tion, Solar Ultraviolet Radiation and Plant Life (Springer-Verlag, Berlin, 1986).

- 2. R. Stolarski et al., Nature 322, 808 (1986).
- 3. J. Calkins and T. Thordardottir, ibid. 283, 563 (1980).
- 4. J. Frederick and D. Lubin, J. Geophys. Res. 93, 3825 (1988)
- 5. Atmospheric Ozone 1985, Assessment of Our Understand-

ing of the Processes Controlling its Present Distribution and Change (National Aeronautics and Space Administration, Washington, DC, 1986).

- One Dobson unit is equal to an ozone column content of 2.69×10^{20} molecules per square meter of horizontal area extending from the ground to the top of the atmosphere.
- 7. J. Farman et al., Nature 315, 207 (1985).
- 8. A. J. Krueger, personal communication (1987); Science 239, 146 (1988).
- B. Diffey, Photochem. Photobiol. 46, 55 (1987)
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The Position of the Gulf Stream During **Quaternary Glaciations**

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Ocean general circulation theories predict that the position of the boundary between subtropical and subpolar gyres (and therefore the position of the Gulf Stream-North Atlantic Current system and the subpolar-subtropical front) is set by the line of zero "Ekman pumping," where there is no convergence or divergence of water in the directly wind-forced surface layer of the ocean. In the present-day North Atlantic Ocean this line runs southwest to northeast, from off the Carolinas to off Ireland. However, during the last ice age (18,000 years ago) the subpolar-subtropical boundary ran more zonally, directly toward Gibraltar. A numerical atmospheric general circulation model indicates that the field of Ekman pumping 18,000 years ago was modified by the presence of a continental ice cap more than 3 kilometers thick such that the line of zero Ekman pumping overlaid the paleogyre boundary. These results demonstrate that the presence of a thick continental ice sheet could have caused changes in sea surface temperatures in the North Atlantic during Quaternary glaciations by altering wind patterns.

n the present-day North Atlantic Ocean, the boundary between subtropical and subpolar gyres runs southwest to northeast, from Hatteras to the Norwegian Sea. The warm Gulf Stream and its extension, the North Atlantic Current system, coincide with this boundary. Together, these currents supply between 50 and 100 W m⁻² of heat to the high latitude North Atlantic (1), and, once cooled, their waters sink to become a major source of bottom water to the world ocean. In contrast, during the last glacial maximum approximately 18,000 years ago, the gyre boundary and associated currents were more zonal and located farther to the south (2, 3), resembling the present-day North Pacific.

The position of the gyre boundary can have important consequences on both sur-

Fig. 1. Present-day January SST compiled by the CLIMAP group (2). The dots are positions of the data points used to make this reconstruction. The heavy solid line is the 10°C isotherm, which was chosen to represent the position of the subpolarsubtropical gyre boundary (10). The heavy dashed line is the present-day position of the line $w_e = \operatorname{curl}(\tau) = 0$ (13). The crossed line represents the circulation pattern of the Gulf Stream-North Atlantic Current system as determined by Sverdrup et al. (14). The 10°C isotherm, maximal thermal gradient, and Gulf Stream-North Atlantic Current system all coincide. Note that the line $w_{\rm e} = {\rm curl}(\tau) = 0$ essentially determines the position of these features.

face water properties and deep and bottom water production. The present-day warmwater influx to high latitudes significantly enhances the evaporation (and cooling) over that of resident cooler waters, resulting in density changes sufficient to produce bottom water (4). The zonal orientation of the gyre boundary 18,000 years ago suggests that the excursion of warm water to high latitudes had ceased. This implies that subpolar surface waters were cool and that deep-water production was reduced. Geological and microfossil evidence supports the first of these implications (3) and geochemical data support the later (5).

Previous studies have suggested that the reason for this realignment is related to atmospheric forcing (6), but the exact mechanism has remained unclear. We suggest that the presence of continental ice may have been responsible for modifying the wind field in such a manner as to cause the line of zero "Ekman pumping"-a dynamically critical parameter to the gyre geometry-to

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become more zonal and, in turn, force a more zonal gyre boundary during the last glacial maximum (7, 8).

