

LETTERS

The Southern Ocean biogeochemical divide

I. Marinov^{1,†}, A. Gnanadesikan², J. R. Toggweiler² & J. L. Sarmiento¹

Modelling studies have demonstrated that the nutrient and carbon cycles in the Southern Ocean play a central role in setting the air–sea balance of CO₂ and global biological production^{1–8}. Box model studies^{1–4} first pointed out that an increase in nutrient utilization in the high latitudes results in a strong decrease in the atmospheric carbon dioxide partial pressure (p_{CO_2}). This early research led to two important ideas: high latitude regions are more important in determining atmospheric p_{CO_2} than low latitudes, despite their much smaller area, and nutrient utilization and atmospheric p_{CO_2} are tightly linked. Subsequent general circulation model simulations show that the Southern Ocean is the most important high latitude region in controlling pre-industrial atmospheric CO₂ because it serves as a lid to a larger volume of the deep ocean^{5,6}. Other studies point out the crucial role of the Southern Ocean in the uptake and storage of anthropogenic carbon dioxide⁷ and in controlling global biological production⁸. Here we probe the system to determine whether certain regions of the Southern Ocean are more critical than others for air–sea CO₂ balance and the biological export production, by increasing surface nutrient drawdown in an ocean general circulation model. We demonstrate that atmospheric CO₂ and global biological export production are controlled by different regions of the Southern Ocean. The air–sea balance of carbon dioxide is controlled mainly by the biological pump and circulation in the Antarctic deep-water formation region, whereas global export production is controlled mainly by the biological pump and circulation in the Subantarctic intermediate and mode water formation region. The existence of this biogeochemical divide separating the Antarctic from the Subantarctic suggests that it may be possible for climate change or human intervention to modify one of these without greatly altering the other.

Recent palaeoceanographic literature points out that different parts of the Southern Ocean have responded differently to climate change^{9–11}. In an attempt to elucidate the complex mechanisms governing Southern Ocean carbon sequestration, we examine: first, which areas of the Southern Ocean control atmospheric p_{CO_2} levels; second, which areas control global biological export production; and third, whether there is a link between atmospheric p_{CO_2} and global export production.

A simple and effective probe for examining these questions is surface nutrient depletion, that is, forcing surface nutrients towards zero by increasing nutrient uptake and converting nutrients to export production. The effect is to reduce p_{CO_2} in surface water, driving CO₂ from the atmosphere into the ocean. Our approach follows previous studies⁵ and gives an upper limit estimate of the oceanic uptake that might result from complete removal of surface nutrients in a specified ocean region. This theoretical approach ignores complex phytoplankton growth limitations that are likely to limit nutrient depletion, such as light supply, iron, zooplankton grazing, and particle aggregation.

We deplete nutrients over nine Southern Ocean regions in the Princeton general circulation model (GCM; Table 1, Methods). The areas of interest are defined as surface waters with densities greater than or lighter than reference potential densities σ_θ of 27.6, 27.4, 27.3 and 27.1 kg m⁻³ (Fig. 1b). Table 1 summarizes the results of the experiments.

We find that atmospheric p_{CO_2} depends strongly on the location where nutrient depletion occurs. If we define a depletion efficiency as the ratio between the atmospheric p_{CO_2} drawdown and the surface area depleted in nutrients, Table 1 shows that nutrient depletion is more efficient at drawing-down atmospheric CO₂ in the southernmost regions (depletion experiments (Exps) S27.6, S27.4, S27.3, S27.1) than in the northern regions (Exps N27.6, N27.4, N27.3, N27.1). This suggests the existence of a Southern Ocean biogeochemical divide, south of which nutrient depletion has most impact on air–sea carbon exchange. How can we explain this finding?

The first order explanation lies with the existing large scale oceanic circulation. As a consequence of wind driven forcing, deep water rich in nutrients and dissolved inorganic carbon (DIC) upwells as Circumpolar Deep Water (CDW) to the south of the Antarctic Polar Front^{12–14}. It has long been known from observations^{14–16} that some portion of this water moves northwards in the surface Ekman layer and is incorporated into Antarctic Intermediate Water (AAIW) and Subantarctic Mode Water (SAMW), while some portion moves south and is subducted as Antarctic Bottom Water (AABW).

