PALEOCEANOGRAPHY

A diminished North Atlantic nutrient stream during Younger Dryas climate reversal

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The high rate of biological productivity in the North Atlantic is stimulated by the advective supply of nutrients into the region via the Gulf Stream (nutrient stream). It has been proposed that the projected future decline in the Atlantic Meridional Overturning Circulation (AMOC) will cause a reduction in nutrient supply and resulting productivity. In this work, we examine how the nutrient stream changed over the Younger Dryas climate reversal that marked the transition out of the last ice age. Gulf Stream nutrient content decreased, and oxygen content increased at the Florida Straits during this time of weakened AMOC. The decreased nutrient stream was accompanied by a reduction in biological productivity at higher latitudes in the North Atlantic, which supports the link postulated in theoretical and modeling studies.

The Gulf Stream and North Atlantic Drift serve as a northward-flowing conduit of nutrient-rich intermediate waters (*1*, *2*). In the subpolar North Atlantic, the density surfaces bearing these nutrients shoal, and the nutrients are incorporated into the deep winter mixed layer (*3*). During the spring bloom, these nutrients drive primary productivity in the sunlit surface ocean. The high-nutrient waters of the Gulf Stream have been called the nutrient stream, and this advective pathway is thought to be the dominant source of nutrients supporting phytoplankton productivity in the subpolar North Atlantic (*4*, *5*). The Gulf Stream originates in the Florida Straits, and as it moves northward along the western boundary of the subtropical gyre, both the mass and nutrient transport of the current are augmented by recirculating water within the North Atlantic basin. However, the ultimate source of the nutrients to the incipient Gulf Stream in the Florida Straits is the import of high-nutrient intermediate-depth waters from the tropics, which are replenished by the high-nutrient Southern Hemisphere intermediate and mode waters as part of the upper (northward) limb of the Atlantic Meridional Overturning Circulation (AMOC) (*2*, *6*). In addition to supplying the nutrient stream, the Southern Hemisphere intermediate and mode waters supply the nutrients that drive much of the primary production at low and mid-latitudes (*7*, *8*).

The AMOC is projected to weaken over the coming century with the increase in anthropogenic greenhouse gases (*9*). Consequently, the nutrient stream is projected to weaken, leading to basin-scale changes in biogeochemistry and decreased primary production. Declines in primary production would affect the important North Atlantic fisheries and may also affect the uptake of anthropogenic CO_2. Although a future decline in North Atlantic export production under future warming scenarios has long been projected (*10*), it has only more recently been recognized that the decline in the nutrient stream is the dominant mechanism driving this change (*11*). Whitt (*5*) has found that, when driven with the high-emissions Representative Concentration Pathway 8.5 (RCP8.5) scenario, the Community Earth System Model (CESM) shows a 35% decline in Gulf Stream nitrate transport at 30° N in 2080 in response to a 39% decline in AMOC and finds that the decreased nutrient stream is the primary driver of the associated decline in North Atlantic export productivity. Tagklis *et al.* (*12*) have shown that the weakening of AMOC over the next century in the multimodel mean of seven CMIP5 models results in reduced upper-ocean phosphate concentration, upper-ocean apparent oxygen utilization (AOU), and primary productivity in the North Atlantic, and they attribute these changes to the decreased nutrient stream. Using biogeochemical data from an ice core, Osman *et al.* (*13*) have reconstructed a decline in North Atlantic primary productivity over the industrial era, which they attribute to a weakening AMOC. There are multiple lines of evidence that the AMOC weakened during the Younger Dryas cold interval that punctuated the transition out of the last ice age (*14*). In this work, we assess the link between the AMOC and nutrient stream for the Younger Dryas event through the reconstruction of nutrient and oxygen concentrations in the deepest waters of the Florida Straits and explore the consequences for North Atlantic productivity. Although the details of the background climate state and timescale of change differ from those of the present day, this past climate event provides an opportunity to test the mechanisms that have been identified in the climate models.

