Biological response to millennial variability of dust and nutrient supply in the Subantarctic South Atlantic Ocean

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Fluxes of lithogenic material and fluxes of three palaeo-productivity proxies (organic carbon, biogenic opal and alkenones) over the past 100 000 years were determined using the $^{230}$Th-normalization method in three sediment cores from the Subantarctic South Atlantic Ocean. Features in the lithogenic flux record of each core correspond to similar features in the record of dust deposition in the EPICA Dome C ice
core. Biogenic fluxes correlate with lithogenic fluxes in each sediment core. Our preferred interpretation is that South American dust, most probably from Patagonia, constitutes a major source of lithogenic material in Subantarctic South Atlantic sediments, and that past biological productivity in this region responded to variability in the supply of dust, probably due to biologically available iron carried by the dust. Greater nutrient supply as well as greater nutrient utilization (stimulated by dust) contributed to Subantarctic productivity during cold periods, in contrast to the region south of the Antarctic Polar Front (APF), where reduced nutrient supply during cold periods was the principal factor limiting productivity. The anti-phased patterns of productivity on opposite sides of the APF point to shifts in the physical supply of nutrients and to dust as cofactors regulating productivity in the Southern Ocean.

1. Introduction

Establishing the contribution by the ocean’s biological pump to past changes in the global carbon cycle, especially the climate-related changes in atmospheric CO$_2$ concentration [1], is a long-sought goal of palaeoclimate research (e.g. [2–4]). Biological utilization of nutrients in the Southern Ocean is particularly important in this regard as it regulates the preformed nutrient inventory for most of the deep ocean and, therefore, the global average efficiency of the biological pump [4,5]. Nutrient utilization is inefficient in the Southern Ocean today, in part because phytoplankton growth is limited by the scarcity of iron (e.g. [6]).

Martin [7] suggested that iron limitation in the Southern Ocean may have been relieved during the Pleistocene ice ages by the greater deposition of continental mineral aerosols (dust) that was discovered in Antarctic ice cores. Dust would have supplied iron to marine phytoplankton. However, early tests of this hypothesis using geochemical indicators of biological productivity extracted from marine sediment cores concluded that the region south of the Antarctic Polar Front (APF) was characterized by lower productivity during the ice ages [8–10], contrary to the expectations from Martin’s hypothesis. The principal exception to this view was derived by examining the species assemblages of diatoms preserved in glacial-age sediments, which suggested greater rather than lower ice-age productivity [11]. Despite this one dissenting finding, the common view is that the increase in dust supply did not enhance biological productivity south of the APF (for a recent synthesis, see [12]).

In contrast to the Antarctic zone, south of the APF, sediment records from Subantarctic sites (defined here as the zone north of the APF, extending as far as the Subtropical Convergence) revealed ice-age enhancement of biological productivity in all sectors of the Southern Ocean [12,13]. This is particularly true in the South Atlantic, where high levels of productivity are inferred from sediments deposited during the last ice age [14]. Initial studies concluded that ice-age productivity in the Subantarctic South Atlantic was stimulated by dust that originated in Patagonia [8], immediately ‘upwind’ of the region and known to have been the primary source of dust in Antarctic ice cores (e.g. [15,16]). However, this view was challenged by a number of studies concluding that most of the lithogenic material in South Atlantic sediments is delivered by ocean currents rather than via the atmosphere [17–27], both during ice ages and during interglacial periods.

Martinez-Garcia et al. [28,29] resurrected the notion that biological productivity in the Subantarctic South Atlantic is stimulated by dust in finding a tight coupling between dust and productivity over the past 4 Myr. Specifically, at ODP Site 1090 (42.913° S, 8.898° E, 3702 m, figure 1) the accumulation rates of iron and of $n$-alkanes (organic compounds derived from leaf waxes of land plants) were correlated with one another across glacial–interglacial cycles, as well as with geochemical indicators of biological productivity. Each of these parameters in ODP 1090 sediments was further correlated with dust deposition in the EPICA Dome C (EDC) ice core. The tight coupling between fluxes of lithogenic material and of leaf waxes, together with
the correlation with EDC dust fluxes, supports the view that most of the lithogenic material in Subantarctic South Atlantic sediments is supplied as dust [8].