Figure 1a taken from ref. 10 summarizes this view of oceanic circulation (see also Methods). In this simple diagram, the lower (blue) circulation comprises the southward moving water subducted as AABW. The upper (red) circulation comprises the upwelling water

Table 1 | Southern Ocean nutrient depletion in the Princeton GCM

Depletion experiments	Region depleted	Area (% total)	Δ Atm. p_{CO_2} (p.p.m.)	Δ Prodn (GtC yr ⁻¹)	Efficiency of depletion (10 ⁻⁶ p.p.m. km ⁻²)
S30S	South of 30°S	29.32	-70.33	0.49	0.66
Antarctic experiments					
S27.1	$\sigma_\theta \geq 27.1$	12.19	-61.29	-1.09	1.4
S27.3	$\sigma_\theta \geq 27.3$	5.9	-47.62	-0.41	2.24
S27.4	$\sigma_\theta \geq 27.4$	3.65	-39.23	-0.06	2.98
S27.6	$\sigma_\theta \geq 27.6$	1.1	-23.10	0.63	5.85
Subantarctic experiments					
N27.1	$\sigma_\theta < 27.1$	17.13	-18.77	2.01	0.3
N27.3	$\sigma_\theta < 27.3$	23.42	-37.03	0.21	0.44
N27.4	$\sigma_\theta < 27.4$	25.66	-43.59	-0.08	0.47
N27.6	$\sigma_\theta < 27.6$	28.22	-53.50	-0.18	0.53

Column 2 defines the region depleted relative to the surface potential density σ_θ . Column 3 is the area depleted as a fraction of the total ocean area. Columns 4–6 show respectively changes in atmospheric p_{CO_2} , total global export production and efficiency of depletion (defined as the ratio of atmospheric p_{CO_2} drawdown and surface area depleted, in absolute value) after each depletion simulation. Antarctic nutrient depletion is more efficient than Subantarctic depletion. Atmospheric p_{CO_2} is calculated relative to an undepleted (control) atmospheric p_{CO_2} of 298.1 p.p.m. Undepleted global production is 9.40 GtC yr⁻¹. Results are shown at equilibrium for our regular gas exchange (standard) model. See Methods for comments on the Weddell Sea experiment (S27.6).

¹Atmospheric and Oceanic Sciences Program, Princeton University, Princeton, New Jersey 08540, USA. ²NOAA/Geophysical Fluid Dynamics Laboratory, PO Box 308, Forrestal Campus, Princeton, New Jersey 08542, USA. †Present address: Program in Atmospheres, Oceans, and Climate, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA.

which moves northward to the rest of the ocean at intermediate depths and returns to the Southern Ocean via the North Atlantic Deep Water (NADW)¹³. The surface separation between the two circulations is somewhere south of the Antarctic Polar Front, and corresponds to the divide between the Antarctic (deep water formation) region to the south from the Subantarctic (intermediate and mode water formation) region to the north.

We propose that this physical separation leads to significantly different responses to nutrient depletion in the two regions—and hence to the biogeochemical divide detected in our experiments. The key to understanding this result lies in the concept of biological pump efficiency.

The biological carbon pump is primarily produced by the photosynthetic formation of organic matter in the surface ocean and its subsequent transport to depth, where it is remineralized. ('Remineralized nutrients' are nutrients added to the ocean interior through remineralization; 'preformed nutrients' are biologically unutilized surface nutrients subducted into the ocean interior via newly formed deep water.) The biological pump acts to decrease surface preformed