Reconstruction of seawater biogeochemistry in the Florida Straits

Sediment core KNR166-2-26JPC was recovered from 24°19.61′ N, 83°15.14′ W in the Florida Straits at 546-m water depth. Because of the high sedimentation rates, this core provides exceptional time resolution over the Younger Dryas climate reversal. The coring site along the Florida margin is currently bathed by Antarctic Intermediate Water (AAIW) (potential density = 27.3 kg m^{-3}), which, at this location, is characterized by high nutrient and low oxygen concentrations and supplies new nutrients to the North Atlantic (*2*, *6*) (Fig. 1). We reconstruct seawater-dissolved oxygen concentration at this location using carbon isotope measurements in paired epifaunal and deep infaunal benthic foraminifera, following an approach pioneered by McCorkle and Emerson (*15*, *16*). *Planulina ariminensis* occupies a habitat on top of the sediments and records seawater $\delta^{13}C$ values, and *Globobulimina* has a habitat deep within the sediments, where the dissolved carbon has much lower $\delta^{13}C$ values and oxygen is reduced to near zero values from the respiration of organic matter within the sediments. The difference between the $\delta^{13}C$ values in the tests of these two benthic foraminifera is used to quantitatively reconstruct past oxygen concentrations (*17*). We also present abundance data for three thermocline-dwelling species of planktonic foraminifera, which are currently abundant in areas with subsurface low-oxygen layers—*Globorotalia menardii*, *Globorotalia tumida*, and *Pulleniatina obliquiloculata* (*18*). At this location, we have previously published Cd/Ca measurements in benthic foraminifera that were used to reconstruct changes in seawater Cd concentration, Cd_w, which mimics the distribution of the major nutrient PO_4 in the ocean (*19*). We have also published benthic foraminiferal Mg/Li (*20*) to reconstruct temperature at this site over the deglaciation. We also use a previously published age model for this core (*21*). We estimate past PO_4 concentrations, using the Cd_w reconstructions, and AOU—a measure of oxygen consumption in the subsurface ocean that is determined from the difference between in situ and saturation oxygen concentration—using the quantitative temperature and oxygen reconstructions. We then use the PO_4 and AOU to separately estimate changes in the PO_4 concentration inherited from the source regions [preformed PO_4 (P_{pre})] and the PO_4 that has been contributed to the subsurface from the remineralization of organic matter. Because intermediate waters leave the surface slightly undersaturated in oxygen, AOU overestimates true subsurface oxygen utilization, and P_{pre}

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can be underestimated by up to 0.2 μM, depending on the climate state. Detailed methods can be found in the supplementary materials.

Weakened Florida Straits nutrient stream during the Younger Dryas

Although the intermediate waters that supply the nutrient stream have high PO_4 and oxygen concentrations (high P_{pre}, low AOU) when they leave the surface in the Southern Hemisphere, these properties change as the waters transit northward through the tropics. Export productivity from overlying surface waters adds PO_4 and consumes O_2 through the oxidation and remineralization of sinking organic matter. Because the productivity is itself fed by a continuous supply of preformed nutrients, the accumulation of remineralized PO_4 and the depletion of oxygen both depend on the northward flow of nutrient-charged intermediate waters (*22*). As the AMOC weakened during the Younger Dryas (*14*), this contribution of nutrient-rich, low-oxygen intermediate water from the south would have diminished, replaced by lower-PO_4 and higher-oxygen intermediate waters formed locally in the North Atlantic. We therefore would expect an increase in the oxygen concentrations in the deep Florida Straits. We reconstruct high oxygen values during the Younger Dryas from the dual carbon isotope approach, and increased oxygenation of the waters in the Florida Straits is also supported by the disappearance of the planktonic foraminifera *G. menardii*, *G. tumida*, and *P. obliquiloculata* (Fig. 2). The small warming of the waters transiting the site of about 2°C during the Younger Dryas interval (*20*) would imply a decrease in oxygen concentration at saturation with the atmosphere, and the decrease in AOU is consequently slightly larger than the increase in oxygen. This is, again, what is expected if the oxygen increase is driven by the diminished contribution of the high-AOU intermediate waters from the tropics.

A more direct measure of the nutrient stream comes from estimates of the concentration of the major nutrient PO_4 in the deep Florida Straits (Fig. 3). This estimate is based on the Cd/Ca in *Hoeglundina elegans*, a different species of benthic foraminifera than was used to reconstruct oxygen through the carbon isotope measurements. The PO_4 at this site reflects contributions of intermediate waters formed in both hemispheres, including the regenerated PO_4 from the remineralization of organic matter in the tropics. We find a strong Younger Dryas decrease in PO_4 and, given that the intermediate water northern and southern end-member values did not change by much over this time period (fig. S2B), the lower PO_4 in the Florida Straits is consistent with the weakened AMOC. To probe this further, we use the AOU to separate the PO_4 concentration into its preformed (P_{pre}) and regenerated ($PO_4 - P_{pre}$) components. The PO_4 reduction primarily reflects a small decrease in P_{pre} and a much larger decrease in the regenerated PO_4, as inferred from the large AOU decrease (Fig. 3). Today, the intermediate waters formed in the Southern Hemisphere have a higher P_{pre} compared with those that form in the North Atlantic, so a lower P_{pre} is expected during a time of weakened AMOC when a larger proportion of Northern Hemisphere–sourced intermediate waters would have bathed the site. Similarly, with a weakened AMOC, we expect a lesser contribution of intermediate waters that have transited through the tropics, where they gain a high regenerated PO_4 content. There may have also been a positive feedback whereby the reduced northward transport of nutrients led to less productivity and remineralization in the tropics. The reduction of both preformed and regenerated PO_4 throughout the intermediate-depth North

