

Nutrient conditions in the subpolar North Atlantic during the last glacial period reconstructed from foraminifera-bound nitrogen isotopes

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[1] Surface nitrate concentration is a potentially useful diagnostic in reconstructing the past circulation of high-latitude North Atlantic waters. Moreover, nutrient consumption in the North Atlantic surface impacts the atmospheric concentration of carbon dioxide. To reconstruct nutrient conditions in the subpolar North Atlantic region during the last ice age, a record of foraminifera-bound $\delta^{15}\text{N}$ was measured in *Neogloboquadrina pachyderma* (sin.) from core V28-73 south of Iceland (57.2°N, 20.9°W). Foraminifera-bound $\delta^{15}\text{N}$ is up to 2‰ lower during the last ice age than during the Holocene, suggesting as much as ~25% less complete nitrate consumption during the former. This is consistent with stronger light limitation associated with a deeper summer surface mixed layer, perhaps related to the formation of Glacial North Atlantic Intermediate Water previously suggested to have occurred near the core site. However, three single-point maxima in $\delta^{15}\text{N}$ in the glacial section and the sharp deglacial $\delta^{15}\text{N}$ rise coincide with Heinrich event layers. This suggests that increased water column stratification during Heinrich events, presumably due to surface freshening, reduced the nutrient supply from below and led to nearly complete nitrate consumption in the summertime mixed layer. The Heinrich layers in V28-73 are not accompanied by $\delta^{18}\text{O}$ minima in either *N. pachyderma* (sin.) or *Globigerinoides bulloides*, which we tentatively attribute to extreme mixed-layer shoaling. The reconstructed subpolar North Atlantic upper water column changes—both glacial/interglacial and millennial—are inverse to those inferred for the Antarctic.

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1. Introduction

[2] Today, the surface waters in most parts of the subpolar North Atlantic are relatively depleted in nitrate (and phosphate) by the end of the spring-to-summer biomass bloom. However, this region has undergone extensive changes since the last ice age. While glacial conditions were variable, the

eastern subpolar North Atlantic region appears to have cooled as much as nearly any other ocean region yet studied [Waelbroeck, 2009], associated with a large southward migration of the Polar Front to a roughly zonal position at 45°N, marked by a thick ice age deposit of ice-rafted detritus (IRD) [Ruddiman and McIntyre, 1977]. In addition, North Atlantic formation of subsurface water differed from the modern formation of North Atlantic Deep Water (NADW). Instead of NADW, a shallower form was produced (glacial North Atlantic Intermediate Water, or GNAIW). GNAIW may have been formed by wintertime convection in the open subpolar North Atlantic [Duplessy et al., 1991; Labeyrie et al., 1992; Oppo and Lehman, 1993] rather than in the Norwegian Sea where a large fraction of NADW currently forms.

[3] An increasing body of data points to the importance of feedbacks between the North Atlantic and the Southern Ocean in controlling high-latitude climate fluctuations and in driving the observed changes in atmospheric CO₂ over glacial cycles [reviewed by Sigman et al., 2007, 2010]. When North Atlantic overturning decreased, it appears that Southern Ocean overturning increased [Broecker, 1998]. In the Southern Ocean, some of the strongest observations for this connection involve ocean biogeochemistry: during

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Heinrich events, when GNAIW formation was interrupted, Southern Ocean export production rose, suggesting increased nutrient supply from below [Anderson et al., 2009].

[4] However, the nature of biogeochemical change in the North Atlantic has been less clear. While bulk geochemical changes are ambiguous regarding export production changes in the North Atlantic [Manighetti and McCave, 1995], benthic foraminiferal data suggest lower productivity during the last ice age relative to the Holocene [Thomas et al., 1995] (Figure 1), as does the accumulation rate of biogenic calcium carbonate [Francois and Bacon, 1994]. The accumulation rates of planktonic and benthic foraminifera and of diatoms as well as species changes in benthic foraminifera suggest that Heinrich events were associated with even lower productivity (Figure 1, inset) [Broecker et al., 1992; Nave et al., 2007; Thomas et al., 1995]. If so, these changes might be attributed either to some form of light limitation or to changes in major nutrient supply from below. These alternatives have completely different implications for upper ocean conditions, the former suggesting a deeper mixed layer and the latter suggesting less exchange between the ocean surface and interior, likely yielding a shallower mixed layer.