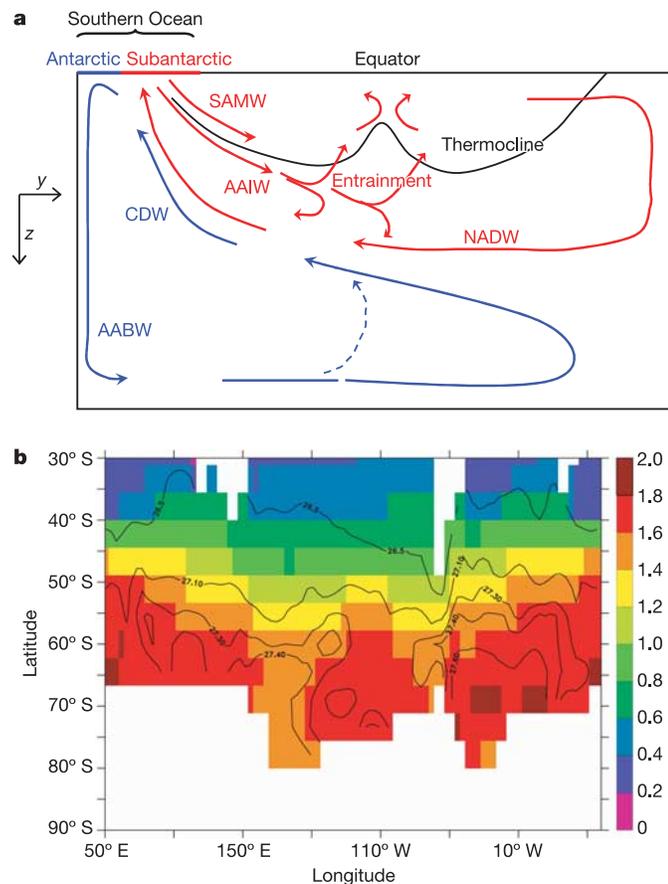


Figure 1 | Global circulation diagram relevant for the carbon cycle, and experimental set-up. a, Circumpolar Deep Water (CDW) upwelling to the Southern Ocean surface is either advected northward as part of the upper circulation (in red), or moves southward as lower circulation (in blue); this panel is adapted from ref. 10. The Antarctic–Subantarctic surface separation at the Antarctic Polar Front roughly corresponds to the $\sigma_o = 27.3$ outcrop in the Princeton GCM. See Methods for the simplifications used in this diagram. AABW, Antarctic Bottom Water; AAIW, Antarctic Intermediate Water; NADW, North Atlantic Deep Water; SAMW, Subantarctic Mode Water. **b**, Undepleted (control) annual mean surface PO_4^{3-} ($\mu\text{mol kg}^{-1}$) shown in colours. Geographical extent of the August σ_o surface outcrops shown as contours in units of kg m^{-3} . Surface nutrients are depleted everywhere south of these density outcrops (Exps S27.1, S27.3, S27.4, S27.6) and between these outcrops and 30° S (Exps N27.1, N27.3, N27.4, N27.6). σ_o is defined as $(\rho_{\text{pot}} - 1,000) + 0.025 (\text{kg m}^{-3})$, where ρ_{pot} is the actual potential density referenced to the surface.

nutrients, converting them to export production and increasing the concentration of remineralized nutrients deeper in the water column. Because of the association of nutrients with carbon in both photosynthesis and remineralization, the more efficient the conversion of preformed to remineralized nutrients, the more efficient the biological pump in sequestering carbon in the deep ocean and reducing atmospheric p_{CO_2} , as recently discussed¹⁷.

Increased surface nutrient depletion in deep water formation regions lowers the concentration of preformed nutrients in newly formed deep waters. Since total PO_4^{3-} is constant in our experiments, a decrease in globally averaged preformed nutrients signals a more efficient conversion to remineralized nutrients, a more efficient biological pump and a stronger decrease in atmospheric p_{CO_2} (Fig. 2a and refs 1–3). The larger the decrease in preformed nutrients, the more efficient the biological pump and the oceanic carbon sequestration.

The most relevant preformed nutrients for the biological pump efficiency and for atmospheric p_{CO_2} are those present in deep water formation areas at the time deep water forms. Concentrations of preformed nutrients in high latitude, deep water formation regions are high, owing to inefficient biology. These nutrients are advected and mixed into the deep ocean; the preformed nutrient concentration relevant for the global biological carbon pump is therefore a linear combination of the surface preformed concentration in each deep water formation area weighted by the corresponding net contribution of the deep water source to the deep reservoir.

