



Figure 1 Northward Ekman transport of surface waters and contours of modern potential density averaged for each ocean zone. The approximate mean latitude of the Polar Front (northern boundary of Antarctic zone) and direction of Ekman and eddy transports that control the rate of deepwater upwelling are shown (lower panel). The relevant eddy transport involves a net southward flow, as opposed to north–south mixing, and ultimately results from the tendency of lighter water to spread over denser water.

upwelling between low and high latitudes^{9,10}; this is consistent with scaling arguments⁵ and global inversions¹¹. Modern southward surface-eddy transport must therefore be of similar magnitude (~15 Sv). In a more stratified glacial ocean, the eddy transport in the surface layer would weaken and upwelling would consequently increase, an opposite change to that suggested by Sigman and Boyle.

The stratification hypothesis could survive in the face of eddy feedbacks if glacial winds were markedly weakened in the relevant latitude band, or if the biological productivity of the Antarctic zone increased sufficiently to prevent CO₂ outgassing despite greater upwelling. However, neither change seems probable given the available evidence. The primary cause of lowered glacial CO₂ may not have been enhanced year-round stratification, but enhanced Antarctic sea-ice coverage¹², which could have suppressed CO₂ outgassing even if glacial Antarctic surface waters were generally less stratified than today, with upwelling into a buoyant surface layer confined to a brief summer season¹³.

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Sigman and Boyle reply — Palaeoceanographic evidence indicates that there was more complete nutrient consumption in Antarctic surface waters during the last ice age^{1,2}, but lower biological production¹. These results suggest that the Antarctic was stratified during glacial times, reducing the transport of sequestered nutrients and CO₂ into the Antarctic surface. By sequestering CO₂ in the ocean interior, this change could explain the observation of lower levels of atmospheric CO₂ during the ice age³. Geological data offer two possible causes for this stratification. First, the Southern Hemisphere westerly winds apparently shifted northwards during glacial times⁴, which would have reduced Ekman-driven upwelling in the Antarctic⁵ (a ‘wind-shift’ mechanism). Second, the Antarctic sea-ice cycle intensified during glacial times⁶, which may have allowed a low-salinity lid to accumulate in the open Antarctic, thus reducing vertical mixing and open-ocean overturning (a ‘sea-ice’ mechanism).

Keeling and Visbeck criticize these mechanisms for Antarctic stratification on theoretical grounds and highlight an alternative hypothesis for lowering glacial CO₂ — prevention of CO₂ release from the Antarctic by covering the ocean with sea ice, thereby blocking ocean–atmosphere CO₂ exchange⁷. Although we cannot be completely confident about the specific mechanisms for stratification outlined above, we believe that Antarctic stratification is a more plausible hypothesis for lower glacial CO₂ than gas-exchange limitation, and it is also more directly supported by palaeoceanographic data³.

With regard to the wind-shift mechanism, Keeling and Visbeck argue that a reduction in winds over the Antarctic was unlikely because of an increase in the Equator-to-Pole temperature gradient during glacial times. However, the modern meridional variation in wind strength across the Southern Ocean is large enough for the observed northward migration in westerly winds during the ice age to have overcome the effects of a global average increase in winds, yielding less wind-driven upwelling in the glacial Antarctic. Winds depend on regional (not global) temperature gradients, and the temperature gradient across the Antarctic may well have been smaller during glacial times, potentially explaining the greater northward persistence of sea ice. But it must be admitted that the wind-shift mechanism is

complex and has inherent thresholds⁸, so this mechanism may have difficulty in accounting for the timing of CO₂ change and its robust, linear relationship with Southern Hemisphere temperature^{4,9}.

Keeling and Visbeck criticize the sea-ice mechanism for stratification on the grounds that it would have been countered by an increase in upwelling because of a response in the southward flux of eddies to a change in ocean-density structure. However, the eddy response is a negative feedback which, at most, would set boundaries on the stratification caused by the sea-ice mechanism. Moreover, the full slope of the density surfaces at the polar front might have changed very little if only the shallowest 30–50 m of the Antarctic surface stratified, in which case there would have been no eddy response. In our opinion, a greater problem with the sea-ice mechanism involves higher-latitude conditions: stratification of the open Antarctic as a result of an enhanced sea-ice cycle might occur at the expense of the coastal Antarctic, making this region more saline and thus more active in ocean ventilation, with an accompanying release of CO₂ into the atmosphere.

Prevention of ocean–atmosphere CO₂ exchange in the Antarctic by sea-ice cover⁷ is unlikely to be the sole mechanism for reducing CO₂ levels during ice ages, because it would require almost complete and continuous ice coverage of the region. For this reason, Keeling and Visbeck refer to the previously described¹⁰ hybrid hypothesis that invokes intense surface stratification and nutrient consumption during the summer, followed by prevention of gas exchange by ice cover during winter. Although promising, this mechanism faces a discrepancy with the evidence of lower productivity in the glacial Antarctic. Without permanent stratification, greater nutrient consumption, even for a brief summer period, would have required a larger annual export of organic matter from the Antarctic surface.

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