[5] While the North Atlantic is the most studied region of the ocean, there is nevertheless much debate regarding how paleoceanographic measurements record conditions there. The $\delta^{18}\text{O}$ of planktonic foraminifera—the most well

developed of our paleoceanographic tools for this purpose—has proven difficult to interpret in some North Atlantic records. Different down-core changes are observed for the two dominant species, *Neogloboquadrina pachyderma* (sinistral) and *Globigerinoides bulloides* (hereafter Nps and Gb) [Hillaire-Marcel and Bilodeau, 2000; Peck et al., 2006]. Moreover, for a given species, different glacial/interglacial and millennial scale changes are observed in different regions of the subpolar North Atlantic. A number of competing explanations exist for these variations [Hillaire-Marcel and de Vernal, 2008; Rashid and Boyle, 2007; 2008]. As will be described below, the balance of the data appear to argue for strengthened vertical density stratification in the northwestern subpolar North Atlantic (and perhaps also the Norwegian Sea) during the last ice age, while there is some evidence for weakened stratification toward the east [de Vernal and Hillaire-Marcel, 2000; de Vernal et al., 2002; Duplessy et al., 1991], for example, off the western coast of the British Isles [Peck et al., 2006]. During Heinrich events, there is evidence for strengthening of stratification along the glacial IRD belt at 42–52°N (Figure 2a) and in the northwestern Atlantic [Bond et al., 1992; Bond and Lotti, 1995], while the conditions north of the IRD belt in the eastern North Atlantic are unclear [Cortijo et al., 1997]. A key goal in the cited studies is to reveal the roles of different regions in forming NADW or