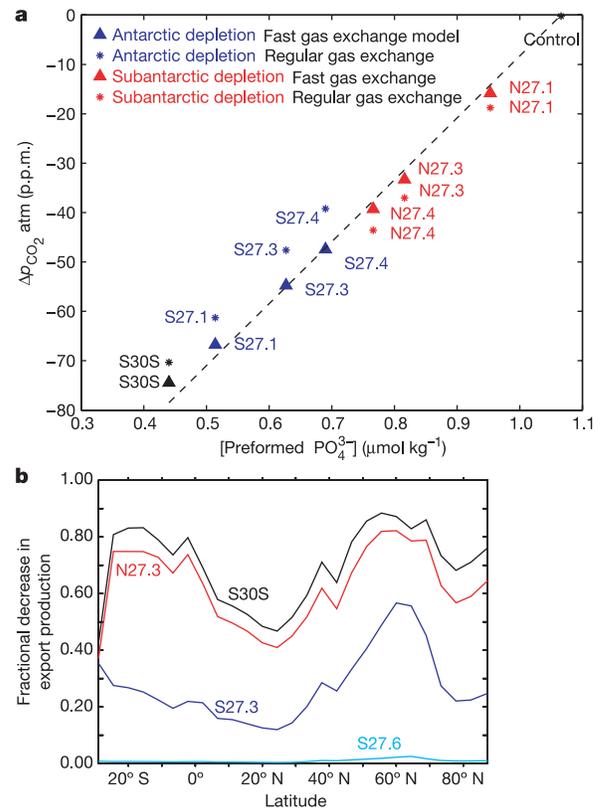


Figure 2 | Oceanic mechanisms for modifying atmospheric CO_2 and global production in the Princeton GCM. a, A decrease in globally averaged preformed PO_4^{3-} results in decreased atmospheric p_{CO_2} . For all simulations, CO_2 drawdown is similar in our regular gas exchange (stars) and fast gas exchange (triangles) models. Antarctic nutrient depletions (blue triangles and stars) generally result in a larger decrease in preformed nutrients and stronger atmospheric p_{CO_2} drawdown than Subantarctic depletions (red triangles and stars). Undepleted/control case also shown (black); see Methods for details. **b**, Fractional decrease in export production following nutrient depletion experiments. Subantarctic depletion (Exp. N27.3) has more impact on global production than Antarctic depletion (Exp. S27.3).

Let us consider the main water masses in Fig. 1a: AABW, NADW, AAIW/SAMW. The balance of preformed nutrients between these sources determines to first order how much CO_2 the deep ocean holds. The surface preformed nutrient concentration is largest in AABW and smallest in the NADW formation region. The AABW ventilates the largest volume of deep water, followed by NADW, AAIW and SAMW. Because of higher surface preformed nutrient concentration and stronger deep ocean ventilation via AABW, Antarctic nutrient depletion has more impact on deep ocean preformed nutrients and results in larger atmospheric CO_2 drawdown compared to the Subantarctic depletion (compare Exps S27.3 and N27.3 in Figs 2a, 3). Interestingly, Antarctic convective regions are very efficient at sequestering atmospheric CO_2 (see Exp. S27.6 in Table 1 and Methods).

We now examine how nutrient depletion affects globally integrated biological export production. Southern Ocean nutrient depletion has two separate effects on export production^{6,18}. Locally, it increases production. Moreover, as the negative nutrient perturbation is advected by the upper circulation, subducted north of the Antarctic Polar Front as intermediate and mode waters and eventually mixed through the thermocline to reach both low latitude surface and high northern latitudes, both nutrients and export production decrease everywhere north of 30°S . The associated fractional decrease in export production outside the Southern Ocean can reach 75% (Fig. 2b), as also discussed in ref. 8.

Because the upper circulation is the primary mechanism by which nutrients are advected into low latitudes, depleting nutrients in

Subantarctic waters (Exp. N27.3) results in much larger decrease in export production north of 30°S than Antarctic depletion (Exp. S27.3). Note that observations of silica^{*8} (defined as $\text{Si}(\text{OH})_4 - \text{NO}_3^-$) and radiocarbon¹⁹ also suggest a large role for Subantarctic nutrients in low latitude production. Figure 2b shows that potential density $\sigma_\theta = 27.3$ (kg m^{-3}) is roughly the Southern Ocean biogeochemical divide in our model, with areas south (north) of this boundary in the Antarctic (Subantarctic) region. Despite its considerable carbon uptake, the Weddell Sea is completely disconnected in terms of nutrient transport from the low latitudes; local nutrient changes do not affect nutrients and production north of 30°S (Exp. S27.6, Fig. 2b).