Although the findings of Martinez-Garcia and co-workers are compelling, correlations across glacial–interglacial cycles may be misleading. Many variables correlate with one another over 100 kyr Milankovitch cycles simply because the enormous variability of climate boundary conditions influences these variables, without any inherent causal connection among them. Consequently, here we expand on earlier work by examining South Atlantic sediment records at much greater temporal resolution, thus affording examination of dust–productivity linkages in the absence of major changes in climate boundary condition (e.g. glacial–interglacial cycles), instead focusing on more subtle changes in forcing at higher frequency. We find a tight coupling between geochemical indicators of biological productivity and the accumulation of lithogenic material in three cores from the Subantarctic South Atlantic Ocean, and we further demonstrate that these features exhibit a close correspondence to dust deposition in the EDC ice core on millennial time scales. We conclude that phytoplankton in the region responded to increased dust supply with an increase in nutrient utilization and increased export production.
2. Material and methods

Accumulation rates of sedimentary constituents were evaluated for three South Atlantic cores (figure 1) using the $^{230}$Th-normalization approach [32]. This approach makes a necessary correction for the redistribution of sediments by deep-sea currents (sediment focusing), which can cause the local accumulation of sediment to exceed the regional average particle rain rate by as much as a factor of 20 in the cores studied here [33]. Concentrations of lithogenic material were estimated for each core using the measured $^{232}$Th concentration. Concentrations of Th isotopes ($^{230}$Th and $^{232}$Th) were measured by isotope dilution using methods described elsewhere [34,35].

Thorium-232 abundance has a fairly narrow range in upper continental crust [36,37], and among dust sources worldwide [38]. Here, we use an average content of 10 ppm to estimate the lithogenic component of each sample, acknowledging that there is a potential uncertainty of as much as 20% in this estimate depending on the source of the lithogenic material. Assessing the temporal variability of lithogenic supply is more important here than the absolute flux, so we accept the uncertainty in the absolute flux inherent in this approach in favour of the precision that it offers for detecting small changes in the lithogenic flux over time. We make no initial assumption about the origin of the lithogenic material. Undoubtedly, for each site some fraction is delivered by ocean currents as well as by dust. We will use the amplitude of the temporal variability that correlates with dust deposition in the EDC ice core [39] to provide semi-quantitative constraints for the fraction of the lithogenic component of sediments that consists of dust.

Mackensen et al. [40] presented an initial estimate of palaeoproductivity for core PS2498-1 (44.15° S, 14.49° W, 3783 m). In addition to thorium (see above), we add to the study of PS2498-1 new measurements of organic carbon (C-org, determined at the Alfred Wegener Institute (AWI)), using an elemental analyser. Biogenic opal was also measured, both at AWI using the method of Müller & Schneider [41] and at the Lamont-Doherty Earth Observatory (LDEO) using the method of Mortlock & Froelich [42]. Opal concentrations measured at LDEO were systematically greater than those measured at AWI, most probably reflecting a difference in the efficiency of Si extraction [43]. Despite the systematic offset, the downcore pattern of opal content derived using the two methods was internally consistent. As for the lithogenic fluxes, the precision with which we can assess temporal variability is more important for our objectives than the accuracy of the opal flux, so the opal results from LDEO are used without implying any judgement about the relative accuracy of the two datasets.

Concentrations of C$_{37}$ alkenones, a suite of organic compounds produced by coccolithophorids, and thorium have been described previously [33] for TN057-06PC4 (42.91° S, 8.9° E, 3751 m) and TN057-21-PC2 (41.13° S, 7.81° E, 4981 m). Here, we report the summed concentration of the C$_{37}$ methyl ketones with two (C$_{37}$:2Me) and three (C$_{37}$:3Me) double bonds, and refer to that quantity simply as ‘alkenones’. Although more than 10 different alkenones and the related alkenoates have been reported in marine sediments, C$_{37}$:2Me and C$_{37}$:3Me are the two compounds used for palaeotemperature reconstructions and are by far the most abundant alkenones in Subantarctic sediments. Those results are supplemented here with additional measurements of thorium for both cores.

