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The Southern Ocean's biological pump during the Last Glacial Maximum

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Abstract

Ice core records from Antarctica show large (~80 ppm) and regular climate-related changes in atmospheric CO_2, with minimum values during glacial periods and maximum values during peak interglacials. The suggested role of the Southern Ocean in driving these changes is based on either the potential for increased utilization of surface nutrients or the potential for decreased ventilation of deep waters during glacial times. Several recent studies have invoked increased stratification of the Southern Ocean to explain lower glacial atmospheric CO_2 levels in terms of reduced exchange of CO_2 between the deep sea and the atmosphere. A northward displacement and/or substantial weakening of the westerly winds during glacial periods are implicit in the scenarios that invoke enhanced stratification. However, both circulation models and proxy results argue against a weakening of the westerlies. In fact, the mean flow of the Antarctic Circumpolar Current and wind-driven upwelling during the Last Glacial Maximum (LGM) are thought to be at least as vigorous as those which exist today. Given these boundary conditions, we offer two (competing) scenarios for ecosystem structure and export production of the glacial Southern Ocean. The first scenario satisfies all proxy records for nutrient utilization and phytoplankton growth rate, and requires increased (relative to today) nitrate utilization south of the Antarctic Polar Front (APF) by phytoplankton other than diatoms, together with a shift in the zone of maximum diatom growth from south (interglacials) to north (glacials) of the APF. The second scenario has reduced growth of all phytoplankton species south of the APF during glacials, and a shift in the zone of maximum export production to the north of the Polar Front. The principal weakness of the first scenario is that there is little sedimentary evidence to support the increased export of particulate organic carbon required by the inferred increase in nitrate utilization south of the APF. The principal weakness of the second scenario is that it requires a change in the isotopic fractionation of nitrogen by phytoplankton growing south of the Polar Front for reasons presently unknown. The Southern Ocean's biological pump at the LGM has yet to be characterized unequivocally. © 2002 Elsevier Science Ltd. All rights reserved.

Résumé

On observe dans les carottes de glace provenant du continent Antarctique des cycles de grandes amplitudes (~80 ppm) dans la concentration atmosphérique du CO_2, qui sont reliés aux cycles climatiques, avec des valeurs minimum durant les époques glaciaires, et des valeurs maximum durant les époques inter-glaciaires. Un rôle de l'océan austral dans ces cycles climatiques a été suggéré, compte tenu du grand surplus de nutriments dans les eaux de surface,

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et de la possibilité que les eaux profondes auraient été moins ventilées pendant les époques glaciaires. Dans les dernières années, plusieurs études ont associées les concentrations moins importantes de CO_2 dans l'atmosphère durant les époques glaciaires à une stratification plus importante de l'océan austral, ce qui aurait réduit l'échange de CO_2 entre l'atmosphère et l'océan profond. En même temps, on remarque un déplacement vers le nord, et/ou une réduction importante de la force des vents d'ouest durant les époques glaciaires. Cependant, des simulations numériques, ainsi que des données proxys, ne supportent pas l'hypothèse d'une réduction des vents d'ouest. Au contraire, pendant le Dernier Maximum Glaciaire (DMG), le forcage des vents auraient entrainé un courant antarctique circumpolaire (ACC), ainsi que des courants ascendants au moins aussi vigoureux que ceux d'aujourd'hui. En tenant compte de ces conditions aux bords, nous proposons deux scénarios possibles de l'écologie et de l'éxportation de carbone dans l'océan austral pendant la dernière époque glaciaire.

Le premier scénario est en accord avec toutes les données proxys ayant attrait a l'utilisation des éléments nutritifs, ainsi que le taux de croissance des phytoplanctons. Ce scénario implique que l'utilisation de nitrate par les phytoplanctons non-diatomés est plus importante durant les époques glaciaires qu'aujourd'hui, et aussi que la zone préférée de diatomées soit au sud du Front Polaire Antarctique (FPA), durant les époques interglaciaires, et au nord du FPA durant les époques glaciaires. Le deuxième scénario, par contre, implique une réduction de la productivité de toutes les espèces de phytoplanctons au sud du FPA durant le DMG, ainsi qu'un déplacement de la zone maximale d'éxportation de carbone au nord du PFA. Le principal point faible du premier scénario est lié à l'absence de données suggérant une augmentation dans l'exportation de carbone organique particulaire, dans les sédiments au sud du PFA. Le principal point faible du deuxième scénario est qu'il requière un fractionnement isotopique de l'azote par les phytoplanctons, au sud du PFA, durant la dernière époque glaciaire qui est différent de celui d'aujourd'hui. Bref, on est toujours à la recherche d'une caracterisation non-équivoque de la "pompe biologique" dans l'océan austral durant le DMG.

1. Introduction

The biogeochemistry and circulation of the Southern Ocean are widely viewed to be sensitive to perturbation by climate change (e.g., Sarmiento et al., 1998). Concerns about changes in the Southern Ocean generally fall within two broad categories, which can be summarized by the following questions:

(1) How do the ecosystem structure and biogeochemical cycles of the Southern Ocean respond to climate change? and;
(2) What role does the circulation and biogeochemistry of the Southern Ocean play in regulating the CO_2 content of earth's atmosphere?

The remarkable correlation between the CO_2 content of the atmosphere and climate over the past 400 kyr (Petit et al., 1999) has stimulated widespread investigation of the mechanisms responsible for controlling the CO_2 content of the atmosphere. Early assessments of the inventories of carbon in various reservoirs exchanging CO_2 with the atmosphere over time scales of 10^3–10^5 years led investigators to conclude that the ocean must be driving the climate-related changes in atmospheric CO_2 (e.g., Broecker, 1982; Sigman and Boyle, 2000). Synchronous changes in atmospheric CO_2 and Antarctic temperature are evident in high-resolution records covering major climate transitions, such as glacial terminations (e.g., Broecker and Henderson, 1998; Petit et al., 1999) and during abrupt warmings of shorter duration (Indermühle et al., 2000; Monnin et al., 2001). These correlations provide strong circumstantial evidence for a Southern Ocean origin for climate-related changes in atmospheric CO_2.

Two features of the Southern Ocean make this region a likely host for processes regulating atmospheric CO_2 over time scales relevant to climate change. First, wind-driven ocean circulation around Antarctica causes deep waters to upwell to the surface (Fig. 1), allowing metabolic CO_2 accumulated during centuries of deep-sea respiration to be released to the atmosphere. Second, wind-driven upwelling also supplies surface waters with abundant dissolved inorganic nutrients. Today, these nutrients are utilized inefficiently by phytoplankton, as evidenced by high nutrient concentrations in surface waters throughout the year (Fig. 2).

A change in the efficiency of the Southern Ocean's biological pump has been long recognized to be a potential source of variability in atmospheric CO_2 (Knox and McElroy, 1984; Sarmiento and Toggweiler, 1984; Siegenthaler and Wenk, 1984). Here, "Biological Pump" refers to the ensemble of processes by which marine organisms consume dissolved inorganic nutrients and CO_2 during photosynthesis and package these elements into organic material, which is then exported, largely by gravitational settling, into the deep sea. The "efficiency" of the biological pump can be viewed as the fraction of nutrients upwelled into surface waters that is consumed there by phytoplankton and exported as organic matter to the deep sea. Nutrients that are not consumed biologically are carried back into the deep sea as "preformed" nutrients during the formation of deep and intermediate water masses. Consequently, the efficiency of the biological pump is influenced both by the rate of nutrient supply by upwelling and by the rate of nutrient loss by biological consumption. High nutrient concentrations today in Southern Ocean surface waters (Fig. 2) reflect that the biological pump is running at less than maximum efficiency. Reduced surface nutrient concentrations in the Southern Ocean, caused either by decreasing the rate of upwelling while nutrient consumption and export of organic

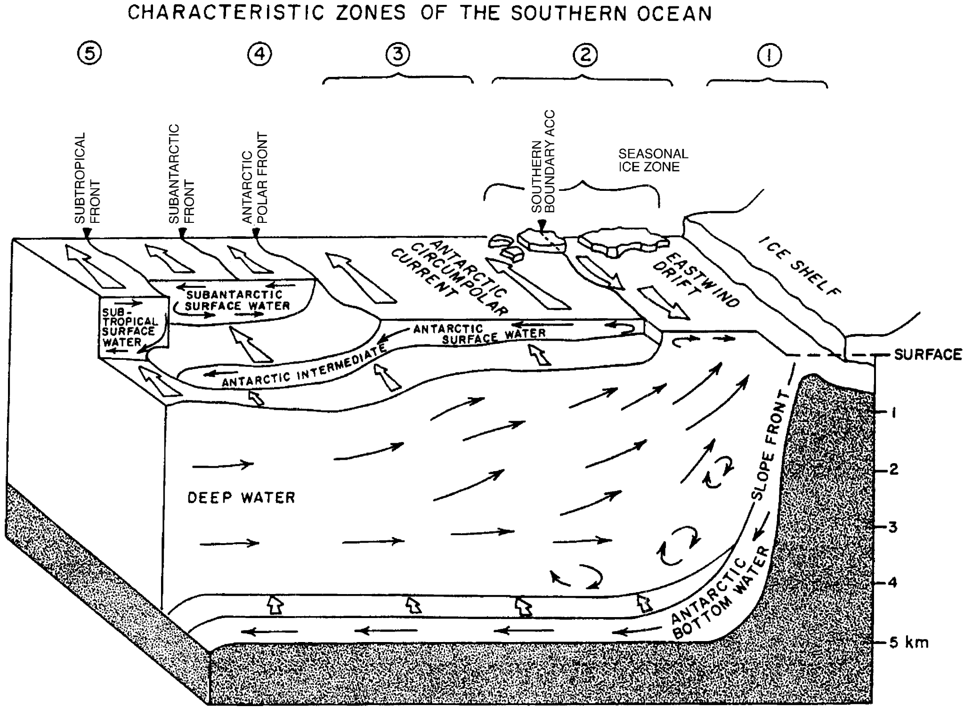


Fig. 1. Schematic illustration of the large-scale circulation of the Southern Ocean (redrawn from Lutjeharms et al., 1985). Circumpolar zones identified by numbers include (1) coastal or continental shelf waters; (2) the seasonal ice zone, which extends from the coast northward into the ACC; (3) the zone between the northern limit of winter sea ice and the APF, referred to as the Permanently Open Ocean Zone; (4) the Polar Front Zone, lying between the APF and the Subantarctic Front; and, (5) the Subantarctic Zone, lying between the SAF and the STF. To simplify the discussion in this paper, the entire region south of the APF is referred to here as the Antarctic Zone, while the entire region between the APF and the STF is referred to as the Subantarctic Zone. Combining the zones in this fashion is justified by the common biogeochemical response to climate change within each of these broadly defined regions.

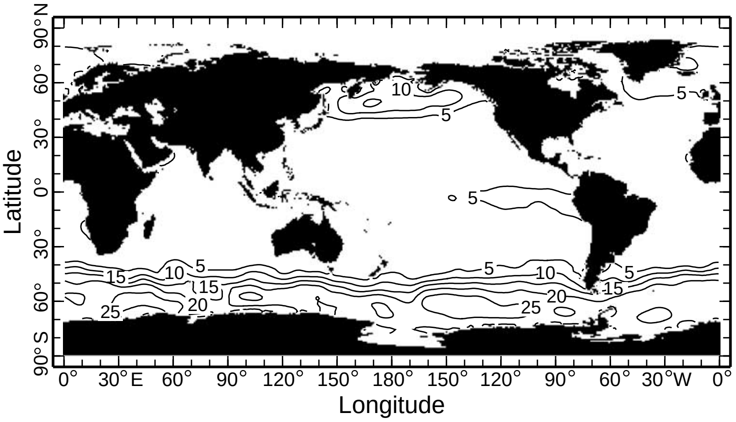


Fig. 2. Annual average surface (10 m) nitrate concentrations in the global ocean. From the World Ocean Atlas (Conkright et al., 1994); processed and made available through http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/.ANNUAL/.NO3/.

matter remain constant, or by increasing consumption and export while holding the rate of upwelling constant, would result in a net transfer of CO_2 from the atmosphere to the deep sea. Either route to an increase in the efficiency of the Southern Ocean's biological pump could contribute to the lower atmospheric CO_2 observed in glacial sections of polar ice cores (see Sigman and Boyle, 2000, Archer et al., 2000, and Elderfield and Rickaby, 2000, for recent reviews as well as a discussion of important feedbacks associated with $CaCO_3$ compensation).