The decrease in atmospheric p_{CO_2} relative to the change in production south of 30°S (Fig. 3a) and north of 30°S (Fig. 3b) further highlights the differential response to depletion of the Antarctic and Subantarctic. Interestingly, there is no meaningful relationship between atmospheric p_{CO_2} and global export production (Fig. 3c). The results of Exps S27.3, S27.4 and S27.6 lie on the same p_{CO_2} versus production branch in Fig. 3a and b, confirming that in our model all points south of $\sigma_\theta = 27.3$ are in the Antarctic and respond similarly to nutrient depletion. For a given increase (decrease) in production south (north) of 30°S , the Antarctic is much better at taking up atmospheric CO_2 than the Subantarctic. The two-branch structure in Fig. 3a and b confirms the existence of two distinct biogeochemical regimes.

The relative contributions of different deep water types to the Antarctic and Subantarctic surface waters, an issue at present debated in the research community (see Methods), might affect the fraction of low latitude production driven by Southern Ocean nutrients (Fig. 2b). However, the existence of the biogeochemical divide is a robust result, which holds across GCMs with different Southern Ocean circulations and box models. Simple box model experiments (see Supplementary Information) show that slow Antarctic–Subantarctic surface mixing and the separation into northward and southward flows at the surface (rather than the separation of the lower and upper circulations at depth), together with the confinement of the AABW formation to the Antarctic, lead to the existence of the biogeochemical divide.

We acknowledge limitations to our model such as coarse resolution, inability to resolve shelf or slope processes and lack of a dynamic ice model. Although the exact sensitivity of atmospheric CO_2 to the global inventory of preformed nutrients (the regression slope in Fig. 2a) may vary among models and between our model and nature²⁰, the efficiency of the biological pump in drawing down atmospheric CO_2 is robustly given, to first order, by the deep ocean inventory of preformed nutrients. In turn, the preformed nutrients inventory depends on both surface unused nutrient concentration and deep ocean ventilation.

Our analysis shows clearly in the context of a realistic GCM that the physical separation between lower and upper oceanic circulations at the ocean surface (Fig. 1a) has a simple translation into a biogeochemical divide. The air–sea carbon balance is primarily determined by the amount of deep water formation and convection in the Antarctic, the unutilized nutrient concentration in this region and the area through which mixing with the deep waters occurs. By contrast, global and low latitude export production are set primarily by the amount of intermediate and deep water formation in the Subantarctic, and by the area and the unutilized nutrient concentration of the Subantarctic region. This suggests that it might be possible for climate change to modify atmospheric CO_2 without greatly modifying low latitude and global export production, and vice versa. We suggest that mechanisms that attempt to explain the lower atmospheric CO_2 during the Last Glacial Maximum—such as changes in deep water formation^{10,21} and oceanic stratification⁹, Fe fertilization²², and reduced ventilation due to increased ice cover²³—should take into account differences in carbon sequestration efficiency between the Antarctic and Subantarctic.

