Evidence from ice cores \(^1\) and deep-sea sediments \(^2\) shows that atmospheric CO\(_2\) concentration has varied by up to 40% over the past few hundred thousand years. As most of the exchangeable carbon resides in the deep sea, large changes in the atmosphere must have their source here. The distribution of carbon in the ocean is linked to biological productivity, the sinking and degradation of organic matter and calcium carbonate, and ocean circulation \(^3\). Carbon-cycle models predict different (and sometimes conflicting) shifts in productivity, and estimates of past productivity constrain the range of possible solutions. Here I use planktonic foraminifera species data in modern and ice-age Atlantic sediments to assess spatial patterns of changes in productivity. Ice-age export productivity was higher than at present by nearly 40% for the whole Atlantic, and by 90% under the Equator. These changes, if extrapolated to the global ocean, support models in which a significant portion of CO\(_2\) changes are driven by variations in biological productivity.

A wide range of models exist to explain ice-age variations in atmospheric CO\(_2\), each of which has implications for past productivity. Early models call on a ~40% increase in nutrient content of the whole glacial ocean relative to the modern ocean. \(^4\) Such models predict increases in productivity nearly everywhere on the globe (although perhaps mostly in upwelling regions). Past nutrient budgets in the ocean are constrained by cadmium/calcium ratios in benthic foraminifera. Estimates range from a 17% increase in the glacial oceans to essentially no change. \(^5\) This excludes nutrient budget models as the sole source of changes in CO\(_2\) concentration, and implies that other mechanisms must exist.

A group of high-latitude models consider Antarctic oceanography as a source of CO\(_2\) change. In the Antarctic, CO\(_2\)-rich deep or intermediate waters reach to the sea surface. \(^6\) Either lower exchange of Antarctic surface and deep waters or higher mixing with warm surface waters could suppress this polar outcrop of the deep ocean. Both would reduce atmospheric CO\(_2\). In the southern oceans, unlike the tropics and subtropics, phosphate and nitrate do not limit biological productivity. More efficient use of these nutrients by the Antarctic biota \(^7\) could comprise a biological mechanism to reduce CO\(_2\). Recent studies suggest that trace iron is a limiting nutrient in this region, \(^8\) in which case a higher input of iron-rich dust last during the ice age may have increased productivity and thus reduced atmospheric CO\(_2\) levels.

All of these high-latitude models permit changes in productivity, but they do not all require it. Comparable CO\(_2\) changes can result either from biological mechanisms or by different modes of circulation independent of the biology. Indeed, in one of the models above, productivity was held constant. Note that model predictions of productivity apply to 'new' production, \(^9\) that is, to the net export flux of carbon out of surface waters. It is reasonable to think that enhanced new production might also mean higher primary production, but this is not a strict requirement of the models.

Other models note the effects of changing productivity in the low latitudes. A three-box model \(^10\) predicts that higher low-latitude upwelling increases productivity and reduces atmospheric CO\(_2\). This result includes the high latitudes, as upwelling in this model forces overturn of the whole ocean. More complex models include the effect of intermediate water masses. Here equatorial upwelling can operate independently of thermohaline overturn. For example, the four-box ocean model of Boyle \(^11\) predicts that doubling the modern shallow upwelling rate in the tropics would produce atmospheric CO\(_2\) by 25 p.p.m. This occurs through transfer of nutrients (and CO\(_2\)) from intermediate to deep waters. As with the high-latitude models, there are less nutrients in the polar outcrop of cold water. The upwelling change (by a factor of two) in this model increases the nutrient flux into warm surface waters (and thus increases new productivity) by 36%. By itself this mechanism does not change atmospheric CO\(_2\), as much as observed, but another 25 p.p.m. CO\(_2\) change in this model could come from a 50% reduction of deep-water formation or from lower temperatures. \(^12\)

Cadmium \(^13\) and carbon isotope \(^14-18\) content of benthic foraminifera from the Atlantic support the idea of ice-age nutrient depletion of intermediate waters. There is no consensus, however, as to whether this reflects formation of glacial North Atlantic intermediate water or outflow of Mediterranean water. Carbon isotope data from the Indian \(^19\) and Pacific \(^20\) oceans suggest that the ice-age nutrient depletion of intermediate waters may have been global.