Regulation of atmospheric CO_2 by the high-latitude oceans has been challenged recently by Archer et al. (2000), who noted that in General Circulation Models (GCMs), in contrast to their box-model predecessors, atmospheric CO_2 levels are relatively insensitive to perturbations of the high-latitude oceans. Whether or not this is true of the real ocean–atmosphere system is unknown. Vertical mixing rates may be overestimated in GCMs, which would increase the importance of the tropical oceans in regulating atmospheric CO_2, and reduce the sensitivity of atmospheric CO_2 to surface ocean conditions at high-latitudes. The degree to which vertical mixing in GCMs is overestimated is unknown, in part because the actual rates of vertical mixing in the oceans remain poorly constrained (Archer et al., 2000). Better constraints on the long-term and large-scale diffusivity of the ocean, and its parameterization in GCMs, are required to improve our understanding of the sensitivity of atmospheric CO_2 to high-latitude processes.

We know that the CO_2 content of the atmosphere changed in the past and that these changes were correlated with changes in temperature over Antarctica. We seek to understand the role of the Southern Ocean, if any, in effecting these changes. Here we review popular strategies and recent efforts to reconstruct past changes in the efficiency of the Southern Ocean's biological pump. We identify limitations inherent in many of these strategies and then offer some plausible scenarios for the circulation and biogeochemistry of the Southern Ocean during the LGM.

2. Assessing the efficiency of the biological pump: difficulties encountered with the "direct approach"

Surface nutrient concentrations provide the most direct measure of the efficiency of the biological pump. Although paleo-nutrient concentrations cannot be measured directly, the carbon isotopic composition (expressed as $\delta^{13}C$) and Cd/Ca ratio of foraminiferal calcite have been proposed as nutrient concentration proxies on the basis of the correlation in the modern ocean between nutrient (nitrate and phosphate) concentrations and the $\delta^{13}C$ of dissolved inorganic carbon (DIC, e.g., Kroopnick, 1985; Curry et al., 1988; Duplessy et al., 1988; Charles and Fairbanks, 1990) as well as with the concentration of dissolved Cd (e.g., Boyle, 1988). If foraminifera shells faithfully record the $\delta^{13}C$ of DIC and the Cd/Ca ratio of ambient seawater during calcification, if the modern relationships between nutrient concentrations and these parameters existed in the past, and if the original composition of foraminiferal calcite is preserved without modification during early diagenesis and burial, then, in principle, one can infer past changes in surface nutrient concentration from the composition of planktonic foraminifera.

2.1. Foraminiferal $\delta^{13}C$

Inferring surface nutrient concentrations from the $\delta^{13}C$ of planktonic foraminifera is complicated by several factors. In high-latitude surface waters, the $\delta^{13}C$ of DIC departs from the global relationship between the $\delta^{13}C$ of DIC and nutrient concentration because of the thermodynamic enrichment of DIC in ^{13}C by gas exchange with the atmosphere at low temperature (Mook et al., 1974; Broecker and Maier-Reimer, 1992; Charles et al., 1993). In addition, multiple factors cause the $\delta^{13}C$ of foraminiferal $CaCO_3$ to depart from that expected for thermodynamic equilibrium with ambient DIC. These factors include the carbonate ion concentration in seawater, the carbon isotopic composition of the foraminifera's diet, and temperature (Spero et al., 1997; see also review by Kohfeld et al., 2000). The $\delta^{13}C$ of *Neogloboquadrina pachyderma*, often the dominant planktonic foraminifera species in polar oceans, is well below that expected for equilibrium with DIC in Antarctic waters (defined as the region south of the Polar Front; Fig. 1), and the amplitude of the isotopic disequilibrium increases equatorward (Kohfeld et al., 2000).

Kohfeld et al. (2000) used a core-top data set to calibrate the sensitivity coefficients for carbon isotope disequilibrium due to temperature and diet. Using these results, together with estimated carbonate ion sensitivity based on laboratory incubations (Spero et al., 1997), Kohfeld et al. showed that the $\delta^{13}C$ in *N. pachyderma* recovered from glacial sediments in the Atlantic sector of the Southern Ocean cannot be used to distinguish differences in surface nutrient concentrations between the LGM and today. When the sensitivity of shell $\delta^{13}C$ to carbonate ion concentration, dietary $\delta^{13}C$, and temperature were each multiplied by the LGM value for the corresponding parameter, the corrected LGM shell $\delta^{13}C$ values were indistinguishable from Holocene values throughout the latitude range examined, from north of the Subtropical Front (STF) to the margin of Antarctica. This conclusion is surprising in light of the large amplitude ($\sim 1‰$) of the glacial–interglacial change in the $\delta^{13}C$ of *N. pachyderma* in this region. This large amplitude, however, reflects the substantial sensitivity of carbon isotope disequilibrium to environmental parameters. More significant, here, is the assessment by Kohfeld et al. that the combined corrections associated with these environmental factors, which must be applied in order to derive $\delta^{13}C$ of DIC from the $\delta^{13}C$ of $CaCO_3$, are three to four times greater than the amplitude of the glacial–interglacial change in $\delta^{13}C$ of *N. pachyderma*. Given that the propagated uncertainty associated with these combined corrections is large compared to the total glacial–interglacial signal (Kohfeld et al., 2000), reliable reconstructions of surface nutrient concentrations cannot presently be obtained for the Southern Ocean using the $\delta^{13}C$ of *N. pachyderma*.

2.2. Foraminiferal Cd/Ca ratios

Interpreting Cd/Ca ratios of foraminiferal calcite suffers from complications as severe as those plaguing the interpretation of $\delta^{13}C$. Analysis of metal/calcium ratios in benthic foraminifera recovered from a series of cores collected at different water depths, corresponding to different levels of bottom water saturation with respect to calcite, led McCorkle et al. (1995) to suggest that foraminiferal shells preferentially lose trace metals such as Cd during partial dissolution, an artifact that may have been exacerbated during the LGM when deep waters of the Southern Ocean were more corrosive toward $CaCO_3$ than today (Howard and Prell, 1994; Oppo and Horowitz, 2000). The results of McCorkle et al. (1995) were derived using a single species of benthic foraminifera, and more recent results suggest that the finding of McCorkle et al. may reflect a sensitivity of metal uptake by that species to bottom-water carbonate ion concentration, rather than the preferential loss of trace metals during partial dissolution of the shells (T. Marchitto, pers. comm.). Therefore, although widely cited in paleoceanographic literature, it is not clear that the results of McCorkle et al. can be applied to planktonic foraminifera. Although evidence for preferential loss of certain metals (e.g., U, Mg) during partial dissolution of planktonic foraminifera growing at lower latitudes is established by several studies (Russell et al., 1994; Brown and Elderfield, 1996; Rosenthal et al., 2000b), the extent to which partial dissolution preferentially releases Cd from polar planktonic foraminifera remains to be determined.

Reconstructing surface nutrient concentrations may be further complicated by a temperature dependence of Cd uptake into foraminiferal shells. Down-core variability in Cd/Ca ratios of Subantarctic planktonic foraminifera bears a strong resemblance to variability in Mg/Ca ratios, which are known to be sensitive to temperature (Rickaby and Elderfield, 1999). Consequently, rather than reflecting climate-related changes in surface-water nutrient concentrations, Cd/Ca ratios measured in planktonic foraminifera (Rosenthal et al., 1997; Rickaby and Elderfield, 1999; Elderfield and Rickaby, 2000) may reflect temperature-related changes in the partition coefficient for uptake of Cd into foraminiferal calcite. If these initial findings are supported by further calibration studies, then independent temperature corrections will be required to reconstruct nutrient concentrations from the Cd/Ca ratios of foraminiferal calcite (Elderfield and Rickaby, 2000).

2.3. Calcification depths

Polar planktonic foraminifera often calcify at depths well below the mixed layer (Kohfeld et al., 1996; Kohfeld, 1998), further complicating the reconstruction of surface nutrient concentrations from the composition of planktonic foraminifera shells. Whereas, it is the concentration of nutrients in the surface mixed layer that provides a measure of the strength of the biological pump, much of the calcite in shells of polar planktonic foraminifera is formed at depths below the mixed layer. Summer mixed-layer depths in the Southern Ocean are generally less than 100 m, and often much less (Levitus and Boyer, 1994). Consequently, the chemical and isotopic composition of the $CaCO_3$ formed by polar planktonic foraminifera at depths much greater than this (Fig. 3) may be defined primarily by nutrient-rich subsurface waters, rather than by conditions in the surface layer.

Better constraints on the sensitivity to environmental variables of the elemental and isotopic composition of polar planktonic foraminifera are clearly needed. Similarly, the depth dependence of foraminifera calcification, and its seasonality, need more complete characterization as well. These issues should be given high priority for future research. Until then, these geochemical proxies must be used with caution when reconstructing

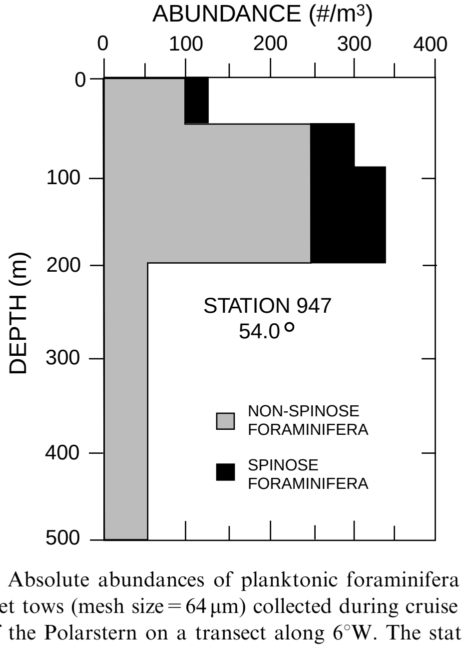


Fig. 3. Absolute abundances of planktonic foraminifera from multinet tows (mesh size = 64 μm) collected during cruise ANT X/6 of the Polarstern on a transect along 6°W. The station is approximately 4° south of the APF. Counts were completed by C. Klaas, Alfred Wegener Institute. Figure redrawn from Kohfeld (1998).

past changes in surface nutrient concentrations in the Southern Ocean.

2.4. An alternative indirect approach

In the absence of unequivocal proxies for surface nutrient concentrations, many investigators have pursued an indirect approach to assess past changes in the efficiency of the Southern Ocean's biological pump. An indirect approach is, of necessity, more complicated, in that changes in circulation and changes in export production must be evaluated independently. In the following sections, we first review the current understanding of the physical setting of the Southern Ocean during the LGM to assess the overall consistency with the physical setting of proposed productivity and circulation scenarios. We then review information concerning proxies of nutrient utilization and phytoplankton growth rate, building toward a limited suite of plausible, though still competing, scenarios describing the Southern Ocean's biological pump during the LGM.

3. Physical setting during the LGM: winds, ocean circulation, and sea ice

3.1. Mean position and strength of the westerlies

Circulation in the Southern Ocean is directly related to the mean position and intensity of the westerlies, as these winds drive both the zonal flow of the Antarctic Circumpolar Current (ACC) and the meridional overturning of deep water associated with Ekman divergence and upwelling. Geostrophic balance in the ACC determines the mean slope of isopycnals and, hence, defines the density surfaces that outcrop south of the Antarctic Polar Front (APF). The rate of upwelling and corresponding flux of nutrients from outcropping deep waters is determined by wind stress and Ekman transport (Gargett, 1991). Additionally, the mean position and intensity of the westerlies regulates the divergence (northward transport) of sea ice, which, in turn, constrains productivity by filtering incident solar radiation. The wind-dependent depth of the mixed layer, combined with the depth penetration of light, determines the balance between photosynthesis and respiration. Likewise, the entrainment and transport of continental dust to an iron-limited Southern Ocean (Martin, 1990) depends on the latitude and intensity of the westerlies.