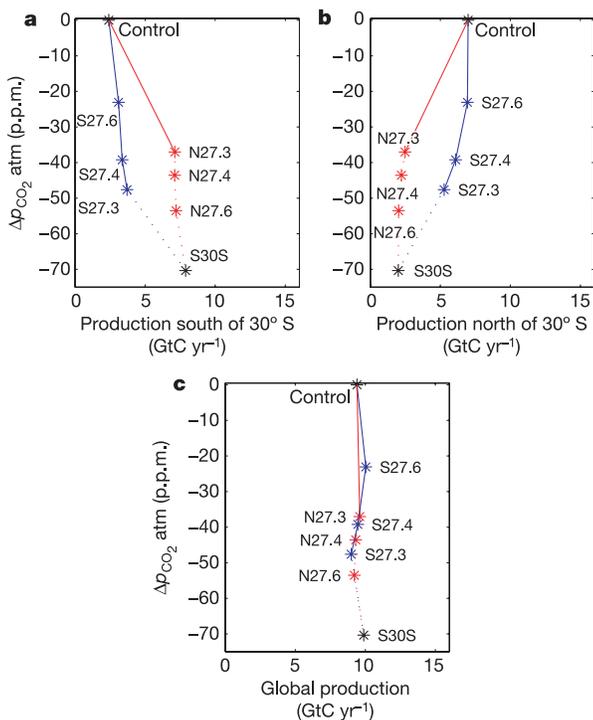


Figure 3 | Change in atmospheric p_{CO_2} versus export production after surface nutrient depletion simulations in the regular gas exchange model. Export production is integrated **a**, south of 30°S ; **b**, north of 30°S ; and **c**, globally. Undepleted/control scenario is shown in black, the Subantarctic branch in red, and the Antarctic branch in blue. A comparison of the two branches in **a** and **b** shows that Antarctic areas take up atmospheric CO_2 more efficiently (Exps S27.3, S27.4, S27.6), while areas primarily in the Subantarctic have a larger impact on global biological production (Exps N27.3, N27.4, N27.6). The rough Antarctic–Subantarctic boundary is $\sigma_\theta = 27.3$. Dotted lines connect scenarios in which nutrients are partially depleted in both Antarctic and Subantarctic areas. There is no robust relationship between global biological production and atmospheric p_{CO_2} .

METHODS

Model set-up. The GCM used in this study is the Geophysical Fluid Dynamics Laboratory Modular Ocean Model version 3 (MOM3) coupled with an OCMIP 2 biogeochemistry model²⁴. A single well-mixed atmospheric box is coupled to the ocean carbon cycle; the total carbon in the atmosphere and ocean is conserved. For a detailed description of our seasonally forced model (KVLW + AILW), which uses the Gent-McWilliams parameterization of subgrid scale processes, see ref. 25. New production in the undepleted case is obtained by forcing PO_4^{3-} towards observed seasonal Levitus values, PO_4^{3-} in the upper 75 m of the model at each time step t , when $\text{PO}_4^{3-} > \text{PO}_4^{3-}$ obs:

$$J_{\text{prod}}(x, y, z, t) = (\text{PO}_4^{3-}(x, y, z, t) - \text{PO}_4^{3-} \text{ obs}(x, y, z, t))/T, \quad z < 75 \text{ m}$$

where $T = 30$ days, and x , y , and z are model longitude, latitude and depth, respectively. In the nutrient depletion cases we replace PO_4^{3-} obs with zero in the above equation. Nutrients in each of the nine simulations are continuously depleted for a few thousand years until a new equilibrium has been achieved; globally integrated nutrients are kept constant during these experiments. Shown are pre-industrial results at equilibrium.

The simulations discussed here are performed with a soft tissue pump model, in which there is no calcium carbonate cycling, and surface temperature and salinity are set to 10 °C and 34.7 p.s.u. (practical salinity units), for the purpose of the gas exchange calculations. We show elsewhere⁶ that these simplifications have a minimal impact on the results. Indeed, this model accounts for most of the atmospheric $p\text{CO}_2$ drawdown following Southern Ocean nutrient depletion in a model that includes the full carbonate and solubility components of the carbon pump. The model includes climatological sea-ice cover at monthly resolution as in OCMIP2²⁴.

The Weddell Sea in our model. The Antarctic region south of $\sigma_\theta = 27.6$ corresponds in our model to the Weddell Sea, a deep water formation region with high preformed nutrients and deep winter convection. Even though the Weddell Sea accounts for only 3.3% of the Southern Ocean, nutrient depletion in this area accounts for 30% of the 70 p.p.m. uptake following depletion of the entire Southern Ocean, suggesting that nutrient depletion in deep convective regions is particularly effective at sequestering CO_2 .