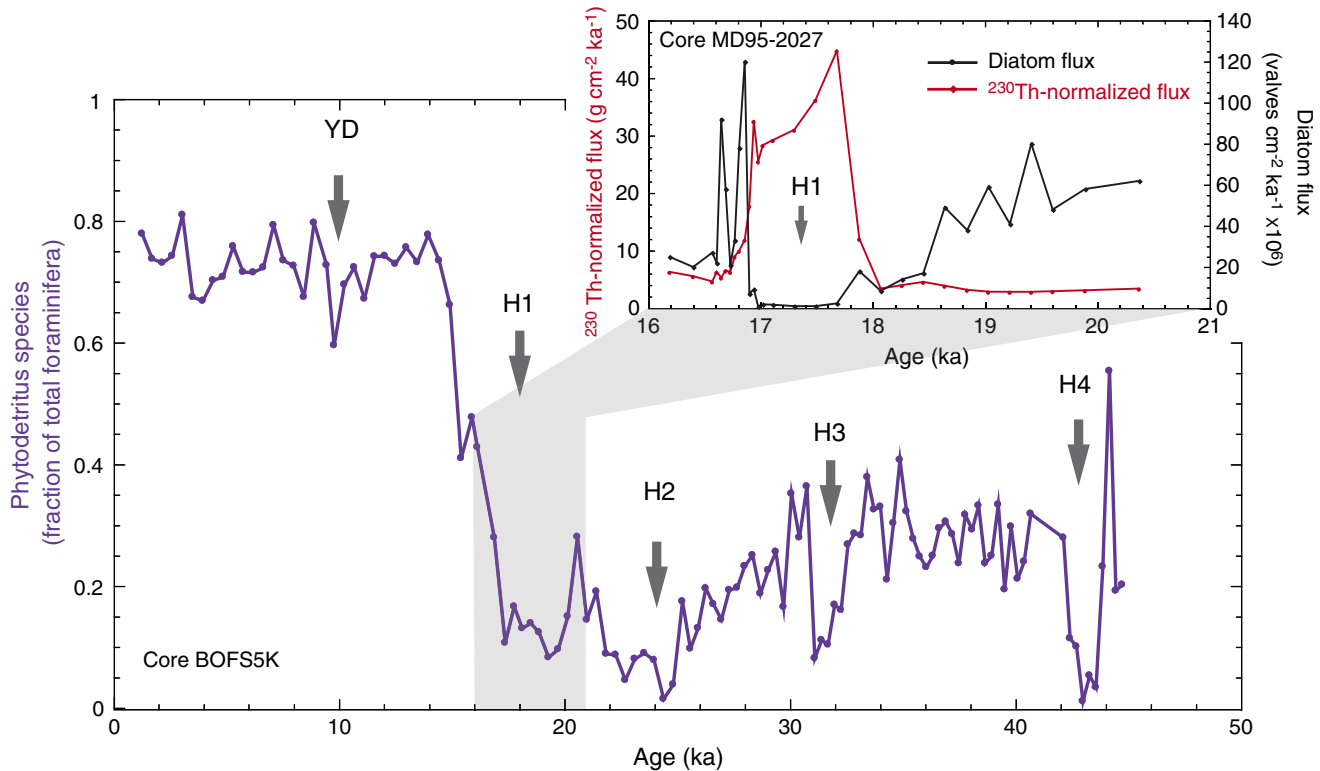


Figure 1. Records of subarctic North Atlantic productivity change since the last ice age. Main panel: abundance of benthic foraminifera species *E. exigua* and *A. weddellensis*, thought to respond strongly to high phytodetritus fluxes, relative to total benthic foraminifera in core BOFS5K [Thomas et al., 1995]. Inset: ^{230}Th -normalized fluxes of total sediment and diatom frustules in core MD95-2027 [Nave et al., 2007] (see Figure 2 for locations). These data reflect the general consensus that subpolar North Atlantic export production was lower during the last ice age than during the Holocene and still lower during Heinrich events (labeled H1 through H4, following Thomas et al. [1995]).