Reconstructions of glacial winds have produced widely divergent views. One view, commonly cited in paleoceanographic literature, is that the westerlies during the LGM were located equatorward of their average modern position (Heusser, 1989a,b) while others (Markgraf, 1987,1989,1993) propose that their mean position was shifted poleward of their present position.

To understand better the nature of LGM wind patterns, the Paleoclimate Model Intercomparison Project (PMIP) ran a suite of atmospheric GCMs for LGM boundary conditions. Using prescribed (CLIMAP) sea-surface temperatures (SSTs), all of the PMIP models showed some degree of southward shift during the LGM of the southern hemisphere westerlies (Valdes, 2000). Some models produced an intensification of the westerlies while others did not.

Additional insights into LGM winds were obtained using the climate model of the UK Universities Global Atmospheric Modeling Program (UGAMP), which has a higher spatial resolution than the models used in the PMIP studies, thereby allowing investigators to examine mid-latitude storm tracks. In this model, the zonal average position of the westerlies during the LGM lay poleward of their present position, and the mean intensity was greater than today, although with substantial zonal variability (Valdes, 2000; Wyrwoll et al., 2000). These changes resulted in part from reduced sea-level pressure within approximately 60°–70°S, which led to an enhanced surface pressure gradient from 40°S to 60°S compared with today (Valdes, 2000). The mean position of the LGM westerlies produced by the model is generally consistent with continental paleoclimate records from Australia (Wyrwoll et al., 2000), and the intensification of the westerlies is supported by the increased wind strengths during the LGM inferred from the concentrations of dust and sea salt extracted from the Vostok ice core (Petit et al., 1981).

Evidence for a LGM position of the westerlies north of their present mean location comes primarily from the extent of mountain glaciers and reconstructed vegetation in southern South America (Heusser, 1989a,b; see also a recent review by McCulloch et al., 2000). Glacial expansions and vegetation indices are interpreted to indicate increased precipitation during the LGM in central Chile, which, in turn, is attributed to a northward shift in the westerlies. However, complex weather patterns around southern South America may have confused the interpretation of the proxy evidence for increased precipitation (Wyrwoll et al., 2000). Results from the LGM run of the UGAMP model show an increase in frequency of storms tracking from the Pacific Ocean into the coast of South America (Valdes, 2000). This, together with the broadening of the latitude belt of the westerlies at the longitude of South America (Wyrwoll et al., 2000), could account for greater precipitation during the LGM. A mean position of the westerlies during the LGM south of their present latitude, together with a possible intensification of the winds, imply that northward Ekman transport of Antarctic surface waters, and the associated wind-driven upwelling, would have been similar to, if not greater than, observed today (Keeling and Visbeck, 2001).

3.2. Circulation of the glacial Southern Ocean

Today, upwelling south of the APF ventilates the deep sea, and supplies nutrients to Antarctic surface waters (Fig. 1). The efficiency of the Southern Ocean's biological pump during the LGM is as sensitive to the rate and location of nutrient supply via upwelling as it is to the consumption of nutrients by biological productivity. It has been proposed that two notable features of Southern Ocean circulation during the LGM may have differed greatly from today: (1) The positions of the major fronts encircling Antarctica, and associated with the ACC, were shifted northward under glacial conditions by several degrees of latitude, and (2) Deep waters of the glacial Southern Ocean were more isolated from ventilation with the atmosphere, involving, perhaps, an increase in shallow stratification south of the APF. We examine here the basis for these interpretations because any assessment of the biological pump depends strongly on the character of overturning circulation.

3.2.1. The position of the Polar Front during the LGM

In the modern ocean, the principal fronts of the ACC (Fig. 1) serve as geographic boundaries for distinct pelagic ecosystems. The sediment record provides unequivocal evidence that these ecosystems migrated equatorward under glacial conditions, illustrated best by the northward shift in the zone of maximum opal deposition (e.g., Charles et al., 1991; Mortlock et al., 1991). This equatorward migration of ecosystems during the LGM has been interpreted to reflect a corresponding northward shift in the mean position of the fronts (Hays et al., 1976; Prell et al., 1980; Howard and Prell, 1992). An opposing view is that the fronts could not have migrated significantly because their position is constrained throughout much of the Southern Ocean by interaction of the flow of the ACC with bottom topography (see review by Moore et al., 1999). Rather than reflecting a migration of the fronts, the northward shift of ecosystems during the LGM would then reflect lower SSTs, altered nutrient concentrations, or other environmental factors affecting the structure of pelagic ecosystems (Moore et al., 2000). Because the APF serves as the northern limit of wind-driven upwelling of deep water, a comprehensive reconstruction of the Southern Ocean's biological pump during the LGM requires an accurate knowledge of the position of the APF at that time.

A recent study of the oxygen isotope composition ($\delta^{18}O$) of foraminiferal calcite helps resolve this issue. The $\delta^{18}O$ of foraminiferal calcite reflects primarily the temperature of calcification (e.g., Lynch-Stieglitz et al., 1999) and, to a lesser extent, the salinity. Temperatures at shallow depths (e.g., 100–200 m) in low latitudes are much greater than those of the deep sea, but decrease rapidly poleward of temperate latitudes. In the modern ocean, temperatures at these shallow depths reach values close to the temperature of the deep sea at about the location of the APF. This relationship is not surprising, given the pervasive upwelling of deep water that occurs south of the APF (Fig. 1). In response to this temperature distribution, one finds today that the $\delta^{18}O$ of planktonic foraminifera in subtropical to temperate waters is well below that of benthic foraminifera living at the same latitudes, but this difference diminishes poleward and effectively disappears at approximately the position of the APF (Fig. 4a). Matsumoto et al. (2001) found no detectable difference between the LGM and the Holocene in the latitude at which $\delta^{18}O$ values of planktonic (*N. pachyderma*) and benthic foraminifera converged in the Atlantic sector of the Southern Ocean (Fig. 4), and concluded that the mean position of the APF during the LGM was essentially unchanged from its present location. These results support the view that the position of the APF is constrained by bottom topography, and that the northward shift in ecosystems that occurred during the LGM-reflected changes in environmental conditions in surface waters (e.g., temperature, nutrient concentrations) rather than a shift in the position of the APF.

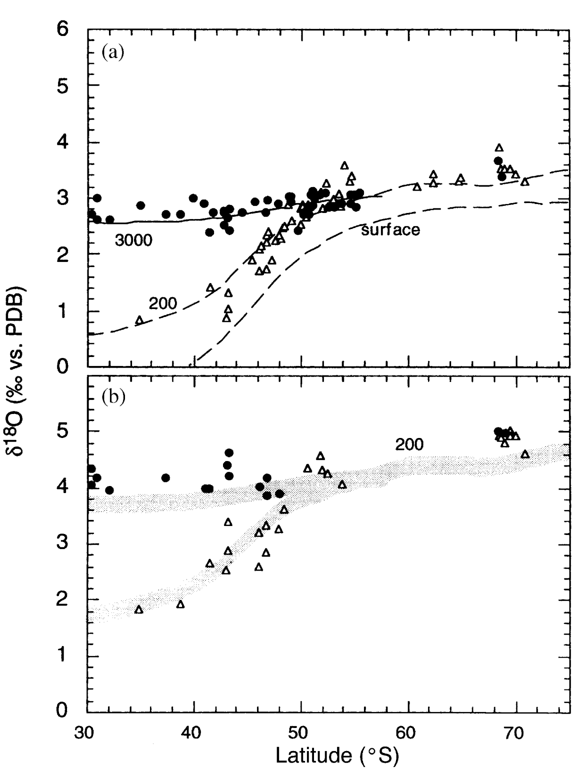


Fig. 4. South Atlantic (A) Holocene and (B) LGM meridional $\delta^{18}O$ distributions of planktonic (*N. pachyderma*; open triangles) and benthic (*Cibicidoides* species; filled circles) foraminifera. Calcite $\delta^{18}O$ in equilibrium with modern seawater is presented in (A) for the surface (dashed line), 200 m (dashed line), and 3000 m (solid line). Thick shaded lines in (B) represent the 200 m and the 3000 m equilibrium calcite $\delta^{18}O$ lines shifted by +1‰ to +1.3‰, the range of estimates for the change in global ocean $\delta^{18}O$ due to the presence of continental ice sheets during the LGM. The APF is located at about 50°S. Figure reproduced from Matsumoto et al. (2001).

3.2.2. *Stratification of the Southern Ocean during the LGM*

Increased stratification of the Southern Ocean has been invoked in several recent studies to account for reduced atmospheric CO_2 during glacial periods. The general principle underlying these scenarios is that increased stratification leads to a reduction in the upwelling that exposes deep waters to the atmosphere, thereby reducing the efflux of metabolic CO_2 and effectively trapping more CO_2 in the deep sea during glacial periods than occurs today. Most "increased stratification" scenarios call upon an increase in the salinity-driven stratification of surface waters south of the APF (Francois et al., 1997; Frank et al., 2000; Sigman and Boyle, 2000), although a glacial scenario encompassing increased stratification of the deep sea also has been proposed (Toggweiler, 1999).

Implicit in the conceptual models invoking increased stratification and reduced upwelling south of the APF is a northward shift in the zone of wind-driven upwelling, accompanied by a shift from deep to intermediate depths in the principal source of upwelled water (Francois et al., 1997; Sigman and Boyle, 2000). This northward shift during the LGM in the zone of upwelling is argued to have been a response, in part, to the contemporary northward position (relative to today) of the mean latitude of the westerlies (Francois et al., 1997; Sigman and Boyle, 2000). This scenario is inconsistent, however, with the evidence for a southerly shift in the position of the westerlies during the LGM (Section 3.1). Under persistent forcing by the winds, any low-salinity cap imposed on Antarctic surface waters would have been removed by northward Ekman transport and replaced by upwelled deep water. Furthermore, although it may seem counterintuitive, an increase in stratification south of the APF would have produced a greater rate of upwelling of deep waters, rather than a reduction, as the reduced baroclinicity of a more-stratified ocean would have shifted the balance between eddy transport across the ACC and upwelling toward increased upwelling (Keeling and Visbeck, 2001). Therefore, it is difficult to envision a combination of factors that would have permitted the inferred reduction in upwelling south of the APF during the LGM, argued to have been as much as an order of magnitude (Francois et al., 1997; Sigman and Boyle, 2000), under conditions where wind forcing was equal to, or greater than, that which exists today (see also Moore et al., 2000).

Reduced upwelling of deep water and a shift toward a shallower cell of meridional overturning called upon by these "increased stratification" models is also inconsistent with diatom production during the LGM inferred from opal burial in Southern Ocean sediments. Biogenic opal has a deeper regeneration cycle than that of organic nutrients, leading to the observed enrichment of dissolved Si in deep waters and an impoverishment of dissolved Si relative to other nutrients in intermediate waters (Broecker and Peng, 1982). Consequently, one would expect the substantial reduction in the upwelling of deep waters, and the corresponding shift to increased upwelling of intermediate waters, invoked by these "stratification" scenarios to have induced an overall decrease in diatom productivity. However, this expectation is not supported by paleoceanographic evidence. Opal burial during the LGM, when corrected for sediment focusing and integrated across the zone of diatomaceous sediments, was no less than today (Kumar et al., 1995; Frank et al., 2000). We interpret the record of opal burial during the LGM to indicate that the supply of dissolved Si to the euphotic zone by the upwelling of deep water was at least as large as that which exists today (see also Section 4.2).

Isolation and reduced ventilation of Circumpolar Deep Water (CPDW) required by the "increased stratification" scenarios would have been accompanied by an increase in concentrations of dissolved nutrients (and in nutrient-related geochemical proxies) and a corresponding reduction in the concentration of dissolved oxygen in deep waters. Evidence to support this view is derived largely from the interpretation of the δ^{13}C of benthic foraminifera. The δ^{13}C values of benthic foraminifera in certain areas of the glacial Southern Ocean were lower than found anywhere else, suggesting that the Southern Ocean had the most nutrient-rich and poorly ventilated (low oxygen concentrations) deep waters of the entire glacial ocean (Michel et al., 1995; Francois et al., 1997; Toggweiler, 1999).