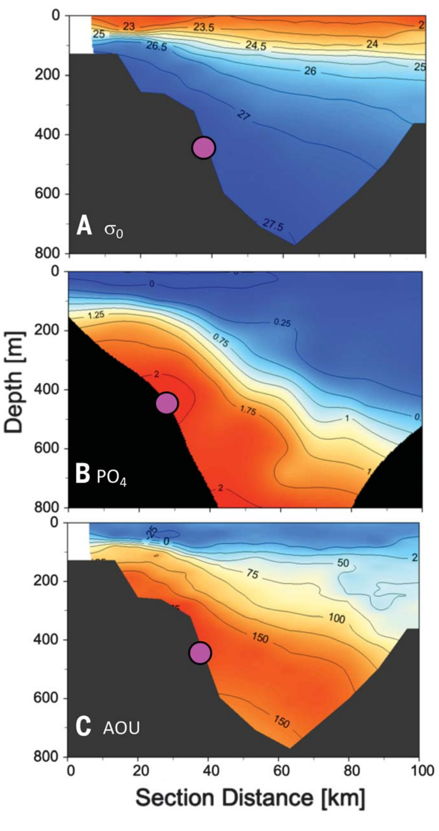

Fig. 1. The nutrient stream in the Florida Straits. The World Ocean Circulation Experiment (WOCE) A5 section across the Florida Current at 26° N from Florida (left) to the Bahamas (right), just downstream of the location of sediment core KNR166-2-26JPC (*29*, *30*). (**A**) Potential density (σ_0) (in kilograms per cubic meter). (**B**) PO_4 (in micromoles per kilogram). (**C**) AOU (in micromoles per kilogram). The depth of core KNR166-2-26JPC on the Florida Margin is indicated with a magenta circle in all panels.

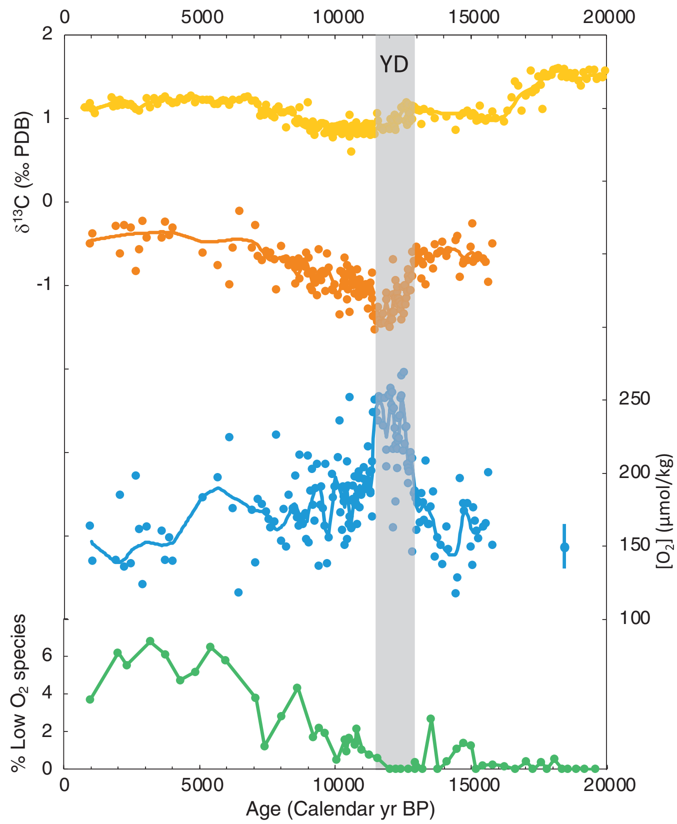

Fig. 2. History of oxygenation in the Florida Straits. The average carbon isotopic composition of tests of the foraminifera *P. ariminensis* (yellow) and *Globulimina* (orange) from KNR166-2-26JPC and the difference in these values converted to oxygen (blue). The 1σ calibration error for the oxygen proxy is indicated in blue. The solid line is a loess smooth through the data. Also shown in green are the proportion of planktonic foraminiferal specimens that are associated with low-oxygen values in the subsurface. The gray bar indicates the Younger Dryas (YD) time period. ‰ PDB, per mil Pee Dee Belemnite; BP, before the present.