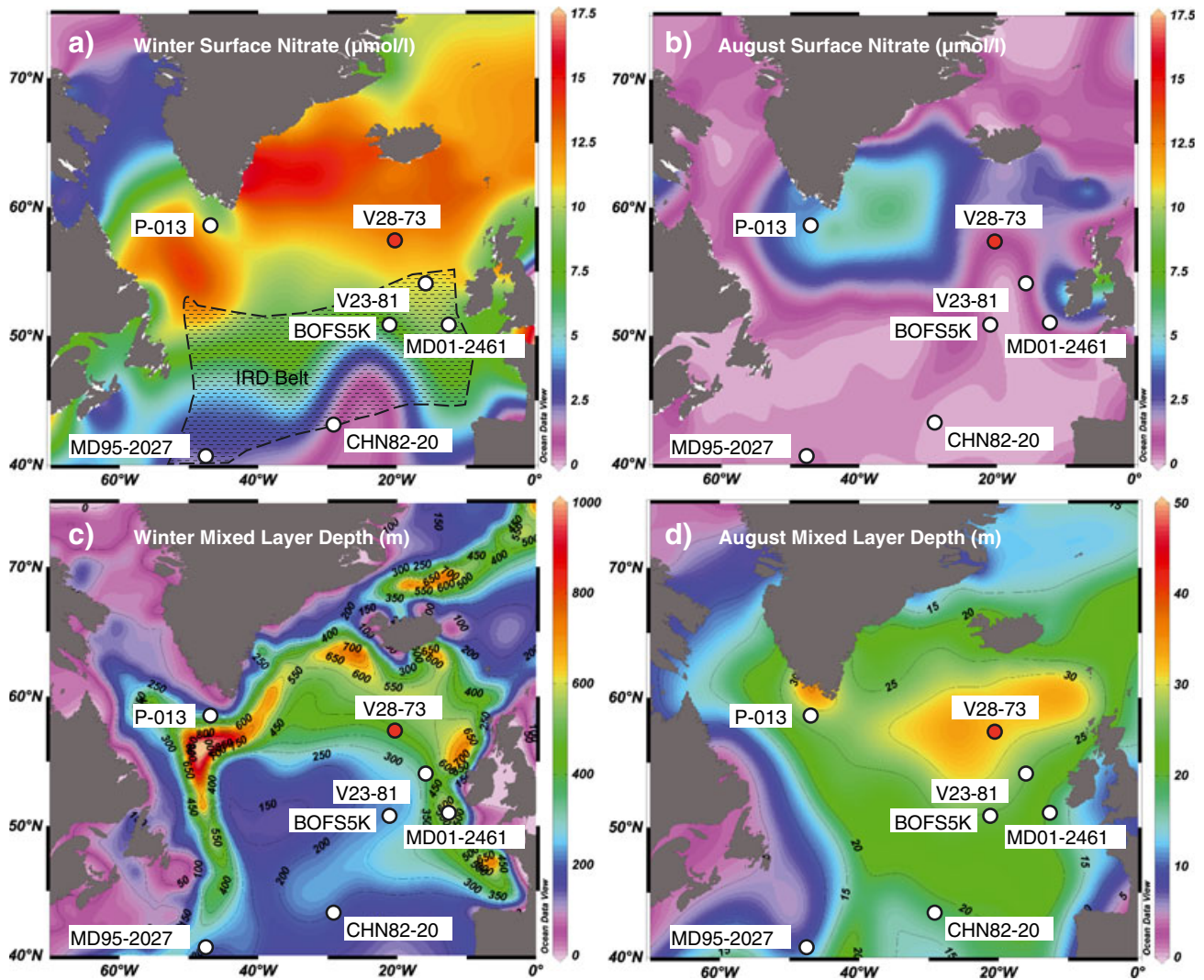


Figure 2. Surface nitrate concentration and mixed-layer depth in the subpolar North Atlantic during the late winter (a, c) and midsummer (b, d) and core locations. Core V28-73 (red circle) was used in this study. Core BOFS5K [Thomas *et al.*, 1995] and core MD95-2027 [Nave *et al.*, 2007] represent core locations of productivity proxies from Figure 1. P-013 [Hillaire-Marcel and Bilodeau, 2000] is representative of the western basin pattern of a larger Nps-Gb $\delta^{18}\text{O}$ difference during the last ice age, suggesting a shallower mixed layer/stronger summer pycnocline in this region [see also de Vernal *et al.*, 2002]. In contrast, MD01-2461 to the southeast is characterized by a decrease in the Nps-Gb $\delta^{18}\text{O}$ difference and is interpreted as an ice age deepening of the mixed layer [Peck *et al.*, 2006]. In core CHN82-20, $\delta^{18}\text{O}$ of different planktonic foraminifera species was taken to indicate mixed-layer deepening during Heinrich events [Rashid and Boyle, 2007]. Core V23-81 shows Nps $\delta^{18}\text{O}$ minima associated with Heinrich events, a well-known pattern suggestive of stratification [Bond and Lotti, 1995] that is nevertheless not apparent in the $\delta^{18}\text{O}$ data from V28-73. Nitrate concentration data and mixed-layer depth estimates are from World Ocean Atlas [Monterey and Levitus, 1997; Garcia *et al.* 2010]. Note the change in depth scale from panel c to d. The location of the ice age “IRD belt” is indicated in panel a [Ruddiman and McIntyre, 1977].

GNAIW and to provide physical mechanisms for changes in the ventilation of the deep ocean by the North Atlantic.

[6] Biogeochemical conditions are a potentially important diagnostic in reconstructing past changes in high-latitude North Atlantic waters. For example, reconstruction of surface nutrients would distinguish whether the apparently reduced export production during the ice age and the Heinrich events during that period were due to stronger light limitation or reduced nutrient supply. This, in turn, would have implications for ocean circulation, in that nutrient supply occurs

by vertical exchange of water between the surface layer and the ocean interior.

[7] Moreover, nutrient consumption in the North Atlantic surface impacts the atmospheric carbon dioxide concentration. Proposed mechanisms for lower atmospheric CO_2 during past glacial periods include reduced overturning and/or reduced ocean/atmosphere gas exchange in the Southern Ocean, which would reduce the leakage of deeply sequestered CO_2 back into the atmosphere from this region [Francois *et al.*, 1997; Stephens and Keeling, 2000]

(reviewed by *Sigman et al.* [2010]). These mechanisms rely on the assumption that the low nutrient concentration observed in the modern North Atlantic surface characterized the ice age North Atlantic as well [*Marinov et al.*, 2008].