Modeling and theoretical studies have shown that the shape and dynamics of the ocean gyres are controlled by the field of Ekman pumping, w_e , the vertical velocity out of the approximately 100-m-thick "Ekman layer" at the ocean surface that is directly forced by the winds. This velocity is given by $w_{\rm e} = \mathbf{k} \cdot \operatorname{curl}(\mathbf{\tau}/f)/\rho$, where **k** is the unit vertical vector, τ is the wind stress vector, f is the Coriolis parameter, and ρ is the density of seawater. For small ranges in latitude (compared to the radius of the earth), f is nearly constant, and the fields of Ekman pumping and wind stress curl are similar and interchangeable [that is, w_e ~ curl(τ)]. Because ρ can be considered as constant, w_e is completely determined by atmospheric parameters, in particular, the wind stress **T**. The actual boundary between gyres tends to lie along the line w_e $= \operatorname{curl}(\mathbf{\tau}) = 0$ (9, 10). South of this line fluid converges in the Ekman layer, defining the subtropical gyre, whereas north of the line fluid diverges, defining the subpolar gyre.

The transition from subtropical to subpolar waters across the gyre boundary is distinct and can be characterized by many property gradients. We chose the position of the maximum thermal gradient to represent the position of the gyre boundary because it offers several advantages: it represents a historical choice (10), and, more importantly, it offers a means of locating the paleoboundary because marine geologic data can provide estimates of past sea-surface temperature (SST). The maximum thermal gradient in the winter SST distribution (11, 12), the 10°C isotherm, the position of the line $w_e = \operatorname{curl}(\tau) = 0$ (13), and the position of the North Atlantic Current (14) all coincide in the present day (Fig. 1).

Held (15), using an Atmospheric General Circulation Model (AGCM) with presentday boundary conditions, suggested that orographic control, particularly the Rocky Mountains, may be important in giving the $w_{\rm e} = 0$ line its southwest to northeast trend. If this is the case, then the presence of a continental ice cap more than 3 km thick would have had important consequences on the wind field during Quaternary glaciations. Manabe and Broccoli (16) have investigated these consequences, using an AGCM that was run with reconstructed boundary conditions from 18,000 years ago, including the presence of continental ice (17). Their model results indicate that the 500-mbar winds retracked from a single jet crossing the North American continent to two jets that straddle the Laurentide ice sheet. The northern branch passed between the Laurentide and Greenland sheets and then over the Labrador Sea, while the southern branch passed south of the ice sheet. The southern branch apparently was significantly stronger than the northern branch (as well as stronger than the present-day single jet).

This restructuring of atmospheric circulation would have affected the field of Ekman pumping as well. Our hypothesis is that the atmospheric circulation changed in such a way as to move the $w_e = \operatorname{curl}(\tau) = 0$ line to a more zonal configuration which, in turn, would have caused a more zonal orientation of the gyre boundary 18,000 years ago. We have reconstructed an estimate of the Ekman pumping field from simulated fields of wind stress, which were predicted by the National Center for Atmospheric Research's AGCM (18). This AGCM predicts cloud cover and includes four separate classes of surface albedo-vegetative, nonvegetative, ice or desert, and water. The boundary conditions that we used are from CLIMAP (2) and include SST and continental orography, reconstructed from 18,000 years ago, for the entire globe. We used only winter simulations. We calculated wind stress for each time step and then averaged the data over 100 days. We then used these averages

to estimate Ekman pumping. This model is not an active ocean model—SSTs are prescribed, rather than predicted.

The simulated $w_e = \operatorname{curl}(\tau) = 0$ line trends zonally (Fig. 2) along 38°N, consistent with a more zonal alignment of the gyre boundary than occurs today. Subpolar regions, characterized by upward pumping $(w_e > 0)$, have expanded to include virtually the entire North Atlantic north of 40°N. As with the present-day configuration, the predicted line of $w_e = \operatorname{curl}(\tau) = 0$ approximates the maximum thermal gradient position as determined by the SST reconstruction of the CLIMAP group (2). The 10°C winter surface isotherm, which best represents the current gyre boundary, is also the isotherm that is most representative of the boundary in the reconstruction.

Even though we suggest that the presence of continental ice was responsible for this realignment, we cannot rule out the possibility that strong thermal gradients at the ocean surface may have driven the line w_e = curl(τ) = 0 to its simulated position through a circular feedback.