Carbon isotopic evidence for reduced ventilation of CPDW during the LGM has been challenged, however, based on the tendency for benthic foraminifera to incorporate isotopically light metabolic CO_2 into their shells when growing under conditions of elevated rain of organic matter, known as the "Mackensen effect" (Mackensen et al., 1993; Bickert and Wefer, 1999). Most glacial benthic δ^{13}C results from the Southern Ocean have been obtained from sites near and just north of the APF, a region where independent evidence suggests that export production during the LGM was greatly elevated compared to today (Kumar et al., 1995; Rosenthal et al., 1995; Anderson et al., 1998; see also Section 4). This evidence for increased export production leads to concern that the δ^{13}C results may not record actual changes in deep-water composition. Indeed, when the global distribution of benthic δ^{13}C was reconstructed for the LGM excluding results from sites suspected of having experienced elevated fluxes of biogenic material to the sea bed, evidence for the isolation of CPDW disappeared; the inferred pattern of global circulation differed only subtly from that which exists today (Matsumoto and Lynch-Stieglitz, 1999). Furthermore, a recent synthesis of new and previously published benthic δ^{13}C results from the Pacific Ocean indicates that, as today, the deep Pacific was ventilated from the south during the LGM (Matsumoto, 2000). These results also show that the deep water ventilating the Pacific during the LGM had much greater δ^{13}C (nutrient concentrations much lower) than inferred previously for CPDW (Michel et al., 1995;

Toggweiler, 1999), adding further evidence that the benthic δ^{13}C results used to infer isolation of CPDW during the LGM had been compromised by the "Mackensen effect" (Mackensen et al., 1993).

The global distribution of benthic δ^{13}C during the LGM, as described above, together with evidence for upwelling south of the APF inferred from the distribution of planktonic and benthic δ^{18}O, lead us to conclude that the major features of ocean circulation in the glacial Southern Ocean differed little from those that exist today. This interpretation is consistent with, if not required by, the inferred wind forcing of ocean circulation during the LGM (Section 3.1). It is also consistent with evidence from the Cd/Ca ratios of benthic foraminifera, which suggest little change between the LGM and the Holocene in the nutrient content of CPDW (Boyle, 1992; Lea, 1995; Rosenthal et al., 1997; Oppo and Horowitz, 2000).

3.3. Sea ice

Sea ice influences the efficiency of the biological pump through obvious direct effects, such as the attenuation of incident solar radiation, but also indirectly through the perturbation of air–sea gas exchange, and through its influence over dynamic processes and thermodynamic budgets dependent on ocean–atmosphere fluxes of heat and momentum. Sea-ice cover is also a primary factor influencing earth's albedo and radiation budget. Early reconstructions of the position of maximum sea-ice cover (for both summer and winter) during the LGM relied on sediment lithology, and its relationship to modern analogs. These reconstructions for the LGM implied an equatorward extension of winter sea-ice of several degrees of latitude, relative to today, and a summer sea-ice cover comparable to that in winter today (CLIMAP Project Members, 1976; Hays et al., 1976; CLIMAP Project Members, 1981; Cooke and Hays, 1982).

Newer sea-ice reconstructions exploit knowledge of the preferred habitat of selected diatom species, whether associated with sea ice or open-water conditions. The maximum winter extent of sea ice during LGM reconstructed using diatom-based transfer functions (Crosta et al., 1998b; Crosta et al., 1998a; Gersonde and Zielinski, 2000) is similar to that derived previously from sediment lithology. All methods place the winter maximum sea-ice extent during the LGM in the vicinity of the APF. Substantial disagreement still exists, however, concerning the summer extent of sea ice during the LGM. Crosta et al. (1998a, b) interpret the open-water species of diatoms preserved in LGM sediments to reflect ice-free conditions during LGM summers nearly as far south as summer ice-free conditions exist today. In contrast, Gersonde and Zielinski (2000) interpret the low rate of opal burial in LGM sediments located more than a few degrees south of the APF to indicate year-round ice cover. According to their reconstruction, summer sea ice during the LGM extended to about the position of maximum winter sea-ice extent today. Further development and application of sea-ice proxies is needed to resolve the extent of summer sea ice during the LGM. Nevertheless, it is clear that sea ice was more extensive during the LGM, and this may have had a substantial impact on the conditions regulating phytoplankton growth.

3.4. Summary of physical setting

An internally consistent picture of the physical setting of the Southern Ocean during the LGM can be described as follows. The mean position of glacial westerlies lay poleward of their modern location, and mean wind velocities were greater than today. In response to colder air temperatures, winter sea ice during the LGM extended further north than today, to the vicinity of the APF. The extent of summer sea ice during the LGM remains unresolved. However, if summer air temperatures warmed during the LGM at least enough to prevent widespread formation of sea ice, then the northward divergence of ice under the influence of the westerlies would have created open-water conditions well to the south of the APF, at least intermittently. Greater production of sea ice during winter, and melting during summer, would have enhanced surface stratification during the LGM relative to today in the principal regions of sea-ice melting. How this would have impacted nutrient utilization and deep-sea ventilation would depend on the amount of sea ice formed and melted each year, as well as on the timing and location of melting. However, the compelling and self-consistent evidence cited above indicates that ocean circulation during the LGM, including the mean position of ACC fronts as well as the upwelling and ventilation of deep water south of the APF, was not radically different from that which occurs today, although subtle differences accompanying the changes in wind and sea ice are to be expected. The task now is to synthesize results from proxies of export production, nutrient utilization efficiency, and phytoplankton growth rate in a way that is consistent with these boundary conditions.

4. Export production

Reconstructions of export production in the Southern Ocean during the LGM have produced substantially divergent results (Table 1). Most studies suggest that export production during the LGM in regions well to the south of the APF was lower than today, while export production in Subantarctic waters, defined here (Fig. 1) as the entire region between the APF and the STF, was greater (Kumar et al., 1995; Rosenthal et al., 1995; Francois et al., 1997; Nurnberg et al., 1997; Anderson et al., 1998; Elderfield and Rickaby, 2000; Frank et al., 2000). However, differences exist among investigators concerning the degree to which export production changed within each zone, and a recent assessment suggests substantially greater export production during the LGM throughout the Southern Ocean (Moore et al., 2000). The principal uncertainties limiting our assessment of the average export production of the entire Southern Ocean during the LGM derive from the paucity of records from the Pacific sector of the Southern Ocean, and from disagreement among investigators concerning the interpretation of different proxies of export production extracted from Subantarctic sediments.

Before examining in greater detail the interpretation of proxy records from Subantarctic sediments, we note that recent results from the SW Pacific sector of the Southern Ocean are generally consistent with the more extensive data base from the Atlantic and Indian sectors. Organic biomarker records from a Subantarctic site on the South Tasman Rise (48°S, 147°E) indicate that export production was greater during the LGM than during the Holocene (Ikehara et al., 2000). In contrast to greater export production during the LGM over the South Tasman Rise, results from cores recovered at sites south of the APF at ~170°W show that accumulation rates of opal, organic carbon, and excess barium, all corrected

Table 1
Export production in the glacial Southern Ocean inferred by previous studies, expressed by comparing LGM levels to a modern (Holocene) standard

	Zone		Proxy(ies) interpreted	Reference(s)
	Subantarctic[a]	Antarctic[b]		
(1)	LGM $\geqslant$ Holocene	LGM $\ll$ H	Opal AR[c]; Pa/Th, xsBa, Δ^{15}N	Francois et al., 1997 and Frank et al., 2000
			Cd/Ca of planktonic foraminifera	Elderfield and Rickaby, 2000
			xsBa	Nurnberg et al., 1997
(2)	LGM $\gg$ Holocene	LGM $<$ H	Opal AR[c]; Corg AR[c]	Kumar et al., 1995 and Anderson et al., 1998
			^{231}Pa/^{230}Th, ^{10}Be/^{230}Th	
			xsBa, UA[d]	
			U_A	Chase et al., 2001
(3)	LGM $>$ H	LGM $>$ H	Modern analog	Moore et al., 2000

[a] North of the modern position of the APF (Fig. 1).
[b] South of the modern position of the APF (Fig. 1).
[c] AR = accumulation rate corrected for sediment focusing.
[d] U_A = authigenic uranium.

for sediment focusing, were much lower during the LGM than during the Holocene (Fig. 5). The principles underlying the interpretation of these proxies will be described in the following section. Here, we note only that these new Pacific records are consistent with results from earlier studies of the Atlantic and Indian sectors of the Southern Ocean.

4.1. Proxies of export production

While several biogeochemical tracers have been proposed to serve as proxies for export production, the burial rates of organic carbon, opal and excess barium have been used most widely. Of these, the basis for using organic carbon is the most straightforward. If the fraction of organic carbon exported from surface waters that is preserved and buried in sediments remains constant through time, then the rate of carbon burial in sediments would scale linearly with export production. Unfortunately, preservation of organic matter is low, highly variable, and cannot be quantified a priori, even with knowledge of past changes in environmental boundary conditions (Lochte et al., in press).

The burial rate of opal is obviously linked to the export, preservation and burial of diatoms, and it has been suggested that the burial rate of opal may serve as a proxy for export production (Ragueneau et al., 2000). This suggestion finds support in recent studies that indicate that diatoms produce much of the organic matter exported from surface waters (Buesseler, 1998; Boyd and Newton, 1999), even in areas dominated by other phytoplankton assemblages. However, like organic matter,

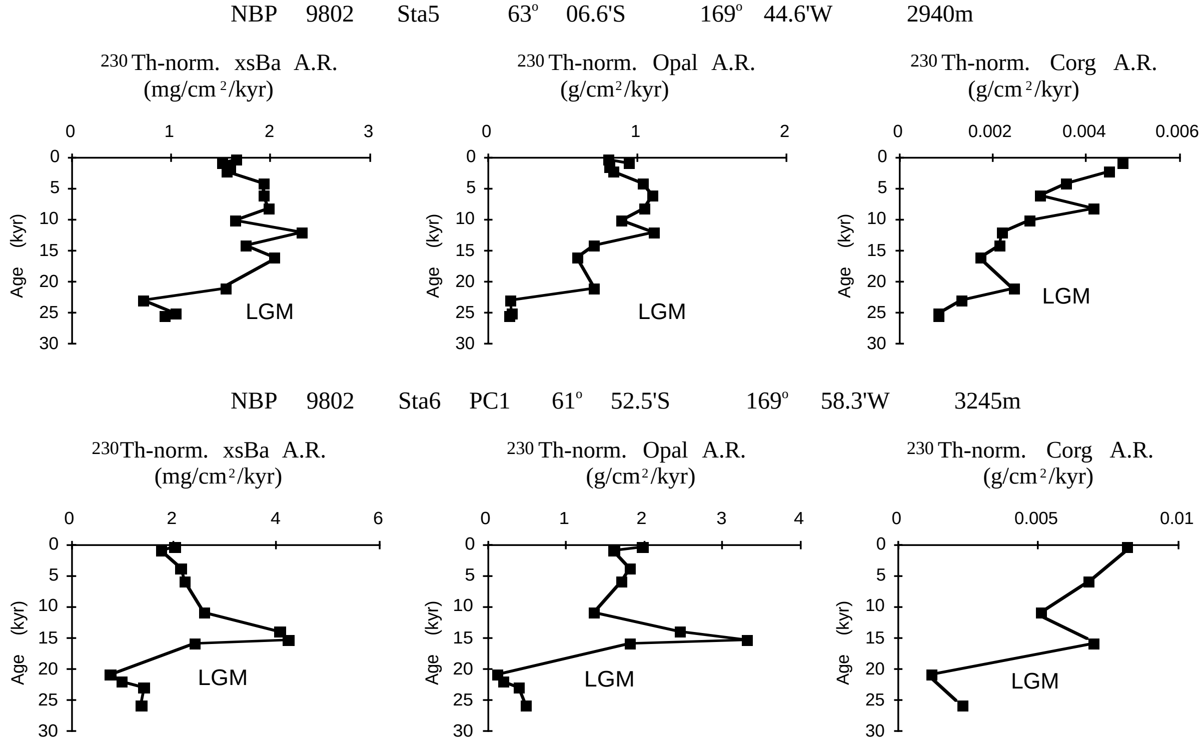


Fig. 5. Accumulation rates of excess barium, opal and organic carbon at two sites in the SW Pacific sector of the Southern Ocean. Both core sites lie south of the APF which, at this longitude, is located between 60°S and 61°S. Accumulation rates have all been normalized to ^{230}Th to correct for sediment focusing. Ages are derived from AMS ^{14}C dates of bulk $CaCO_3$ and are expressed in calendar years. Results replotted from Chase et al. (submitted).

preservation of opal is low and variable, and cannot be predicted a priori (Sayles et al., 2001).