[8] Due to isotope fractionation during nitrate assimilation, the $\delta^{15}\text{N}$ of surface ocean nitrate covaries with the degree of nitrate consumption [*Sigman et al.*, 1999], and the $\delta^{15}\text{N}$ of phytoplankton biomass and sinking matter generally tracks this variation [*Altabet and Francois*, 1994; *Altabet et al.*, 1991], albeit with some specific exceptions for sinking N ([*Altabet et al.*, 1991; *Lourey et al.*, 2003] ($\delta^{15}\text{N} = [(^{15}\text{N}/^{14}\text{N}_{\text{sample}})/(^{15}\text{N}/^{14}\text{N}_{\text{reference}})] - 1$), where the reference is atmospheric N_2). The $\delta^{15}\text{N}$ of organic matter bound within the walls of planktonic foraminiferal tests covaries with the $\delta^{15}\text{N}$ of nitrate consumed in the euphotic zone across the global ocean, through grazing and predation of phyto- and zooplankton in the upper ocean [*Ren et al.*, 2009, 2012a]. “Foraminifera-bound” $\delta^{15}\text{N}$ (hereafter FB- $\delta^{15}\text{N}$) measurements have just begun in core top sediments from high-latitude regions. The demonstrated $\delta^{15}\text{N}$ connections between nitrate consumption and surface particles in these regions and between surface particles and FB- $\delta^{15}\text{N}$ in the low-latitude and midlatitude ocean, taken together, argue that down-core records of FB- $\delta^{15}\text{N}$ should capture surface nutrient changes in the high-latitude oceans. The results to date support this covariation of FB- $\delta^{15}\text{N}$ with nitrate consumption, so far most convincingly for Nps (H. Ren, unpublished results). While bulk sedimentary $\delta^{15}\text{N}$ has been used in the same context [*Altabet and Francois*, 1994], this approach is of questionable robustness in environments where the preservation of sedimentary organic matter is low [*Altabet*, 2006] and/or terrigenous inputs are high [*Schubert and Calvert*, 2001]. Indeed, bulk sedimentary N fails to capture signals recorded by FB- $\delta^{15}\text{N}$ in low-latitude North Atlantic and South China Sea records [*Meckler et al.*, 2011; *Ren et al.*, 2009, 2012b]. The Heinrich layers in high-latitude North Atlantic sediments are known to be contaminated with terrigenous N [*Huon et al.*, 2002], and terrestrial organic matter is generally more abundant in the North Atlantic sediments during the last ice age than during the Holocene [*Villanueva et al.*, 1997]. While diatom frustule-bound N represents an alternative to foraminifera-bound N as a protected, upper ocean-derived form of N in deep sea sediments, the low biogenic opal content in the subarctic North Atlantic sediments makes it a less promising analytical target in this region.

[9] In an effort to provide new constraints on surface nutrient consumption in the subpolar North Atlantic during the last ice age, we have measured a down-core record of FB- $\delta^{15}\text{N}$. The record is the first of its kind from a polar/subpolar environment, and it shows changes that are of fundamental significance to our understanding of the subpolar North Atlantic during the last ice age.

2. Materials and Methods

[10] Core V28-73 was raised in 1970 from 57.18°N 20.87°W and 2063 m depth, and it is curated at the Lamont-Doherty Deep-Sea Sample Repository (Figure 2, red circle). Twenty-two samples were collected for foraminifera picking. The upper 1 m was sampled roughly every 10 cm and then at less regular intervals down to 3.45 m, according to the condition of core working half. The core