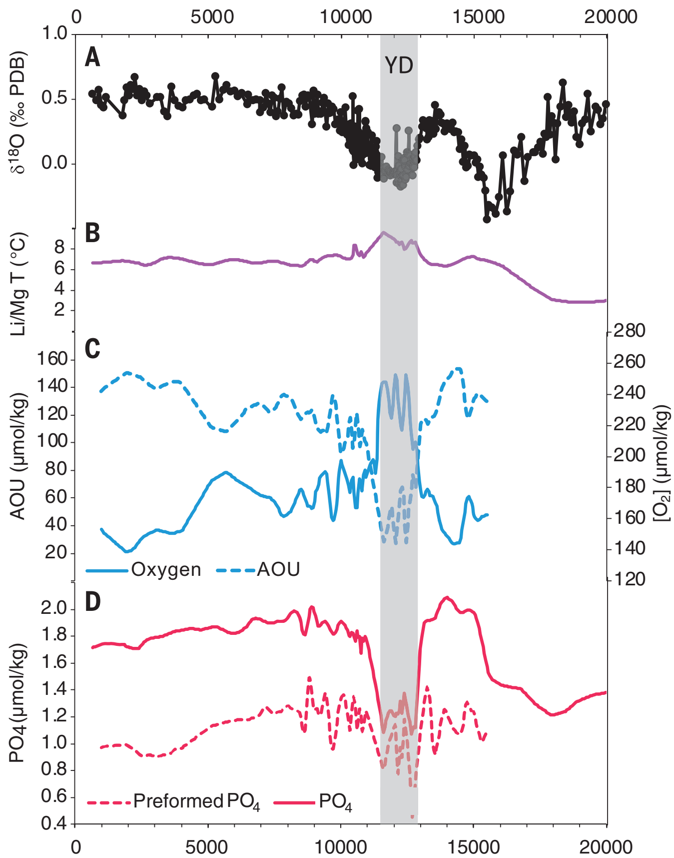

Fig. 3. Florida Straits circulation and biogeochemistry over the deglaciation. (**A**) The ice volume–corrected oxygen isotope ratio of benthic foraminifera on the Florida Margin at KNR166-2-26PC, which reflects changes in the density contrast across the Florida Straits and the strength of the upper branch of the AMOC (*14*, *26*, *31*). (**B**) Temperature (T) estimate from Li/Mg (*20*). (**C**) Smoothed reconstructed oxygen time series as in Fig. 2 (solid line) and the AOU based on Li/Mg temperature reconstruction (dashed line). (**D**) PO_4 estimated from Cd/Ca ratio (*19*) and preformed PO_4 estimated using AOU. The gray bar indicates the Younger Dryas time period.