3. Age models

Lithogenic fluxes in PS2498-1, on the age model of Mackensen et al. [40] (figure 2b), share a number of features with the EDC dust record (figure 2a); for example, elevated fluxes during the intervals approximately 18–30 ka and approximately 60–70 ka, as well as three shorter intervals of elevated flux between 30 and 60 ka. Given the similarity of the records, we selected a number of tie points to align lithogenic fluxes in PS2498-1 with EDC dust fluxes (solid black lines in figure 2). In addition, the age model was modified using radiocarbon ages reported by Gersonde et al. [44] for the core.
top down to a depth of 151 cm (age of 22 ka). The original age–depth relationship for PS2498-1 is compared with the revised age model in figure 3. Oxygen isotope data for PS2498-1 [40] placed on the adjusted age model fitted the stacked record of Lisiecki et al. [45], the benchmark for Pleistocene chronology of deep-sea sediments, at least as well as when using the original age model (not shown, but available from the lead author).

For TN057-06PC4, we began with the age model of Hodell et al. [46] as modified by C. Charles (2000, personal communication). Further adjustments to the age model were made to align the lithogenic fluxes of TN057-06-PC4 with dust deposition in the EDC record (figure 2, dashed grey lines). As for PS2498-1, the oxygen isotope record for the adjusted age model fitted the Lisiecki stack at least as well as with the original. The revised age–depth relationships for PS2498-1 and TN057-06 exhibit less variability over time than with the original age models (figure 3). While a more uniform accumulation rate does not necessarily mean that an age model has been improved, the internal consistency among all results following the adjustments to these age models (see also below) supports the use of the new age models.

Several age models have been published for TN057-21-PC2. Building upon previous work [47,48], we first tied features in the TN057-21 record to features in the oxygen isotope record of the North GRIP ice core. The absolute age of both records beyond 60 ka was then adjusted by aligning the North GRIP oxygen isotope record with the northern Alps (NALPS) speleothem record [49], which has absolute age control from U–Th dating [50]. Adjustments to the age model of the EDC ice core were then made to place it on the NALPS chronology as well, maintaining the relationship between EDC and North GRIP developed by previous studies. While further adjustments to the absolute age of the records may be necessary, more important is that all of the marine and ice core records used here have been tied to a common age model to facilitate intercomparison of the various results.
Figure 3. Age–depth relationships for (a) PS2498-1 and (b) TN057-06. Original age models from Mackensen et al. [40] for PS2498-1 and from C. Charles (2000, personal communication) for TN057-06 are shown in grey. Age control points for the adjusted age models are shown as triangles for PS2498-1 and as squares for TN057-06. For PS2498-1, the revised age model was fitted to the radiocarbon dates of Gersonde et al. [44] to a depth of 151 cm. Age control points for depths greater than 151 cm in PS2498-1, and for all depths in TN057-06, were derived by tuning to the EDC dust record (figure 2).

4. Results

Lithogenic fluxes in the three Subantarctic cores are compared with the EDC dust flux record in figure 4. Fluxes of opal and of C-org in PS2498-1, as well as the lithogenic flux, are shown with the EDC dust record in figure 5. Alkenone fluxes from TN057-06 and from TN057-21 are presented in figure 6, together with the lithogenic fluxes from each core, to compare with the EDC dust record. Alkenone concentrations are also shown in figure 6d to show that variability of the $^{230}$Th-normalized alkenone flux is determined mainly by variability in the concentration of alkenones rather than by variability of $^{230}$Th-normalized mass flux.

5. Discussion

(a) Sources of lithogenic material

Cores PS2498-1 and TN057-06 were recovered from sites on the eastern flank of the Mid-Atlantic Ridge [40] and on the Agulhas Ridge [46], respectively. Their location on elevated topography and their distance from continental margins isolates these sites from turbidites and from contour currents delivering sediment from continental sources. Therefore, one can have confidence that lithogenic sediment delivered to these sites was transported either via the atmosphere or by major ocean currents, such as the Antarctic Circumpolar Current, allowing for minor contributions from material transported by icebergs.
Figure 4. (a) Flux of dust in the EPICA Dome C ice core [39]. Fluxes of lithogenic sediment in Subantarctic South Atlantic cores (b) PS2498-1, (c) TN057-06 and (d) TN057-21 estimated from $^{230}$Th-normalized fluxes of $^{232}$Th (see text for details). Age models for PS2498-1 and TN057-06 were tuned to the EDC dust record as illustrated in figures 2 and 3. The age model for TN057-21 was derived by tuning to the North GRIP ice core (see text) and, therefore, it is independent of the EDC dust record.