Simplification of complex overturning circulation. Figure 1a is a simplified two-dimensional diagram of a complex overturning circulation. The composition of the water upwelling in the Southern Ocean, and of the resulting waters moving northward and southward, are a matter of great debate in the oceanographic community. Numerical models such as ours^{25,26}, observations of silica⁸ and radiocarbon¹⁹ and older observational syntheses¹⁶ suggest that a considerable amount of deep water (in particular of the NADW type) is transformed into lighter water in the Southern Ocean and entrained northward into the AAIW and SAMW. By contrast, recent data-based estimates²⁷ and inverse model studies²⁸ suggest that the Southern Ocean transformation might be quite small. These studies also suggest that a percentage of NADW is converted into surface waters south of the Antarctic Polar Front area where Upper Circumpolar Deep Water upwells, such that the lower and upper circulations in Fig. 1a are interconnected rather than separate. Box model studies (Supplementary Information) tend to suggest that this would have little impact on the biogeochemical divide.

Preformed nutrients and atmospheric $p\text{CO}_2$. Nutrient depletion simulations were separately run in two models: one with regular gas exchange and one with fast gas exchange (where oceanic CO_2 at each time step is set equal to atmospheric CO_2 calculated at the previous time step), as shown in Fig. 2a. For both models, a larger decrease in preformed nutrients signals a stronger biological uptake of atmospheric CO_2 and a more efficient biological pump^{1–3,17}.

If gas exchange is infinitely fast, surface DIC is in equilibrium with the atmosphere and the surface to deep DIC difference and atmospheric $p\text{CO}_2$ levels are entirely due to increased remineralization. Global mean preformed nutrients are the difference between total globally averaged nutrients (a constant in all our experiments) and global mean remineralized nutrients. Global mean remineralized nutrients are calculated as the surface to deep DIC difference in the fast gas exchange model divided by the Redfield ratio, $r_{\text{C:P}}$. Since the time step of the model limits how fast gas exchange is, there is a maximum error of 5–10% associated with this method.

While atmospheric $p\text{CO}_2$ is linearly related to preformed PO_4^{3-} in the fast gas exchange model, results for the regular gas exchange model are slightly off the fast gas exchange line. The deviation of these results from the fast gas exchange line is due to surface DIC disequilibrium (relative to the atmosphere) at the time of subduction. The small deviation of the regular model from the fast gas exchange line shows that in this particular GCM the oceanic CO_2 uptake is primarily driven by changes in remineralized nutrients. Changes in carbon uptake due to changes in surface DIC disequilibrium with nutrient depletion are relatively small.

Received 4 May 2005; accepted 16 May 2006.