The position of the "polar front" 18,000 years ago, as reconstructed by Ruddiman and McIntyre (3), corresponds to our recon-



Fig. 2. January SST for 18,000 years ago, as reconstructed by the CLIMAP group (2). The dots are positions of the data points used to make this reconstruction. As in Fig. 1, the heavy solid line represents the 10°C isotherm and the heavy dashed line is the position of the model-predicted $w_e = \operatorname{curl}(\tau) = 0$ line. The crossed line represents the position of the polar front 18,000 years ago, as determined by Ruddiman and McIntyre (3). We assume that the 10°C isotherm, maximal temperature gradient, and the presence of the polar front all correspond with the position of the Gulf Stream–North Atlantic Current system 18,000 years ago. Note the close correspondence between the model-predicted $w_e = \operatorname{curl}(\tau) = 0$ line and these features.

structed position of the North Atlantic Current and the gyre boundary (Fig. 2). This suggests that the glacial subpolar gyre took on polar characteristics when the subpolarsubtropical gyre boundary shifted to a more zonal orientation and the northward excursion of warm subtropical waters into the subpolar region ceased. This allowed a southern migration of water with polar characteristics. The polar front represents the southern limit of this migration, which occurred at the subpolar-subtropical gyre boundary. This interpretation is consistent with that of Ruddiman and McIntyre (3).

We speculate on why the North Atlantic had a more zonally oriented $w_e =$ $\operatorname{curl}(\tau) = 0$ line 18,000 years ago. In the present-day North Atlantic, the position of the line where $w_e = \operatorname{curl}(\boldsymbol{\tau}) = 0$ corresponds to the location of strong eastward wind stresses (produced by westerlies) and occurs where the meridional gradient of these stresses vanishes (19). These strong stresses are due to continental storms. In turn, the southwest to northeast trend of the line is due to the storm tracks, which have a similar pattern. However, in our runs, strong eastward stresses occur only in the eastern central North Atlantic, centered on approximately 35°W, 45°N, as if the present-day pattern had swung to the south. This suggests that the storm tracks 18,000 years ago ran more zonally and farther to the south than they do now, which is consistent with interpretations based on geological data (20)

Central to our hypothesis is that the buildup of a substantial ice cap is necessary before the paleowind fields can be expected to shift and, in turn, alter the orientation of the gyre boundary. Changes in ice volume should precede changes in SST. Using oxygen isotope analyses and assemblages of planktonic foraminifera from the same core, Ruddiman and McIntyre (3) have shown that continental glaciation preceded changes in SST as far north as 60°N in the North Atlantic during the isotopic 5 to 4 and 5e to 5d transitions approximately 120,000 years ago. This sequence of events implies that the ocean passively responds to continental ice conditions rather than actively driving an ice age and the consequential buildup of continental ice. Our interpretation accounts only for changes in the ocean over the relatively long time scales of continental ice buildup and decay. It does not explain the much more rapid (approximately 1000-year) Younger Dryas event, which did not correspond with any substantial change in ice coverage (21).

Our scenario for the role of the ocean during glaciation can be summarized as follows. Low summer insolation causes accumulation of snow and ice through the summer, which in turn increases the volume of ice and overall earth albedo. The ice volume eventually becomes large enough to influence thermal and orographic steering of the $w_{\rm e} = {\rm curl}(\tau) = 0$ line, causing it and, by consequence, the subtropical-subpolar gyre boundary to move southward. Finally, such a shift shuts off the supply of warm and salty waters to the high-latitude North Atlantic, resulting in a drop in SST and a cessation of bottom water production in the high latitudes. Deglaciation follows a similar, but reversed, sequence (22).

REFERENCES AND NOTES

- 1. A. V. Bunker and L. V. Worthington, Bull. Am. Meteorol. Soc. 57, 670 (1976). CLIMAP, Geol. Soc. Am. Map Ser. MC-36 (1981). W. F. Ruddiman and A. McIntyre, J. Geophys. Res.
- 3. 82, 3877 (1977)
- B. A. Warren, J. Mar. Res. 41, 327 (1983)
- For a review, see B. H. Corliss, D. G. Martinson, T. Keffer, Geol. Soc. Am. Bull. 97, 1106 (1985).
- 6. W. F. Ruddiman, in North America and Adjacent Oceans During the Last Deglaciation, W. F. Ruddiman and H. E. Wright, Jr., Eds. (Geological Society of America, Boulder, CO, in press).
- T. Keffer, B. H. Corliss, D. G. Martinson, Eos 67, 44 (1986)
- K. E. Nowell and J. Hsiung, in Abrupt Climatic Change, W. H. Berger and L. D. Labeyrie, Eds. (Reidel, Dordrecht, 1987), pp. 67–87.
 W. H. Munk, J. Meteorol. 7, 79 (1950).
- H. Stommel, The Gulf Stream (Univ. of California 10. Press, Berkeley, 1965).
- 11. The CLIMAP (2) geological indices have been used