Figure 5. (a) Flux of dust in the EPICA Dome C ice core [39]. Fluxes of (b) lithogenic sediment, (c) organic carbon and (d) biogenic opal in Subantarctic South Atlantic core PS2498-1. Fluxes of sediment constituents were estimated by $^{230}$Th normalization (see text for details).
Lithogenic fluxes in PS2498-1 and in TN057-06 (figure 4b,c) exhibit a close correspondence to the pattern of dust deposition in the EDC ice core (figure 4a), including two major intervals of elevated dust flux (approx. 18–35 ka and 60–70 ka), two shorter but intense episodes of dust deposition centred at approximately 41 ka and at approximately 50 ka, as well as smaller features (e.g. 55–60 ka and approx. 89 ka). The observed correspondence is consistent with an aeolian source for a large fraction of the lithogenic material in PS2498-1 and TN057-06. Furthermore, during intervals of maximum lithogenic flux, fluxes are nearly twice as large on the Mid-Atlantic Ridge (PS2498-1) as on the Agulhas Ridge (TN057-06), in agreement with previous observations of an eastward decrease in lithogenic flux across the Subantarctic South Atlantic during the Last Glacial Maximum (LGM) [8], and consistent with expectations, as dust is washed out of the atmosphere while transported downwind from a South American source.

In contrast to the other cores, TN057-21 was recovered from a drift deposit in the deep Cape Basin where contour currents deposit sediment entrained along the margin of Africa [52]. Mineralogical [22] and isotopic [25] composition of lithogenic material at this location are consistent with an African source for a portion of the sediment, with an additional time-varying source of material originating at higher latitudes [22]. This combination of two major sources of lithogenic material at the site of TN057-21 creates a record of lithogenic accumulation (figure 4d) that has a smaller amplitude of variability compared with the other cores (figure 4b,c).
Building on the prior work of Kuhn & Diekmann [22], we interpret the record of lithogenic accumulation in TN057-21 to reflect a time-varying aeolian component, similar to the record in TN057-06, superimposed on a relatively constant source of sediment from Africa. Despite its reduced amplitude of variability, the record of lithogenic flux in TN057-21 contains most of the features that correspond to the EDC dust record, including some of the smaller peaks (e.g. approx. 30 ka).

Our results do not permit us to quantify precisely the fraction of lithogenic material in the marine cores that was delivered as dust. Future studies involving geochemical provenance tracers will help in this regard. Nevertheless, based on our finding that the principal features in the lithogenic flux record correspond to features in the EDC dust record, we conclude that the majority of the lithogenic material in PS2498-1 and in TN057-06, as well as a large fraction of lithogenic material in TN057-21, was delivered by atmospheric transport, most probably from South America.

(b) Biological response to dust

Biogenic constituents of the sediments are interpreted as indicators of biological production. Accumulation of biogenic material in marine sediments is influenced by preservation as well as by production, and preservation is difficult to quantify. Therefore, rather than attempt to quantify preservation, we employed two biogenic tracers (opal and organic carbon) for which preservation is not expected to covary. Preservation of opal is sensitive to temperature, but in the cold stable environment of the abyssal ocean the preservation of opal depends mainly on sediment accumulation rate [53]. Preservation of organic carbon, on the other hand, is most sensitive to the concentration of oxygen in bottom water [54], which is not expected to covary with sediment accumulation rate. Therefore, covariability of opal and of C-org is interpreted to reflect changes in production rather than variable preservation.