Excess (non-lithogenic) barium (Ba) forms within biogenic aggregates by mechanisms not yet completely understood (Dehairs et al., 1980; Bishop, 1988). Early calibration studies (Dymond et al., 1992; Francois et al., 1995) found a good correlation between the flux of excess Ba and that of organic carbon collected by sediment traps. Combined with evidence that preservation of excess barium is much greater than that of organic carbon or opal (Dymond et al., 1992), these findings led to the development of algorithms to derive export production from the burial rate of excess Ba (Dymond et al., 1992; Francois et al., 1995). Excess Ba has since been used widely in paleoproductivity studies, although more recent work has shown that the correlation between excess Ba and organic carbon in the expanded data base derived from analysis of sediment trap samples is much reduced (Dymond and Collier, 1996). The use of excess Ba as a paleoproductivity proxy is further weakened by the recent discovery that preservation of excess Ba in sediments plummets under suboxic conditions (McManus et al., 1998). McManus et al. identified the presence of authigenic uranium (U_A; defined below) as a criterion to judge when redox conditions in sediments had reached the level where preservation of excess Ba declines, at which point the use of excess Ba as a productivity proxy becomes unreliable.

4.2. *Organic carbon, opal, and excess barium in southern ocean sediments*

With this background in mind, the historical difficulty in reconstructing glacial export production can be illustrated by comparing records of each proxy in a suite of cores recovered from the Atlantic sector of the Southern Ocean (Fig. 6). Accumulation rates of each proxy have been normalized to ^{230}Th to correct for sediment focusing (e.g., Suman and Bacon, 1989; Francois et al., 1990), which is pervasive throughout the Southern Ocean (Frank et al., 1999). At sites well to the south of the APF, represented by the core at ~54°S in Fig. 6, the burial rates of all proxies during the LGM were much lower than today. These results are consistent with those from other studies (Francois et al., 1997; Frank et al., 2000; Fig. 5) that have concluded that export production in the zone well south of the APF during the LGM was substantially lower than found today. Therefore, for the remainder of this section we focus on reconciling proxy records from the Subantarctic zone, where distinctly different interpretations arise from each proxy.

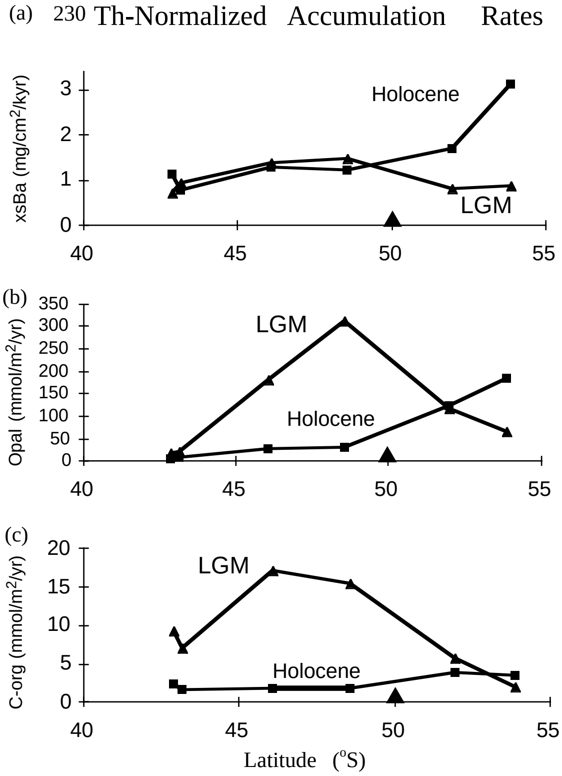


Fig. 6. Accumulation rates of (A) excess Ba, (B) opal and (C) organic carbon in six cores from the Atlantic sector of the Southern Ocean, collapsed onto a meridional transect for illustration. Accumulation rates are normalized to initial unsupported ^{230}Th to correct for sediment focusing (Suman and Bacon, 1989; Francois et al., 1990). Holocene values are presented as squares; LGM values as triangles. The triangle on the *X*-axis at 50°S marks the approximate position of the APF. In the South Atlantic, the Subantarctic Front is at ~45°S, while the STF is at ~40°S. Core IDs and locations: RC15-94 (42°54′S, 20°51′W); V22-108 (43°11′S, 03°15′W); RC15-93 (46°06′S, 13°13′W); RC13-254 (48°34′S, 05°07′E); RC13-271 (51°59′S, 04°31′E); RC13-259 (53°53′S, 04°56′W). Plotted data are from Kumar (1994) and Anderson (unpublished).

North of the APF there was no significant change between the LGM and the Holocene in burial of excess Ba (Fig. 6). Unlike excess Ba, however, the burial rates of opal and of organic carbon during the LGM were greater than during the Holocene (Fig. 6). Between the Subantarctic Front (~45°S) and the APF (~50°S), glacial burial rates of opal and of organic carbon were both several fold greater than those occurring during the Holocene. North of the Subantarctic Front, the glacial increase in opal burial was small in absolute terms, though still significant, whereas the burial rate of organic carbon during the LGM in this region was much greater than during the Holocene, both in a relative sense and in absolute terms. Clearly, the burial rate of each of these proxies cannot scale linearly with export production. Other factors must have influenced these records, and these factors must be understood before a reliable reconstruction of export production can be achieved.

4.3. Reconciling barium with opal and organic carbon

The recent discovery that preservation of excess Ba is poor under suboxic conditions (McManus et al., 1998) helps reconcile the excess Ba record with those of the other proxies. South Atlantic sediments at all but the southern-most site in Fig. 6 were enriched in U_A during the LGM (Kumar et al., 1995; Anderson et al., 1998). Failure of excess Ba to record accurately the higher glacial levels of export production north of the APF indicated by the accumulation rates of opal and of organic carbon (Fig. 6) consequently reflects the reduced preservation of excess Ba in the suboxic LGM sediments. Holocene sediments at these sites, in contrast to those deposited during the LGM, lack U_A (Kumar et al., 1995; Anderson et al., 1998), and preservation of excess Ba in Holocene sediments was much greater than in sediments deposited during the LGM. Since preservation of excess Ba at these sites has varied and because it cannot be evaluated quantitatively, excess Ba cannot be used reliably to reconstruct export production.

4.4. Authigenic uranium

Suboxic conditions leading to enrichment of U_A (and depletion of excess Ba) occur in sediments where oxygen is consumed by respiration faster than it can diffuse into sediments from bottom waters. Below the depth of anoxia, respiration is dominated by anaerobic bacteria, which produces the chemically reducing conditions under which dissolved U is precipitated from pore waters (Klinkhammer and Palmer, 1991). Although the presence of U_A indicates the unequivocal existence of suboxic conditions within the sediments, one cannot discern from the presence of U_A alone whether the suboxic conditions in glacial Subantarctic sediments were created by elevated respiration, fueled by high levels of export production and rain of organic matter to the sea bed, or by lower concentrations of oxygen in bottom waters. Furthermore, respiration within sediments does not discriminate between organic matter supplied vertically, by gravitational settling of biogenic material exported from surface waters, and that supplied laterally, advected by the strong deep currents that lead to extensive sediment focusing in the Southern Ocean (Frank et al., 1999, 2000).

By examining the pattern of U_A burial at a large number of sites distributed throughout the South Atlantic Ocean, Chase et al. (2001) were able to constrain more completely the conditions responsible for U_A enrichment in LGM sediments. Chase et al. ruled out sediment focusing as the primary factor leading to the formation of U_A because glacial Subantarctic sediments were found to be enriched in U_A whether glacial sediment accumulation rates were greater or less than those occurring during the Holocene. The ubiquitous presence of U_A in LGM sediments at sites located between the APF and the STF was found to be in stark contrast to the absence of U_A in LGM sediments at sites located north of the STF or south of the APF (Chase et al., 2001). The geographic limits on U_A deposition indicate that the suboxic sediment conditions required for U_A formation resulted primarily from elevated export production in the zone between the APF and the STF rather than from reduced oxygen concentrations in bottom waters, which would have influenced sites south of the APF and north of the STF as well.

Further support for elevated glacial export production in Subantarctic waters was obtained from a core (V22-109) recovered from the Discovery Seamount (41.97°S, 0.25°W) at a depth of 733 m. Relative to Holocene levels in this core, glacial sediments were enriched both in organic matter and in U_A (Chase et al., 2001). This site lies within Antarctic Intermediate Water, which was well ventilated during the LGM (Lynch-Steiglitz et al., 1994). Consequently, the elevated concentrations of organic carbon and of U_A in glacial sediments at this site cannot be attributed to reduced oxygen concentrations in waters bathing the sediments. Rather, these features can be explained only by a high rate of benthic respiration, driven by a rate of export production during the LGM that was much greater than that exists today at this site. The distribution of U_A in glacial sediments is, therefore, consistent with the substantial increase in export production in the Subantarctic zone inferred from organic carbon burial (Fig. 6).

4.5. *Variable organic carbon/opal ratios*

Burial rates of opal and organic carbon (Fig. 6) as well as authigenic uranium (Chase et al., 2001) provide strong evidence for substantially greater glacial rates of export production throughout the Subantarctic zone than those during the Holocene. However, there remains a potential inconsistency in that the relative change in organic carbon burial is much greater than the corresponding change in opal burial, particularly within the northern Subantarctic region (Fig. 6), a situation that would not be expected if the majority of export production is fueled by diatoms (Buesseler, 1998; Boyd and Newton, 1999).

One way to reconcile the organic carbon and opal records is to invoke iron fertilization associated with increased supply of dust from Patagonia during the LGM (Kumar et al., 1995). Recent studies have shown that diatoms reduce their Si/C ratio upon relief of iron stress (Hutchins and Bruland, 1998; Takeda, 1998; Franck et al., 2000). Therefore, natural fertilization of South Atlantic waters during the LGM by Fe released from Patagonian dust may have created conditions under which, compared to today, relatively more organic carbon was exported per unit opal buried.

Alternatively, one must consider the possibility that phytoplankton other than diatoms contributed significantly to export production, particularly in the northern Subantarctic zone. While a comprehensive study of organic biomarkers diagnostic of phytoplankton taxa has yet to be undertaken, preliminary results from a site within the northern Subantarctic zone show that the concentration and flux of alkenones in sediments deposited during the LGM were both an order of magnitude greater than during the Holocene (Fig. 7). As alkenones are produced primarily, if not exclusively, by coccolithophorids, this suggests that an increase in abundance and production of coccolithophorids may have contributed significantly to the elevated export of organic carbon in the northern Subantarctic zone during the LGM, thereby reconciling the opal and organic carbon records (Fig. 6). Additional studies are needed to determine if the results in Fig. 7 are generally representative of the northern Subantarctic zone throughout the Southern Ocean.