to calculate present-day SSTs (12). In the region of interest, these geologically based SSTs are nearly indistinguishable from the observed SSTs, except for an area southeast of Newfoundland where the geologically based estimates are warmer than observed by $\geq 1.2^{\circ}$ C.

- 12. B. Molfino et al., Quat. Res. (N.Y.) 17, 279 (1982). A. Leetma and A. F. Bunker, J. Mar. Res. 36, 311 13. (1978).
- 14. H. U. Sverdrup, M. W. Johnson, R. H. Fleming, The Oceans (Prentice-Hall, New York, 1942). 15. I. M. Held, *Icarus* 50, 449 (1982).
- 16. S. Manabe and A. J. Broccoli, J. Geophys. Res. 90, 2167 (1985).
- 17. For examples of other atmospheric simulations for 18,000 years before present, see J. Williams et al. [J. App. Meterol. 13, 305 (1974)], W. L. Gates [Science **191**, 1138 (1976)], and J. E. Kutzbach and P. J. Guetter [*J. Atmos. Sci.* **43**, 1726 (1986)].
- 18. E. J. Barron and W. M. Washington, J. Geophys. Res. 89, 1267 (1984).
- 19. This is because of the dominance of zonal winds and the near similarity of Ekman pumping and wind stress curl. This allows Ekman pumping to be approximated as $w_e \sim \operatorname{curl}(\tau) \sim \partial \tau(x) / \partial y$. Hence, where the meridional gradient of zonal wind stress $\left[\frac{\partial \tau(x)}{\partial y}\right]$ equals zero, w_e will tend to equal zero.
- 20 W. F. Ruddiman and A. McIntyre, Science 204, 173 (1979)
- 21. W. S. Broecker, D. M. Peteet, D. Rind, Nature 315, 21 (1985)
- 22. We thank E. Barron and L. Sloan (both at Pennsylvania State University) for providing wind stress values for 18,000 years before present. This research was initially supported by a grant from the Woods Hole Occanographic Institution Center for the Analysis of Marine Systems. Additional support came from NSF grants OCE 83-15369 and OCE 85-15642 (T.K.), and OCE-84-19595 and OCE-86-14162 (B.H.C.). This is University of Washington, School of Oceanography contribution number 1776 and Lamont-Doherty Geological Observatory number 4299

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Direct Measurement of O₂-Depleted Microzones in Marine Oscillatoria: Relation to N₂ Fixation

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Among the nitrogen (N₂)-fixing cyanobacteria, the filamentous, nonheterocystous marine Oscillatoria spp. (Trichodesmium) appears enigmatic; it exhibits N2 fixation in the presence of oxygenic photosynthesis without structural protection of the N2-fixing apparatus (nitrogenase) from potential inhibition by molecular oxygen (O2). Characteristically, N₂ fixation is largely confined to aggregates (bundles) of filaments. Previous work has suggested that spatial partitioning of photosynthesis and of N2 fixation occurs in the bundles as a means of allowing both processes to occur contemporaneously. The probing of freshly sampled bundles with O₂ microelectrodes directly confirmed such partitioning by showing the presence of O₂-depleted (reduced) microzones in photosynthetically active, N2-fixing bundles. Bundle size was directly related to both the development of internal reduced microzones and cellular N2 fixation rates. By enhancing microzone formation, bundles optimize N2 fixation as a means of supporting Oscillatoria spp. blooms in surficial, nitrogen-depleted tropical and subtropical waters.

ROPICAL AND SUBTROPICAL NITROgen-depleted marine waters periodically support near-surface blooms of the filamentous oxygenic cyanobacterium Oscillatoria (Trichodesmium) spp. Blooms are confined to calm periods when buoyant filaments accumulate at the surface as reddish-brown aggregates or bundles. The filaments in the bundles are oriented in a parallel fashion (Fig. 1). Characteristically, N_2 fixation is associated with bundles (1).

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