized by results from an iron fertilization experiment, reproduced glacial atmospheric CO_2 levels remarkably well [*Watson et al.*, 2000]. Our data provide support for the validity of this paleoceanographic model and highlight the need for longer-term, species-oriented, in situ iron fertilization experiments to further validate proxies and test hypotheses linking biogeochemical and ecological processes.

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