4.6. *Multiproxy overview*

Based on the multiproxy evidence described above, as well as evidence presented elsewhere (Kumar et al., 1995; Anderson et al., 1998; Chase et al., 2002), we conclude that export production in the Subantarctic South Atlantic during the LGM was much greater than anywhere in the Southern Ocean of today, with the exception of coastal regions that regularly support large phytoplankton blooms (Sullivan et al., 1993). Diatoms were clearly major contributors to export production in the southern Subantarctic zone, as indicated by elevated rates of opal burial between the SAF and the APF (Fig. 6). Diatoms growing during the LGM may have been more effective than today at exporting organic carbon due to natural iron fertilization. In addition, other species, such as coccolithophorids, may have served as major contributors to export production in the northern

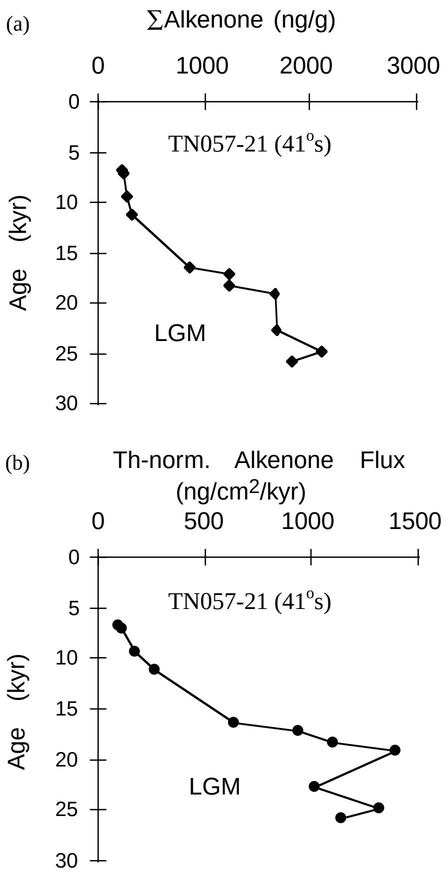


Fig. 7. (A) Concentration and (B) ^{230}Th-normalized accumulation rate of total alkenones in core TN057-21PC2 (41°08′S 7°49′E). Unpublished data of Sachs and Anderson.

Subantarctic zone. To support these conclusions, we must identify mechanisms to supply the requisite nutrients to fuel the inferred levels of export production in glacial Subantarctic waters. This issue is explored in the following section.

5. Nutrient cycles and export production in the glacial Southern Ocean

Before considering nutrient cycles and export production in the glacial Southern Ocean, it is instructive to review principles learned form the study of nutrient cycles in the modern Southern Ocean.

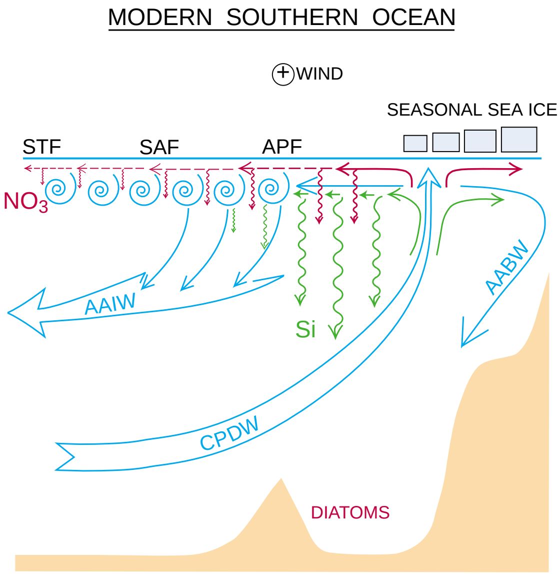


Fig. 8. Schematic illustration of nutrient cycles in the modern Southern Ocean. Meridional overturning is illustrated (in blue) by upwelling of Circumpolar Deep Water south of the APF, and sinking of surface waters in regions where Antarctic Bottom Water and Antarctic Intermediate Water are formed, near Antarctica and north of the APF, respectively. AAIW may be formed only in limited regions of the Southern Ocean. The APF is shown in a typical position overlying a topographic high. Other major fronts include the Subantarctic Front and the STF. Upwelling of CPDW supplies surface waters south of the APF with high concentrations of dissolved inorganic nutrients (nitrate illustrated in red, dissolved Si in green). Nutrients are consumed biologically as waters move northward under the influence of Ekman pumping. Organic carbon and nutrient elements are exported to depth as sinking biogenic particles (wavy arrows pointing downward). Most of the upwelled Si is utilized south of the APF, whereas most of the upwelled nitrate avoids utilization south of the APF and is mixed northward across the APF, either to be consumed within the Subantarctic zone (the region between the APF and the STF) or to be returned to depth with sinking intermediate and mode waters.

5.1. Modern nutrient cycles

Upwelling supplies surface waters south of the APF with high concentrations of major dissolved nutrients (Figs. 1, 2 and 8). Approximately, one-third of the nitrate and phosphate upwelled to the surface within the Antarctic zone is consumed there biologically and exported to depth as organic matter (Sigman et al., 1999b). The remainder is carried northward across the APF, where some is consumed in Subantarctic waters and some returns to the deep sea, carried downward in newly formed intermediate and mode waters (Fig. 8). Unlike nitrate and phosphate, most of the dissolved Si upwelled south of the APF is consumed there and exported to depth as particulate biogenic opal (Brzezinski et al., 2001; Sigmon et al., 2002). Relatively little of the upwelled Si survives biological consumption south of the APF, so modern Subantarctic waters are generally impoverished in Si during summer months, limiting diatom growth and the export of diatom-generated organic matter (Boyd et al., 1999; Franck et al., 2000; Nelson et al., 2001).

5.2. *Glacial Si cycle and diatom production*

It has long been recognized from the sedimentary record that the zone of maximum opal deposition during the LGM lay north of its present position by several degrees of latitude (Charles et al., 1991; Mortlock et al., 1991; Fig. 6). If, as we contend, circulation in the glacial Southern Ocean was not fundamentally different from that which exists today, then we must identify a mechanism to supply dissolved Si to diatoms growing north of the APF (Charles et al., 1991). Subantarctic surface waters could be supplied with abundant Si if, under glacial conditions, utilization of dissolved Si by diatoms growing south of the APF were greatly diminished (see below). Then, by analogy with modern processes supplying nitrate to Subantarctic waters (Section 5.1), Si upwelled south of the APF during the LGM may have been supplied to Subantarctic surface waters by mixing across the APF.

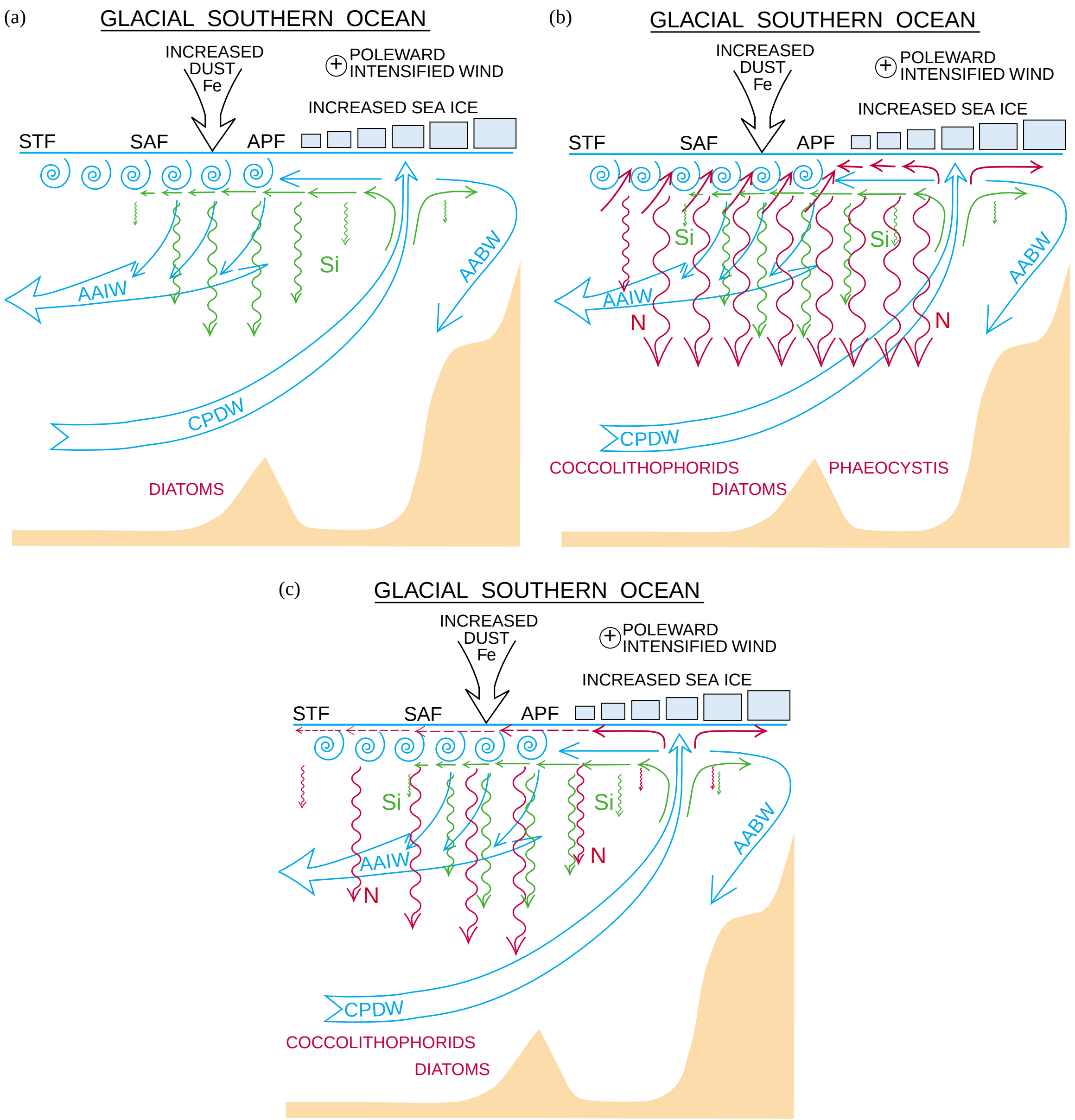
Glacial conditions in the Southern Ocean may have contributed to reduced growth of diatoms south of the APF (illustrated schematically in Fig. 9A). The greater extent of winter sea ice during the LGM (Section 3.3), together with the reduced duration of open-water conditions in summer, may have limited the growth of diatoms. At the same time, the southward position and intensification of the westerlies (Wyrwoll et al., 2000) may have increased the average depth of the mixed layer, thereby further reducing the growth of light-limited diatoms (e.g., Smith and Sakshaug, 1990; Mitchell et al., 1991).

Several lines of evidence support the notion that diatom growth south of the APF was lower during the LGM than today. As noted above, glacial rates of opal burial south of the APF were substantially

Fig. 9. (A) Schematic illustration similar to that in Fig. 8 showing principal features of glacial boundary conditions (see text) and the Si cycle during the LGM. The maximum winter extent of sea ice during the LGM was equatorward of its present position, whereas the mean position of the westerlies lay poleward of their present position. The positions of the principal fronts remained unchanged, due to topographic control, as did the general meridional overturning of the Southern Ocean. Conditions south of the APF were unfavorable for diatom growth, leaving a large fraction of upwelled Si available for transport across the APF. Conditions north of the APF were favorable for diatom growth, possibly nurtured by an increased supply of iron released from dust. Dissolved Si was largely consumed south of the SAF, as indicated by the glacial pattern of opal burial in sediments. (B) Schematic illustration similar to that in Fig. 8 showing principal features of glacial boundary conditions (see text) and a scenario where nitrate utilization south of the APF was greater than today. Although conditions south of the APF were unfavorable for diatom growth, they may have been amenable to blooms of other phytoplankton species such as *Phaeocystis antarctica*, whose growth left surface waters depleted in nitrate, as recorded by the N isotopic composition of diatoms. Nitrogen required to support the growth of diatoms, and of other phytoplankton taxa, such as coccolithophorids, north of the SAF, was supplied by a combination of northward mixing of surface waters together with nitrate supplied by winter convection. Principal phytoplankton taxa responsible for export production within each zone are indicated near the bottom. This scenario is similar to that described by Moore et al. (2000). (C) Schematic illustration similar to that in Fig. 8 showing principal features of glacial boundary conditions (see text) and a scenario where nitrate utilization south of the APF was less than today. Conditions well to the south of the APF were unfavorable for growth of all phytoplankton taxa due to extensive ice cover. Deep mixed layers, associated with intensified westerlies, may have contributed to poor growing conditions as well. Nutrients upwelled south of the APF were largely unused there but were transported northward by mixing across the APF. Conditions north of the APF were favorable for diatom growth, possibly nurtured by an increased supply of iron associated with dust. Conditions remained favorable for phytoplankton growth after Si depletion, allowing for levels of export production north of the SAF much greater than occurs today by taxa such as coccolithophorids.

lower than during interglacial periods (Figs. 5, 6 and 10, see also Charles et al., 1991; Mortlock et al., 1991; Kumar et al., 1995; Anderson et al., 1998; Frank et al., 2000). If upwelling of Si-rich deep waters south of the APF during the LGM were no less than today (Section 3.2), then the lower glacial rates of opal burial would imply rates of Si utilization lower than today.