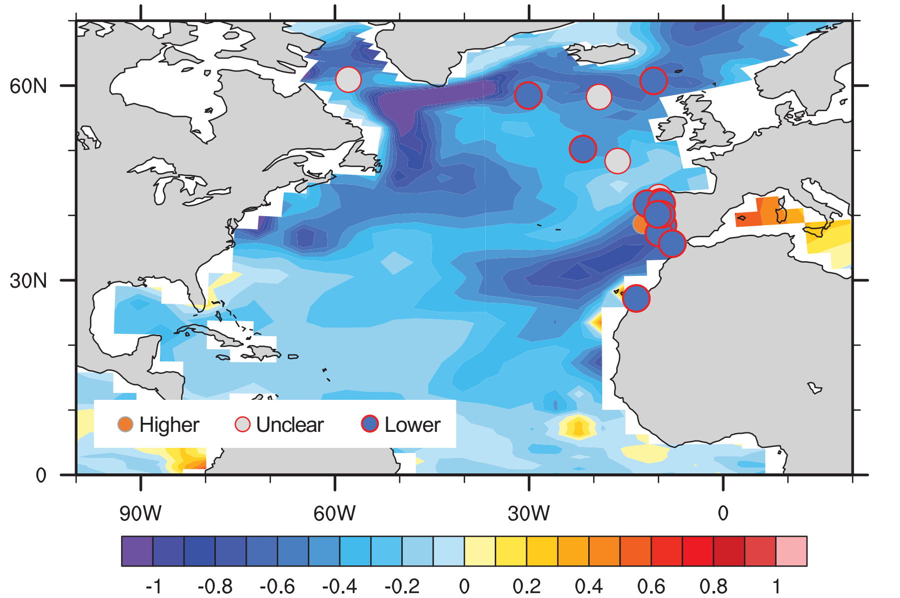

Fig. 4. Younger Dryas productivity anomaly. Circles are sediment core locations where reconstructed productivity is clearly lower than that in time periods before and after the Younger Dryas (blue), where reconstructed productivity is higher than that in the time periods before or after (orange), or where there is no clear anomaly relative to the time before and after (gray) (table S1). The background is anomaly in the flux of particulate organic carbon (in moles per square meter per year) between a time in the C-iTRACE simulation (*26*) with a weak AMOC [17.5 thousand years ago (ka)] and a strong AMOC (19.5 ka).

Atlantic, coupled with a decreased contribution of intermediate waters from the Southern Hemisphere, is also inferred for the Last Glacial Maximum, based on an inversion of the spatially more extensive dataset for that time period (*23*).

Biogeochemical consequences of a weakened versus collapsed AMOC

Although it has been established that the surface branch of the AMOC replenishes the modern nutrient stream and that a future century-scale weakening of the AMOC will result in a weaker nutrient stream and lower North Atlantic productivity, it is not immediately apparent that these concepts and expectations translate directly to the Younger Dryas, a millennial-scale event that occurred on the deglaciation. Schmittner (*24*) simulated a millennial-scale AMOC collapse and recovery using freshwater forcing in an intermediate-complexity model. Although a productivity decline is observed, the mechanism behind this decline under a collapsed AMOC differs from the simulations for a future weakening of the AMOC. The decline in productivity in this case is attributed to strong near-surface density stratification, and the intermediate water nutrient content in the upper 1 km of the North Atlantic is higher over the duration of the shutdown rather than lower, as in the future scenarios. Another set of equilibrium experiments under Last Glacial Maximum boundary conditions in a different intermediate-complexity model confirmed this behavior for a simulation where the large-scale AMOC is completely collapsed because of strong freshwater forcing (*25*). However, when the AMOC is weakened but not shut down completely, the PO_4 in the upper 2 km of the North Atlantic is lower than that in the control state, consistent with the pattern seen for the future transient (*12*) and with that seen in our reconstruction for the Younger Dryas. The transient response of a long paleoclimate simulation using CESM1 (*26*) can be used to explore the relationship between the AMOC, biogeochemical properties in the upper North Atlantic, and productivity. In this simulation, as the AMOC and nutrient stream weaken, the nutrient content of the upper North Atlantic and primary productivity both decline (fig. S2A). However, when the AMOC is almost absent, a state with low productivity and high open ocean North Atlantic intermediate water nutrient content is seen, as in the AMOC collapse scenarios of the intermediate-complexity models. The intermediate water Cd_w records in the Florida Straits and those in the open ocean North Atlantic converge at low values during the Younger Dryas, consistent with what the model shows for a very weak AMOC and diminished nutrient stream but not consistent with a fresh water–induced collapse (fig. S2B).

Impact of weakened Younger Dryas nutrient stream on North Atlantic productivity

Finally, we examine paleoclimate records that have been interpreted as indicators of export productivity. These include records of fluxes of organic components to the sediments as well as microfossil assemblages associated with different productivity regimes. Most of the records that resolve the Younger Dryas climate oscillation show decreased productivity relative to the millennia immediately before and after the event (Fig. 4 and table S1). Although changes in oceanic conditions influencing productivity over the Younger Dryas may have influenced each site differently, the overall reduction of productivity in the region is consistent with the diminished supply of nutrients. This provides observational support of the causal chain inferred from global climate model simulations—that AMOC weakening leads to reduced advective supply of nutrients and declining North Atlantic primary productivity. We also highlight that whereas North Atlantic primary productivity is expected to decline in the case of either a weakening or a collapse in the AMOC, the sign of biogeochemical changes in the intermediate waters of the open ocean North Atlantic will be different. The data for the Younger Dryas are consistent with a weakened rather than a collapsed AMOC. Although most climate models suggest a weakening of the AMOC over the coming century, a collapse has not been ruled out (*27*, *28*), and it is worth noting the nonlinear response of some biogeochemical impacts between these two scenarios.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S4
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Data S1

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