Keir's \(^21\) fifteen-box model resolves surface, intermediate and deep waters in the Pacific, Atlantic and Indian oceans, as well as polar outcrop areas in both hemispheres. Keir explores a number of options, but favours one in which Antarctic export productivity is two to three times greater than now and the ratio of Antarctic bottom water to North Atlantic deep water is higher than now. This model is similar to Boyle's \(^22\) in that it reduces intermediate water nutrients. It does this by fixing nutrients in the Antarctic, however, and does not require the increase in intermediate-water formation suggested by Boyle. Keir's model.

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Table 1: Regional changes in productivity between the ice age and present

<table>
<thead>
<tr>
<th>Area</th>
<th>Grid points</th>
<th>Primary productivity (g C m(^{-2}) yr(^{-1}))</th>
<th>New productivity (g C m(^{-2}) yr(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Modern 18 kyr +% change</td>
<td>Modern 18 kyr +% change</td>
</tr>
<tr>
<td>Equatorial</td>
<td>40</td>
<td>70 96 +37</td>
<td>12.3 23.0 +87</td>
</tr>
<tr>
<td>Subtropical</td>
<td>193</td>
<td>47 57 +21</td>
<td>5.5 8.1 +47</td>
</tr>
<tr>
<td>Subpolar</td>
<td>82</td>
<td>62 67 +8</td>
<td>9.6 11.2 +17</td>
</tr>
<tr>
<td>Eastern boundary</td>
<td>51</td>
<td>74 75 +1</td>
<td>13.7 14.1 +3</td>
</tr>
<tr>
<td>Total</td>
<td>366</td>
<td>57 67 +18</td>
<td>8.1 11.2 +38</td>
</tr>
</tbody>
</table>

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**Fig. 1** Calibration of foraminiferal transfer function FAP-6 for primary productivity. The error envelope (mean absolute value of residuals) (dashed line) is ±128 C m\(^{-2}\) yr\(^{-1}\).
decreases warm-ocean productivity by 13 to 43% globally, or by 26 to 50% in the Atlantic sector.

The various models of the carbon system discussed above imply different regional changes in productivity. For the high latitudes, results range from no change to an increase by a factor of three. In the low latitudes anything from a factor-of-two increase to a 50% decrease at the glacial maximum is possible. An obvious test of these model predictions is to reconstruct past productivity.

Initial attempts at reconstructing productivity have used organic-carbon data. This is a logical choice, as organic-carbon accumulation rates in the deep-sea sediments should in some way relate to the export flux of organic carbon from the sea surface. A recent summary of organic-carbon data suggests that higher productivity occurred in many places at the last glacial maximum. This inference, although useful, has not met universal acceptance. Possible causes of poor signal preservation include the diverse composition of bulk organic matter, the effects of deep-sea oxygen sensitivity to errors in sedimentation rates, and contamination with organic matter from the continents.

Because of these uncertainties regarding organic carbon, I have estimated past productivity in a different way. A transfer function may be used to relate the modern planktonic foraminiferal data found in deep-sea sediments to modern productivity. The equation coefficients are constants, found by multiple regression of the core-top foraminiferal assemblages on the modern productivity values from each site.

To estimate past productivity, down-core species abundances are first reduced to factor assemblages as defined by the core tops; these are operated on the productivity transfer function. Both the assemblages and the productivity equation are similar in form to the transfer functions used to estimate sea surface temperatures from the same foraminiferal data. Both temperature and productivity may be estimated from the same data set if the two parameters are statistically independent, which is the case here. In the modern world, productivity and mean sea surface temperature are not correlated on a large scale. For the 356 calibration sites used here, the correlation between productivity and sea surface temperature is essentially zero (r = -0.11). Thus, the productivity transfer function, if designed properly, is independent of variations caused by temperature changes.

Calibration of the transfer function requires a map of modern productivity. Berger et al. have compiled primary-productivity data based on 14C incubation. They note the uncertainties involved with this method, but assert that the large-scale patterns are reasonably reliable. Using these data and a model based on nutrient concentrations, light intensity, and continental influence, they develop a global map of productivity. Although some assumptions were made to derive this map, I use it here for calibration because it is the only available map that has global coverage and uniform smoothing. It is very similar to earlier global productivity maps, but includes much more recent data. Further studies will no doubt expand on the modern data set, and this will improve future attempts at calibrating the geological record.

Transfer function FAP-6 (Foraminiferal Atlantic Productivity equation Six) is used here (Fig. 1). Full documentation of the factor and equation coefficients appears elsewhere

Fig. 2. Atlantic primary productivity, in g C m⁻² yr⁻¹, using equation FAP-6 and CLIMAP foraminiferal species data. a. Core tops (modern). b. Last glacial maximum (>18 kyr BP). c. The productivity difference (glacial minus modern). Positive values indicate higher ice-age productivity.