New proxies for dissolved Si utilization support the view that diatom growth in Antarctic waters was reduced during the LGM. In a pioneering application of the stable isotopic composition of diatomaceous Si, De La Rocha et al. (1998) concluded that the low values of δ^{30}Si in opal deposited south of the APF during the LGM indicated reduced utilization of upwelled Si. This



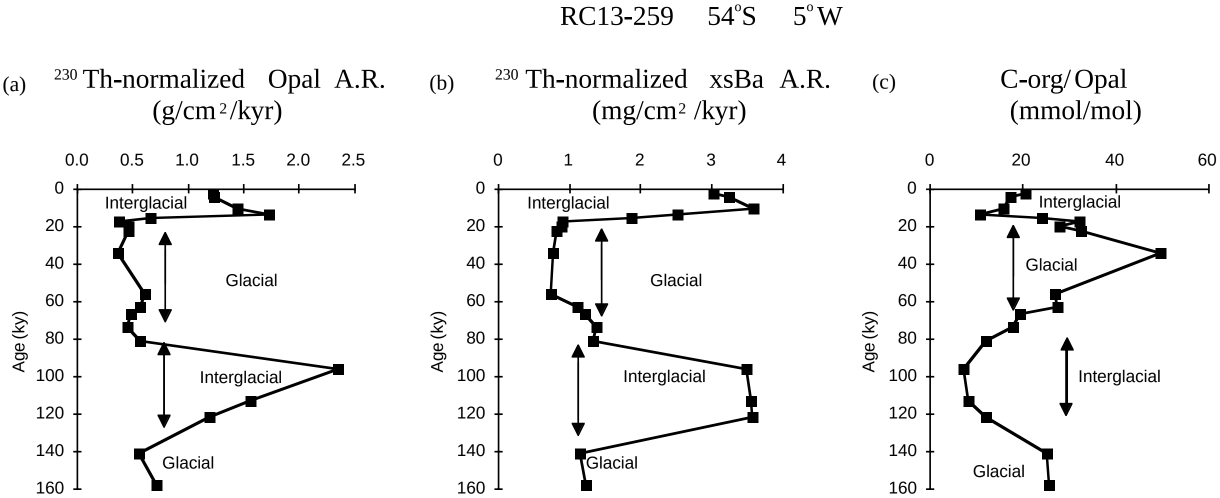


Fig. 10. Accumulation rates (normalized to ^{230}Th to correct for sediment focusing) (A) of opal and (B) of excess barium in core RC13-259 (53°53′S, 04°56′W) illustrate the amplitude of the glacial-to-interglacial changes in these proxies of export production at a site located approximately 4°S of the APF. Sediments at the location of this core lack the enrichment of authigenic uranium characteristic of Subantarctic sediments, so there is no reason to suspect that the xsBa record at this site is compromised. (C) Molar ratios of organic carbon/opal also exhibit substantial glacial–interglacial variability. Glacial periods of minimum opal accumulation are characterized by maxima in organic carbon to opal ratios. Either diatoms growing during glacial times carried a much larger C/Si ratio than their interglacial counterparts, or glacial sediments are enriched in organic matter originating from phytoplankton other than diatoms. Surface C/Si ratios may be high because the loss of unprotected organic matter during early diagenesis is incomplete at these depths.

implies during the LGM that a larger fraction of Si upwelled remained available for transport north of the APF.

The carbon isotopic composition of opal-intrinsic organic matter (i.e., the organic template upon which diatoms build their opal tests) suggests that the lower Si utilization in glacial Antarctic waters was associated with substantially lower diatom growth rates than today. De La Rocha et al. (1998) showed that the LGM minimum in δ^{30}Si was well correlated with a minimum in δ^{13}C of opal-intrinsic organic matter. Rosenthal et al. (2000a) subsequently showed that the glacial minimum in δ^{13}C of opal-intrinsic organic matter occurred in all sectors of the Southern Ocean south of the APF. The δ^{13}C of organic matter produced during photosynthesis depends on several factors, but the two principal variables relevant to Southern Ocean diatoms are the aqueous concentration of CO_2 and the growth rate of the phytoplankton cells, with lower growth rates and higher CO_2 concentrations leading to lower δ^{13}C. As shown by Rosenthal et al. (2000a), even if aqueous CO_2 concentrations in surface waters at the LGM remained at Holocene levels, despite reduced atmospheric CO_2, a lower LGM diatom growth rate is required to account for the observed δ^{13}C values in opal-intrinsic organic matter. If aqueous CO_2 concentrations in Antarctic surface waters were lower than today, following the downward trend in atmospheric CO_2 during glacial times, then an even greater reduction of diatom growth rate would be required (Rosenthal et al., 2000a). While uncertainty in the aqueous CO_2 concentration limits our ability to constrain the growth rate of diatoms, the carbon isotopic results provide strong evidence for lower diatom growth rates during the LGM, reflecting the unfavorable growing conditions (e.g., increased sea-ice cover, increased mixed-layer depth) in Antarctic waters at that time.

The paleoceanographic evidence described above, including reduced opal burial as well as the isotopic proxies of Si utilization and diatom growth rate, is consistent with reduced Si utilization south of the APF during the LGM, thereby leaving a larger fraction of upwelled Si to be transported north of the APF. In contrast to conditions south of the APF, elevated opal burial rates (Fig. 6) and a positive shift in the δ^{13}C of opal-intrinsic organic carbon (Rosenthal et al., 2000a) point to increased diatom growth in Subantarctic waters, indicating favorable conditions (e.g., sufficient light and nutrients) there during the LGM.

5.3. Inconsistencies among proxies of nutrient utilization and growth rate

If diatoms were the primary consumers of nitrate, then the glacial Si scenario described above implies reduced utilization of nitrate as well as Si south of the APF during the LGM. However, the nitrogen isotopic composition of organic matter deposited south of the APF during the LGM has been interpreted to indicate greater utilization of nitrate in Antarctic surface waters, rather than less, than today. This interpretation is supported both by a large data base derived from the analysis of the isotopic composition of bulk organic matter (Francois et al., 1997) and by more recent results derived from the analysis of opal-intrinsic organic nitrogen (Sigman et al., 1999a). The analysis of opal-intrinsic organic N is deemed to be more robust because the organic matter is protected from alteration during sediment diagenesis.

No simple explanation reconciles the interpretation of all of the nutrient-utilization and growth-rate proxies. Any scenario invoked to satisfy at least two of the proxy records violates the interpretation of the third. For example:

(1) Relief from Fe limitation during the LGM may have lowered the Si/N utilization ratio of diatoms (Hutchins and Bruland, 1998; Takeda, 1998; Franck et al., 2000), leading to greater nitrate utilization during the LGM than today while at the same time Si utilization was less. However, Fe fertilization also should have increased diatom growth rate, which is inconsistent with the opal-intrinsic δ^{13}C results.

(2) Slow growth of diatoms within a confined environment of limited nutrient availability (e.g., shallow mixed layer) would satisfy the δ^{13}C indication of reduced growth rate, as well as the evidence for reduced opal burial during the LGM, while permitting increased utilization of nitrate. However, Si should have been depleted within the confined growth environment as well, and this is inconsistent with the δ^{30}Si results.

(3) Consumption of a large fraction of the nitrate in Antarctic (south of the APF) surface waters by phytoplankton other than diatoms would satisfy the δ^{15}N indicator of increased nitrate utilization while allowing for lower growth rates of diatoms (satisfies δ^{13}C) and reduced Si utilization (satisfies δ^{30}Si). However, this explanation is inconsistent with the burial rates of organic carbon and of excess Ba in this region, which suggest that levels of export production during the LGM were much lower than today (e.g., Figs. 5, 6 and 10).

We can think of no plausible scenarios built upon explanation (1) or (2) above, so they will be considered no further. Evidence in support of explanation (3) is discussed in the section below, followed by a discussion of the possibility that our interpretation of one or more proxies may be inaccurate.

5.4. Glacial N cycles: two competing hypotheses

5.4.1. Increased nitrate utilization south of the APF

Increased nitrate utilization south of the APF by phytoplankton other than diatoms, such as *Phaeocystis antarctica* (Fig. 9B), would not necessarily be inconsistent with the environmental conditions inferred to have existed during the LGM. Studies in the Ross Sea have shown a tendency for spatial segregation of regions dominated by diatoms from those dominated by *Phaeocystis*. While some coexistence is common, several studies have reported that *Phaeocystis*-dominated regions tend to have greater mixed-layer depths than diatom-dominated regions (DiTullio and Smith, 1996; Arrigo et al., 1998, 1999; Sweeney et al., 2000). *Phaeocystis antarctica* have a high photosynthetic efficiency (Palmisano et al., 1986) and quantum yield (Moisan and Mitchell, 1999) under low light conditions. *Phaeocystis* also seem to be more efficient at quenching high irradiance levels with no apparent change in their chlorophyll-*a* specific absorption coefficient (Moisan et al., 1998), an advantage when mixed from depth to the surface, where other species suffer photoinhibition. These characteristics, which give *Phaeocystis* a competitive advantage under both low and variable levels of irradiance, have been invoked to explain their dominance in regions of greater mixed-layer depth (Arrigo et al., 1999). However, this general relationship is sometimes violated, in that at least one study of the Ross Sea has found *Phaeocystis* to be dominant in more stratified regions (Smith and Asper, 2001), indicating that a complex matrix of factors, rather than a single parameter, regulates species abundance. Nevertheless, a summer Antarctic zone with deep mixed layers and intermittent ice cover may have provided an environment favorable for growth of *Phaeocystis* during the LGM. In addition to depleting surface waters of nitrate, widespread *Phaeocystis* blooms would have increased the production of methane sulfonic acid, consistent with the elevated concentrations of this compound in the glacial sections of Antarctic ice cores (Legrand et al., 1991; Legrand, 1997).

The principal problem with this scenario is that glacial sediments deposited south of the APF fail to show the expected increase in organic carbon deposition (Figs. 5 and 6). To reconcile the sediment record with this scenario, one must propose either that *Phaeocystis*-derived organic matter was largely regenerated before sinking to the sea bed, or that virtually all of the organic matter reaching the sea bed was regenerated, with very little preserved and buried. Although recent studies in the Ross Sea suggest that *Phaeocystis* can be exported efficiently to depths of several hundred meters (DiTullio et al., 2000), there is insufficient information to predict the fate of a *Phaeocystis* bloom if one were to have occurred in deep waters of the ACC. Furthermore, the low burial rates of excess Ba during the LGM at sites well to the south of the APF (Figs. 5, 6 and 10) are inconsistent with high export production. Reduced preservation of excess Ba cannot be invoked because authigenic U is generally absent in these sediments (Rosenthal et al., 1995; Chase et al., 2002; note that Pacific cores in Fig. 5 also lack authigenic U in glacial sediments, RFA and ZC, unpublished data). Therefore, production and export of excess Ba during the LGM must have been much lower than today in waters well south of the APF. This can be reconciled with increased nitrate utilization by *Phaeocyctis* only if the production and degradation of *Phaeocystis*-derived organic matter failed to produce much excess Ba. This is possible if, for example, the rate of formation of excess Ba is linked to the abundance of diatom frustules (Bishop, 1988).

Increased utilization of nitrate south of the APF during the LGM by phytoplankton other than diatoms is not entirely without supporting evidence, however. At two sites located south of the APF, where ^{230}Th-normalized rates of opal accumulation during the LGM were less than or equal to those during the Holocene, Francois et al. (1997) found detectable enrichment of authigenic U in sediments deposited during the LGM, but not during the Holocene. Francois et al. invoked low oxygen concentrations in circumpolar deep waters to account for the suboxic sediment conditions required to form authigenic U. However, increased rain of organic matter derived from phytoplankton other than diatoms also could have produced the suboxic sediments under which U_A was formed.