Accumulation rates of C-org (figure 5c) and of opal (figure 5d) in PS2498-1 are correlated with one another, as well as with the accumulation rate of lithogenic material (figure 5b) and with EDC dust deposition (figure 5a). For the eastern sites (TN057 cores), we use alkenones, long-chained ketones produced exclusively by certain haptophyte algae, predominantly the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica* in the open ocean [55,56], as a palaeoproductivity indicator (figure 6). Alkenones were also employed as a palaeoproductivity indicator by Martinez-Garcia et al. [28,29] in their study of ODP1090 (figure 1). Features in TN057-06 are less well defined because of the roughly fivefold lower accumulation rate in this core compared with TN057-21, which allows for greater smoothing of the record by bioturbation. Nevertheless, despite the differing depositional regimes (pelagic deposition on a topographical elevation versus deep drift deposit), the principal features of the TN057-06 alkenone record (figure 6e) are consistent with those in TN057-21 (figure 6df, 33), supporting the validity of these tracers as indicators of time-varying changes in biological productivity.

Palaeoproductivity proxy records in each Subantarctic core exhibit features that covary with the lithogenic flux in the same sediment core, even over millennial time scales (figures 5 and 6). Tight coupling over short time intervals lessens the potential influence of changes in global climate boundary conditions, thereby strengthening the view that the productivity record reflects a biological response to varying supply of dust, and to the iron that it carries [8,28]. However, factors other than dust may also regulate biological productivity in the Southern Ocean, and these are discussed in the next section.

Before proceeding, we want to reiterate that, whereas the age models for PS2498-1 and TN057-06 were adjusted by tuning to the EDC dust record, the age model for TN057-21 was tuned only by alignment with the oxygen isotope record of the North GRIP ice core [49]. Therefore, the correspondence of the palaeoproductivity record of TN057-21 (figure 6df) with the records from the other cores (figures 5 and 6), as well as with the EDC dust record (figure 6a), supports the reliability of tuning the age models of PS2498-1 and TN057-06 to the EDC dust record.
Figure 7. Concentration of alkenones (grey) and $\delta^{13}C$ of planktonic foraminifera *G. bulloides* (black) in TN057-21. Alkenone concentrations are from [33] and carbon isotope data are from [59].

(c) Supply and utilization of nutrients

The Subantarctic zone is a region of persistently high nitrate concentrations (figure 1a; phosphate, not shown, has a similar distribution). Therefore, the greater fluxes of organic material during periods of elevated dust flux, which correspond to the colder intervals in Antarctica [39], could reflect a more efficient utilization of nitrate due to relief from iron limitation, or a greater supply of nutrients, or both. Nitrogen isotopes in foraminifera-bound organic matter from ODP1090/TN057-06 have been interpreted recently to indicate greater nitrate utilization efficiency during periods of elevated dust supply [57], providing compelling evidence for iron fertilization.

Although the results presented here are consistent with a strong sensitivity of biological productivity to dust supply in the Subantarctic South Atlantic Ocean, dust supply cannot be the sole factor regulating productivity. For example, all of the core sites are located in regions where surface waters today are impoverished in dissolved silicon (Si, figure 1b). At the site of PS2498-1, the flux of opal during the late glacial period (20–35 ka; 0.25–0.30 g cm$^{-2}$ kyr$^{-1}$) was about sixfold greater than during the last 10 kyr (approx. 0.05 g cm$^{-2}$ kyr$^{-1}$; figure 5d). Nearly identical results were reported previously for a site further to the east (PS2082-2, 43°13.2′S, 11°44.3′E, [9]). Substantially greater opal fluxes during the LGM are recorded at sites further south, but still well to the north of the APF (approx. 50° S in this region), ranging between 0.6 g cm$^{-2}$ kyr$^{-1}$ (PS1754-1/2, 46°46.2′S, 7°36.7′E, [9]) and 1.6 g cm$^{-2}$ kyr$^{-1}$ (RC15-93, 46°06′S, 13°13′W, [8]). Opal fluxes this large require a source of Si much greater than exists today to sustain the diatom productivity implicated by the opal flux.