- Sarmiento, J. L. & Toggweiler, J. R. A new model for the role of the oceans in determining atmospheric $p\text{CO}_2$. *Nature* **308**, 620–624 (1984).
- Knox, F. & McElroy, M. B. Changes in atmospheric CO_2 : Influence of the marine biota at high latitude. *J. Geophys. Res.* **89**, 4629–4637 (1984).
- Siegenthaler, U. & Wenk, T. H. Rapid atmospheric CO_2 variations and ocean circulation. *Nature* **308**, 624–626 (1984).
- Joos, F., Sarmiento, J. L. & Siegenthaler, U. Estimates of the effect of Southern Ocean iron fertilization on atmospheric CO_2 concentrations. *Nature* **349**, 772–775 (1991).
- Sarmiento, J. L. & Orr, J. C. Three-dimensional ocean model simulations of the impact of Southern Ocean nutrient depletion on atmospheric CO_2 and ocean chemistry. *Limnol. Oceanogr.* **36**, 1928–1950 (1991).
- Marinov, I. *Controls on the Air-Sea Balance of Carbon Dioxide*. PhD thesis, Princeton Univ. (2005).
- Caldeira, K. & Duffy, P. B. The role of the Southern Ocean in uptake and storage of anthropogenic carbon dioxide. *Science* **287**, 620–622 (2000).
- Sarmiento, J. L., Gruber, N., Brzezinski, M. A. & Dunne, J. P. High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature* **427**, 56–60 (2004).
- Sigman, D. M. & Boyle, E. A. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature* **407**, 859–869 (2000).
- Toggweiler, J. R., Russell, J. L. & Carson, S. R. Mid-latitude westerlies, atmospheric CO_2 and climate change during the Ice Ages. *Paleoceanography* **21**, PA2005, doi:10.1029/2005PA001154 (2006).
- Kohfeld, K. E., Le Quere, C., Harrison, S. P. & Anderson, R. F. Role of marine biology in glacial-interglacial CO_2 cycles. *Science* **308**, 74–78 (2005).
- Gordon, A. in *Antarctic Oceanology I* (ed. Reid, J. L.) Antarctic Res. Ser. Vol. 15, 169–203 (American Geophysical Union, Washington DC, 1971).
- Toggweiler, J. R. & Samuels, B. Effect of Drake Passage on the global thermohaline circulation. *Deep-sea Res.* **142**, 477–500 (1995).
- Wyrtki, K. The thermohaline circulation in relation to the general circulation in the oceans. *Deep-Sea Res.* **8**, 39–64 (1961).
- Sverdrup, H. U., Johnson, M. W. & Fleming, R. H. *The Oceans, Their Physics, Chemistry, and General Biology* (Prentice-Hall, New York, 1942).
- Schmitz, W. J. On the interbasin-scale thermohaline circulation. *Rev. Geophys.* **33**, 151–173 (1995).
- Ito, T. & Follows, M. J. Preformed phosphate, soft tissue pump and atmospheric CO_2 . *J. Mar. Res.* **63**, 813–839, doi:10.1357/0022240054663231 (2005).
- Dutkiewicz, S., Follows, M. J. & Parekh, P. Interactions of the iron and phosphorus cycles: a three dimensional model study. *Glob. Biogeochem. Cycles* **19**, GB1021, doi:10.1029/2004GB002342 (2005).
- Toggweiler, J. R., Dixon, K. & Broecker, W. S. The Peru upwelling and the ventilation of the South Pacific thermocline. *J. Geophys. Res.* **96**, 20467–20497 (1991).
- Toggweiler, J. R., Murnane, R., Carson, S., Gnanadesikan, A. & Sarmiento, J. L. Representation of the carbon cycle in box models and GCMs—Part 2. Organic pump. *Glob. Biogeochem. Cycles* **17**, 1027, doi:10.1029/2001GB001841 (2003).
- Toggweiler, J. R. Variation of atmospheric CO_2 by ventilation of the ocean's deepest water. *Paleoceanography* **14**, 571–588 (1999).
- Martin, J. H. Glacial-interglacial CO_2 change: the iron hypothesis. *Paleoceanography* **5**, 1–13 (1990).
- Stephens, B. B. & Keeling, R. F. The influence of Antarctic sea ice on glacial-interglacial CO_2 variations. *Nature* **404**, 171–174 (2000).
- Najjar, R. & Orr, J. Design of OCMIP-2 simulations of chlorofluorocarbons, the solubility pump and common biogeochemistry. (<http://www.cgd.ucar.edu/ocmip/ocmip/design.pdf>) (1998).
- Gnanadesikan, A., Slater, R. D., Gruber, N. & Sarmiento, J. L. Oceanic vertical exchange and new production: a comparison between models and observations. *Deep Sea Res.* **1149**, 363–401 (2002).
- Gnanadesikan, A., Slater, R. D. & Samuels, B. L. Sensitivity of water mass transformation and heat transport to subgridscale mixing in coarse-resolution ocean models. *Geophys. Res. Lett.* **30**, 1967, doi:10.1029/2003GL018036 (2003).
- Speer, K., Rintoul, S. R. & Sloyan, B. The diabatic Deacon cell. *J. Phys. Oceanogr.* **30**, 3212–3222 (2000).
- Sloyan, B. M. & Rintoul, S. R. The Southern Ocean limb of the global deep overturning circulation. *J. Phys. Oceanogr.* **31**, 143–173 (2001).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements I.M. was supported by the DOE Office of Science while at Princeton University, and by the NOAA Postdoctoral Program in Climate and Global Change, administered by the University Corporation for Atmospheric Research, while at MIT. We thank R. Slater for help with the Princeton GCM, D. Sigman and M. Follows for discussions, and R. Anderson for comments that improved the manuscript.

Author Information Reprints and permissions information is available at npg.nature.com/reprintsandpermissions. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to I.M. (imarinov@mit.edu).