Although ^{230}Th-normalized accumulation rates of organic matter at sites well south of the APF were lower during the LGM than during the Holocene (Figs. 5 and 6), glacial–interglacial changes in sedimentary organic-carbon/opal ratios (Fig. 10C) are consistent with the accumulation during glacial periods of non-diatom organic matter. The most compelling evidence for increased supply during the LGM of organic matter from sources other than diatoms comes from Sigman et al. (1999a), who measured both total organic nitrogen and opal-intrinsic organic N in cores from sites south of the APF. In contrast to Holocene sediments, where virtually all of the organic matter not protected within an opal matrix is regenerated during early diagenesis, they found small but readily detectable amounts of non-opal-intrinsic organic matter in LGM sediments. Preservation of unprotected organic matter in LGM sediments provides qualitative evidence that the supply of organic matter from sources other than diatoms may have been greater than during the Holocene.

5.4.2. Reduced nitrate utilization south of the APF

Factors other than those we understand today may have affected the records of elemental and isotopic proxies preserved and buried in the past. The recent discovery of reduced preservation of excess Ba under suboxic conditions is a good illustration of this point. Stable isotopes of Si are still under development as a proxy for Si utilization, so it is difficult to assess the reliability of the interpretations based on δ^{30}Si described above. Growth rate is only one of many factors influencing the isotopic composition of carbon produced during photosynthesis, and unknown factors may be responsible for the reduced δ^{13}C of diatoms growing in Antarctic waters during the LGM, or may have caused the δ^{13}C of opal-intrinsic organic matter to vary independent of the isotopic composition of the whole cell. Recent field calibrations find that the fractionation of nitrogen isotopes by phytoplankton during uptake of nitrate varies little throughout the ocean (Sigman et al., 1999b). However, laboratory studies have found a large range of fractionation factors among different phytoplankton species (Montoya and McCarthy, 1995). If a change in species composition, or a change in growth conditions, reduced the fractionation of N isotopes during nitrate consumption by diatoms growing in Antarctic waters during the LGM, then this, rather than increased nitrate utilization, could explain the observed enrichment in δ^{15}N in glacial sediments (Francois et al., 1997; Sigman et al., 1999a).

One hint that a previously unrecognized factor may have influenced the nitrogen isotopic composition of organic matter during the LGM can be seen in the spatial distribution of sedimentary δ^{15}N (Fig. 4 in Francois et al., 1997). In Holocene sediments, δ^{15}N of bulk organic matter increases monotonically from south to north across the ACC. In contrast, during the LGM there was a systematic minimum in δ^{15}N of organic matter deposited near the APF. The monotonic northward increase in δ^{15}N seen in Holocene sediments is consistent with the modern cycle of nitrate supply and consumption. Nitrate is supplied by upwelling south of the APF and transported northward at the surface by mixing across the APF (Sigman et al., 1999b). Lowest sedimentary δ^{15}N values are found today in the south, associated with the highest concentrations of nitrate in surface waters and the lowest fraction utilized. As the pool of surface nitrate is depleted by phytoplankton during its northward transport, the δ^{15}N of residual nitrate becomes progressively enriched (Sigman et al., 1999b). This northward increase in the δ^{15}N of the surface nitrate is reflected, in turn, by the corresponding northward increase in δ^{15}N of organic N preserved and buried in Holocene sediments.

If the overturning circulation of the Southern Ocean during the LGM was not fundamentally different from today (Section 3.2), then the supply and consumption of nitrate also would have followed a pattern similar to that which exists today (Fig. 8). An interruption at the APF of the northward increase in δ^{15}N of organic nitrogen implies one of two things: either there was an additional supply of nitrate due to upwelling near the APF (Francois et al., 1997) or, under glacial conditions, the isotopic fractionation during uptake of nitrate by phytoplankton was much lower than today throughout the region well to the south of the APF. Because the fractionation factor for nitrate uptake has been observed in the lab to vary under different conditions and among different species, this possibility cannot be ruled out.

Supporting evidence for an environmental factor influencing N isotopic fractionation is provided by the recent results of Holmes et al. (2000 and unpublished results), who discovered that plankton growing south of the Southern ACC Front (SACCF; near the southern boundary of the ACC; Fig. 1) are enriched in ^{15}N by as much as 4–5 ‰ compared to plankton growing further north within the ACC. Similarly, sedimentary organic N south of the SACCF is enriched in ^{15}N by >2‰, indicating that the observed ^{15}N enrichment in plankton is a persistent feature of this region.

These enrichments of ^{15}N south of the SACCF are as large as the glacial–interglacial changes in δ^{15}N recorded in sediments south of the APF. As the higher values of δ^{15}N south of the SACCF cannot be explained by greater nitrate utilization (nitrate concentrations are not depleted by biological utilization), they reflect a response to environmental conditions in this region that cause lower isotopic fractionation during nitrate consumption than elsewhere. While the specific conditions leading to ^{15}N enrichment in plankton south of the SACCF remain to be established, a potential expansion of these conditions during the LGM offers a basis to propose that the larger δ^{15}N values of glacial organic matter south of the APF was caused by reduced isotopic fractionation rather than by increased nitrate utilization.

Our second scenario for the glacial Southern Ocean (Fig. 9C) lacks abundant *Phaeocystis* south of the APF and therefore invokes substantially lower nitrate utilization south of the APF than exists today, accompanied by reduced N isotopic fractionation during the LGM. Under this scenario, export production in Antarctic waters during the LGM was much lower than today, consistent with the measured accumulation of organic carbon, opal, and excess Ba (Figs. 5, 6 and 10). Nitrate was supplied to Subantarctic waters by mixing across the APF, much as occurs today (Fig. 8), and as is proposed for the glacial Si cycle (Fig. 9A).

5.5. Implications for the Southern Ocean's biological pump

The first nitrate scenario above for the glacial Southern Ocean, involving increased utilization south of the APF by phytoplankton other than diatoms (Fig. 9B), leads to much greater export production averaged over the entire Southern Ocean than today. This scenario is similar to that proposed by Moore et al. (2000). The impact on atmospheric CO_2 under this scenario remains uncertain. Whereas, mass budget calculations by Moore et al. (2000) suggest that the increased export production of the glacial Southern Ocean could have accounted for the lower atmospheric CO_2 at that time, model results of Watson et al. (2000) suggest that increased export production in response to Fe fertilization would have accounted for only about half of the observed glacial reduction in atmospheric CO_2. One key difference between these results is that export production in the model of Watson et al. is limited by Fe, whereas the estimates of Moore et al. lack this constraint. While existing data are insufficient to refine these estimates, it is clear that the first scenario would have had a substantial impact on atmospheric CO_2.

Under the second nitrate utilization scenario described above (Fig. 9C), export production south of the APF during the LGM was substantially lower than today. Although the zone of opal burial during the LGM lay north of its present position, the overall rate of opal burial was not much different from that which exists today (Fig. 6). This is to be expected if the rate of opal burial in the Southern Ocean scales with the rate at which dissolved Si is supplied to surface waters by upwelling and if the rate of upwelling during the LGM was not much different from that which exists today (Section 3.2). Despite similar rates of opal burial, however, export of organic matter from Subantarctic waters during the LGM was much greater than the modern export of organic carbon from Antarctic waters. Elevated accumulation rates of organic matter (Fig. 6), together with the widespread presence of authigenic U (Chase et al., 2001), suggest that export production and the rain of organic matter to the sea bed within the Subantarctic zone during the LGM was several times greater than today (see also Kumar et al., 1995; Anderson et al., 1998).

Nutrient utilization efficiencies in glacial Subantarctic surface waters may have been greater than today in part because Fe limitation was relieved by Fe released from dust (Fig. 9; see also Martin, 1990; Kumar et al., 1995). As suggested by the results of in situ iron enrichment experiments (Coale et al., 1996; Boyd et al., 2000), diatoms would have responded most significantly to the increased supply of iron, and would most likely have been the primary consumers of nitrate until the available supply of Si was exhausted. Because export of organic matter produced by diatoms is more efficient than export of organic matter produced by other phytoplankton taxa (Buesseler, 1998; Boyd and Newton, 1999), iron fertilization also may have increased the fraction of exported organic matter reaching the sea bed, thereby contributing to the elevated accumulation rates of organic matter as well as the accumulation of authigenic uranium in glacial Subantarctic sediments. Under this scenario, however, the Southern Ocean's biological pump would not have been the primary factor responsible for the lowered atmospheric CO_2 levels during glacial times because a large reservoir of unused nutrients would have existed in surface waters south of the APF.

6. Summary

A direct assessment of past changes in the strength of the Southern Ocean's biological pump using proxies of nutrient concentrations in surface waters is limited by factors that influence both the generation of the proxy records as well as their preservation. In surface waters, both the carbon isotopic composition and the Cd/Ca ratio of planktonic foraminifera are affected by multiple environmental parameters, and the sensitivity of these proxies to changes in environmental parameters remains poorly constrained. Furthermore, planktonic foraminifera in Antarctic waters frequently calcify below the mixed layer, at depths too great to record the surface nutrient concentrations required to assess the strength of the biological pump.

The indirect reconstruction of past changes in the biological pump, i.e. using proxies of export production and of nutrient utilization efficiency, requires independent constraints on ocean circulation and related boundary conditions (e.g., winds and sea ice). This approach has not produced a general consensus, as proxies of export production are subject to differing interpretations, and the reconstruction of ocean circulation and related boundary conditions during the LGM is controversial as well.

Multiple and conflicting scenarios for circulation in the glacial Southern Ocean have been proposed. We reject the notion that upwelling of deep water south of the APF during the LGM was much less than today, in favor of the view that circulation in the glacial Southern Ocean was not radically different from modern conditions. This view is based on the oxygen isotopic composition of planktonic and benthic foraminifera, together with evidence supporting a vigorous ventilation from the south of the deep glacial Pacific Ocean. This view is consistent, as well, with evidence for a southward shift and intensification of the Southern Hemisphere westerlies during the LGM. Further examination of the consequences of glacial boundary conditions is still needed. Specifically, the response to increased seasonality and extent of sea ice coinciding with a poleward shift and intensification of the westerlies should be explored in a high-resolution model of the Southern Ocean.

With the realization that the use of excess barium as a productivity proxy is compromised by reduced preservation in suboxic sediments, the remaining proxies present a consistent picture of export production during the LGM in the Subantarctic Zone, located between the STF and the APF. There, glacial export production was greatly elevated compared to modern conditions. Export production during the LGM was dominated by diatoms in the southern Subantarctic zone, but other phytoplankton species, such as coccolithophorids, may have been the dominant agents of export in the northern Subantarctic zone. Unfavorable conditions for diatom growth south of the APF during the LGM left a large fraction of the upwelled Si unused and therefore available for northward transport to the Subantarctic zone.

It is difficult to construct a glacial scenario for Antarctic waters (south of the APF) that is consistent with all proxies. If a conventional interpretation is applied to the nitrogen isotopic composition of glacial organic matter, then nitrate concentrations in glacial Antarctic surface waters were drawn down to levels below those found there today by phytoplankton species other than diatoms (e.g., *Phaeocystis antarctica*). This scenario requires that very little of the material exported from surface waters, whether generated by *Phaeocystis* or by other phytoplankton, was preserved and buried in the sediments. An alternative scenario is that the isotopic fractionation of nitrogen during nitrate uptake by diatoms was reduced under glacial environmental conditions in Antarctic waters. While a mechanism to account for reduced isotopic fractionation cannot be provided at this time, if true, then the nitrogen isotope results can be reconciled with evidence from multiple export proxies indicating much lower glacial levels of export production in Antarctic waters than those that exist today.

Glacial scenarios proposed in this review, while still speculative, are consistent with our understanding of the physical setting of the glacial Southern Ocean, and provide specific hypotheses to be tested by future research. In addition to the general need for improvement in our understanding of proxies for export production, nutrient concentration, nutrient utilization, and growth rate, there are specific needs for biomarkers diagnostic of *Phaeocystis* and other phytoplankton taxa to better assess their role in the biological pump of the glacial Southern Ocean. Finally, the role of increased sea ice as a barrier to CO_2 exchange with the atmosphere (Stephens and Keeling, 2000) also requires further investigation.

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