A greater supply of nutrients to the Subantarctic zone during glacial periods has also been inferred from the carbon isotopic composition ($\delta^{13}C$) of planktonic foraminifera in TN057-21 [58,59]. Many of the features in the alkenone record of TN057-21 are correlated with the $\delta^{13}C$ of *Globigerina bulloides* in this core, in the sense that increasing productivity corresponds to increasing concentrations of nutrients (decreasing $\delta^{13}C$; figure 7). However, $\delta^{13}C$ of planktonic foraminifera is sensitive to other factors in addition to nutrient concentration (e.g. [60,61]), so a nutrient–productivity correlation cannot be inferred unambiguously. Furthermore, over two intervals (approx. 65–60 ka and approx. 18–10 ka), the palaeoproductivity indicator drops dramatically while the $\delta^{13}C$ remains low (consistent with, but not necessarily requiring, high nutrients). Over these intervals, the palaeoproductivity indicator correlates much better with dust supply (figures 5 and 6).

On the other hand, there are occasions when this correlation breaks down. In TN057-21, for example, alkenone concentrations are relatively high during times of low or declining lithogenic flux at approximately 39, 48 and 57 ka (figure 6). In PS2498-1, elevated fluxes of opal and of C-org also persist until approximately 39 ka, despite declining dust flux (figure 5). Each of these intervals, corresponding to Heinrich Stadials 4, 5 and 5A, coincides with low $\delta^{13}C$ in *G. bulloides* (figure 7), which we interpret to indicate that nutrient supply may play at least as great a role as dust flux in regulating productivity at these times. Enhanced upwelling south of the APF...
during these intervals [62] may have injected nutrients into the Subantarctic zone [51] as well as in the Antarctic zone. We conclude, therefore, that both increased supply of nutrients and increased nutrient utilization efficiency, stimulated by dust, contributed to the rise in Subantarctic productivity during cold periods, including relatively cold intervals of millennial duration during Marine Isotope Stage (MIS) 3 (approx. 30–60 ka) and late MIS 5 (prior to approx. 80 ka) as well as throughout MIS 2 and 4.

(d) Contrasting conditions across the Antarctic Polar Front

Subantarctic productivity can now be considered in the context of a substantial body of work describing patterns of productivity throughout the entire Southern Ocean. In contrast to modern (Holocene) conditions, when export production south of the APF exceeds that of the Subantarctic zone, the situation was reversed during the LGM, when export production of the Subantarctic zone was much greater than to the south of the APF (e.g. [8–10]). Kohfeld et al. [12] provide a comprehensive synthesis of the evidence for the last glacial period, whereas Jaccard et al. [63] show that the seesaw pattern of productivity across the APF was a regular response to climate variability throughout the late Pleistocene.

Two general scenarios have been proposed to explain lower export production of the Antarctic zone during glacial periods. First, expansion of sea ice during glacial periods [64] may have limited the growth of phytoplankton in the Antarctic zone (e.g. [10,65]). Implicit in this scenario is the corollary that a greater fraction of the nutrients upwelled south of the APF would remain unused and thus be subjected to Ekman transport northward into the Subantarctic zone. That is, the greater supply of nutrients to the Subantarctic zone during glacial periods could simply reflect lower utilization in the Antarctic zone superimposed on conditions of upwelling and surface water transport similar to those that exist today. The principal alternative scenario is that nutrient supply by upwelling south of the APF was reduced during glacial periods (e.g. [66]), most probably tied to increased stratification of the polar ocean (for reviews, see [67,68]).

Nitrogen isotopes archived in Southern Ocean sediments have been interpreted to favour the second hypothesis (reduced nutrient supply). Throughout the Antarctic zone, the nitrogen isotopic composition of organic compounds preserved within diatom frustules indicates greater nitrate utilization during glacial periods, coincident with lower export production, compared with interglacials [69–71]. Relatively efficient utilization of nitrate during glacial periods is inconsistent with inhibition of phytoplankton growth by sea ice, but it allows for iron fertilization in response to the greater supply of dust. That is, the lower rate of nutrient supply during glacial periods trumps the effect of iron fertilization, reducing export production within the Antarctic zone compared with iron-limited interglacial periods.

The combination of lower supply and greater utilization of nitrate south of the APF during glacial periods eliminates the northward transport of unused nutrients as the primary source to fuel Subantarctic productivity. Instead, during glacial periods, nutrients must have been supplied to the Subantarctic zone by mixing from below.