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carbonate fluxes (thought to reflect lower productivity) on the Sierra Leone Rise. Because the sites off north-west Africa which were studied for organic carbon are mostly under coastal upwelling, whereas the cores used in this work are mostly offshore, the two data sets are not easily comparable. It is possible that the histories of coastal and offshore productivity are different.

High productivity at the Equator is consistent with ice-age cooling. Upwelling could drive both effects. Cooling also occurred off north-west Africa, however, where the foraminiferal data suggest lower productivity. Cooling here may reflect advection of cool surface waters from higher latitudes instead of upwelling of cold nutrient-rich sub-surface waters. Again, note that the cores used here are not under the coastal upwelling system, but are offshore. Ice-age productivity appears to have increased not only in the equatorial upwelling area but also in the subtropics (Fig. 2c), so equatorial upwelling is not the only mechanism contributing to the change. Although cadmium data preclude large variations in nutrient budgets, small changes remain possible. In addition, stronger ice-age winds may have enhanced vertical mixing outside of the upwelling zones.

Table 1 lists changes in productivity by area. The equatorial area has boundaries of 60° W, 0° W, 8° S, 8° N. The other areas have parts in both the Northern and Southern Hemispheres. The subtropical boundaries are 90° W, 25° W, 8° N, 40° N and 80° W, 0° E, 40° S, 8° S. For the subpolar regions the boundaries are 80° W, 0° E, 40° N, 65° N and 70° W, 0° E, 60° S, 40° S. The eastern boundary current (EBC) regions are defined as 25° W, 0° E, 8° S, 40° N and 0° E, 20° E, 40° S, 0° S. The major increases in primary productivity at the last glacial maximum occur in the equatorial and subtropical areas, with increases of 37% and 21% respectively. The subpolar and EBC regions change little on average. For the EBC this reflects a slight increase in productivity in the Southern Hemisphere and a slight decrease in the Northern Hemisphere. Over the whole Atlantic, the mean glacial primary productivity (67 ± 1.6 g C m⁻² yr⁻¹) was 18 ± 5% higher than at present (57 ± 1.0 g C m⁻² yr⁻¹).

Only the portion of the organic matter exported to the deep sea, or "new" productivity, drives partitioning of CO₂ in the ocean. We cannot yet constrain the recycling of carbon within near-surface waters in the past, but modern primary and new productivity may be related. If we use the proposed model relationship, the 18 ± 5% glacial-interglacial change in primary productivity amplifies to a 38 ± 12% increase in new productivity. For the equatorial band, glacial new productivity is nearly twice that at present (Table 1). The transform between primary and new productivity is uncertain even for the present ocean, and is only an approximation. Some conclusions can be drawn, however. The changes suggested here agree with models in which atmospheric CO₂ is driven lower by increasing low-latitude productivity. They are not consistent with models that require lower warm-ocean productivity at the last glacial maximum.

This study covers the Atlantic ocean alone, which accounts for about one-third of the present total oceanic production (both primary and new productivity). If productivity in the Pacific and Indian oceans varied in a different fashion to that in the Atlantic, the inferences made here could be in error. A recent global study of organic carbon reconstructs an ice-age increase in new productivity of 45 ± 6% over the modern value. Although the spatial patterns disagree in detail with the estimates made here, the average change is remarkably consistent with the 38 ± 12% increase suggested by the foraminiferal data. To further understand the mechanisms responsible for these changes, we must work toward global reconstructions with regional resolution. From the reconstruction presented here, it appears that equatorial upwelling and vertical mixing in the subtropics are two possible mechanisms. I appreciate assistance from C. Peterson on foraminiferal species data and counts analysis. Discussions with W. Berger, S. Emerson, M. Sarnthein and E. Suess, and a review by L. Labeyrie added to this paper. This research and curation of cores was supported by the NSF.

NGC 1951 Model explores several mechanisms for lower glacial PCO₂ and produces a range of effects on nutrient fluxes to the warm surface ocean (and thus on new productivity). These vary from an ~20% decrease (in cases without enhanced upwelling) to an ~120% increase (for a case with higher glacial upwelling) relative to modern values. The reconstruction presented here is most similar to, but less extreme than, the cases with enhanced tropical upwelling.