Today, the zone of maximum upwelling and nutrient supply is located to the south of the APF [72]. Two scenarios can be envisioned to account for the northward displacement of nutrient supply during glacial periods. First, the APF may have migrated northward by several degrees of latitude (reviewed by Gersonde et al. [64]), carrying the band of upwelling with it into latitudes more favourable for phytoplankton growth. Alternatively, the hydrographic features associated with the APF may have remained locked roughly in their present position through interaction with bottom topography [73]. Under this scenario, a northward shift of the southern westerlies [74] may have decoupled the zone of upwelling from the APF. Upwelling, driven primarily by wind stress curl in the Subantarctic zone under these conditions, may have ventilated much shallower layers of the deep ocean than occurs today. While this scenario is speculative, ventilation of shallower water masses in the Southern Ocean during glacial periods is consistent with a growing body of evidence for greater mid-depth stratification during the LGM [75,76]. Of
course, the two scenarios are not mutually exclusive, as the westerlies and the frontal systems may have migrated concurrently.

Lastly, we note that the seesaw pattern of nutrient supply across the APF that is evident over glacial–interglacial cycles is also apparent over much shorter time scales, with some exceptions. Anderson et al. [62] interpreted opal fluxes to indicate increased upwelling south of the APF during the most intense Northern Hemisphere stadials of the last glacial cycle, which correspond to relatively warm Antarctic Isotope Maxima (AIM). Dust fluxes to Antarctica are at relative minima during AIM events, and peak during the coldest intervals [39]. Therefore, if the lithogenic fluxes to Subantarctic sites correspond to dust fluxes in Antarctica, then the covariance between dust, export production and nutrient supply (figures 5–7) indicates maximum supply of nutrients to the Subantarctic zone during Antarctic cold intervals, opposite to the pattern observed south of the APF. The principal exceptions, noted in the previous section, occur during Heinrich Stadials 4, 5 and 5A, when nutrient supply to the Subantarctic zone remained high during the transition into Antarctic warm intervals. Records with greater temporal resolution will be needed to resolve the precise phasing between temperature, dust, nutrients and productivity at these times.

6. Summary and outlook

Accumulation rates of lithogenic material in three sediment cores from the Subantarctic South Atlantic Ocean exhibit features over the past 100 000 years that correspond to the pattern of dust deposition in the EPICA Dome C ice core, indicating that most of the lithogenic material in the sediments was derived from South American dust sources. Accumulation rates of biogenic opal and of organic indicators of biological productivity also correlate with the lithogenic fluxes in these cores. Combining these results with evidence for nutrient utilization [57] and for nutrient supply, we conclude that export production in the Subantarctic zone was stimulated during cold periods by the synergistic effects of greater nutrient supply together with increased nutrient utilization, supported by elevated dust fluxes.

Nutrient supply and export production south of the APF varied in a pattern that was anti-phased with their variability in the Subantarctic zone, whereas nutrient utilization was high in both regions during the LGM and, presumably, during earlier cold intervals as well. Conditions south of the APF indicate that export production during the LGM was limited more by the supply of macronutrients than by iron. The anti-phased pattern of nutrient supply on opposite sides of the APF, combined with the dust fluxes presented here, further indicates that the physical forcing that brings nutrients to the surface varied almost concurrently with dust supply.

Climate-related shifts in the latitude of the Southern Hemisphere westerlies have been suggested to influence nutrient supply in the Subantarctic South Atlantic [47,77] as well as in the Antarctic zone [62]. Meridional shifts in the southern westerlies may also have modulated the growth and retreat of mountain glaciers in the mid-latitudes of the Southern Hemisphere [78–81], which, in turn, may have regulated the source of glaciogenic sediments entrained by the winds as they passed over Patagonia [82]. Thus, a north–south displacement of the southern westerlies provides a unifying hypothesis that is consistent with the palaeoclimate records described earlier. Future studies should consider why these features do not appear to be prominent in model simulations (for recent discussion, see [83,84]).

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Data accessibility. Results presented here that have not been published previously will be submitted to the PANGAEA (http://pangaea.de/) and NCDC (http://www.ncdc.noaa.gov/) data archives. Data from core PS2498-1 are available at PANGAEA DOI via the link: http://doi.pangaea.de/10.1594/PANGAEA.832084. DOIs for data from cores TN057-21 and TN057-06 are not yet available.
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