has previously yielded few significant paleoceanographic results, its sedimentation rate is modest, and its use required us to generate a number of basic ancillary measurements (see below). These shortcomings beg the question of why this core was used, given the relative abundance of higher resolution, well-studied North Atlantic sediment cores. A number of issues were at work. First, V28-73 is in the subarctic North Atlantic region that has significant wintertime mixing today (Figure 2a and c), increasing the potential for major changes in surface nutrient concentration in the past relative to, for example, sites in the ice age IRD belt [Figure 2a, *Ruddiman and McIntyre*, 1977]. Second, V28-73 is in the region suspected to be involved in GNAIW formation [*Oppo and Lehman*, 1993]. Third, we sought to avoid the region of high summertime surface nitrate off the southern tip of Greenland (Figure 2c), the origin and significance of which is not clear. Future work will focus on higher-quality sediment cores with higher accumulation rates. Nevertheless, it should be noted that FB- $\delta^{15}\text{N}$ analysis is well suited to cores that are no longer useful for sedimentary geochemical studies, as foraminifera-bound N is unaffected by storage.

2.1. Foraminifera-Bound N Isotope Analysis

[11] The sediment samples were sieved for the size fraction $>63\ \mu\text{m}$. From this coarse fraction, planktonic foraminifera species Nps were picked under a binocular microscope. Nps was the most abundant species, with Gb uniformly present but not as abundant. Three to seven milligrams of foraminifera (i.e., 800–1000 specimens) per sample were used to carry out the analyses.

[12] Samples were cleaned and analyzed for FB- $\delta^{15}\text{N}$ and N content following the protocol of *Ren et al.* [2009]. The cleaned samples were dried overnight at 60°C. Three to seven milligrams of cleaned sample were weighed into a previously combusted vial and dissolved in 4 N HCl (40–60 μL per sample). Basic potassium persulfate oxidizing solution (see below) was then added to each vial and to vials containing organic standards and procedural blanks. The persulfate oxidizing solution for organic N conversion to nitrate was made up at the time of processing; 1 g ACS-grade sodium hydroxide and 1 g potassium persulfate were dissolved in 100 mL deionized water (DW). For the samples measured here, we used 1 mL of persulfate reagent for the blanks, oxidation standards, and foraminifera samples. The vials were autoclaved for 1 hour (1.5 hours including warm-up and cool-down time) on a slow vent setting. For nearly all samples, replicates were partitioned after the cleaning step. Two replicates of each sample were oxidized and analyzed several weeks apart.

[13] With each set of replicates, oxidation standards of known nitrogen concentration and isotopic composition were run to correct for the nitrogen blank of the persulfate reagent and sample processing. The organic standards used here were USGS 40 and USGS 41, as well as two in-house standards composed of a solution mixture of 6-aminocaproic acid and glycine, with a $\delta^{15}\text{N}$ of 3.4‰ and 5.4‰ (determined by analysis of the concentrated standard solutions with EA-IRMS). The standard sizes were chosen to match to the expected N content of the foraminifera samples. A minimum of 10 organic standards and three to five blanks were analyzed per batch of samples, allowing for a

correction for the persulfate blank. The Nps samples had N contents of 3–5 $\mu\text{mol N}$ per gram sample, typically yielding nitrate concentrations in the oxidation solutions of 10–20 μM , whereas the blank ranged between 0.3 and 0.7 μM . Average $\delta^{15}\text{N}$ for each sample depth is shown; error bars indicate the estimated standard deviation from oxidation replicates (Figure 3).

[14] Bulk sediment $\delta^{15}\text{N}$ was measured every ~ 10 cm. The total N content of the sediment was liberated and analyzed as N_2 using a Thermo Fisher elemental analyzer Series 1112 coupled to a Thermo Delta V Plus mass spectrometer (Thermo Fisher Scientific, Waltham MA) at ETH Zurich. Between 40 and 60 mg sediment was analyzed. Standards of atropine and peptone were measured in the same run. Standard deviations for both standards were $< 0.2\%$. These data are compared with the FB- $\delta^{15}\text{N}$ results in Auxillary Figure A1.

2.2. Foraminiferal and Bulk Sediment Carbonate Oxygen Isotope Analysis

[15] Oxygen isotopes of the planktonic foraminifera species Nps and Gb were measured at ETH Zurich. Between 30 to 40 individual foraminifera species were cleaned using the following approach: 1000 μL DW was added to each sample which then was ultrasonicated for 3–5 s. After

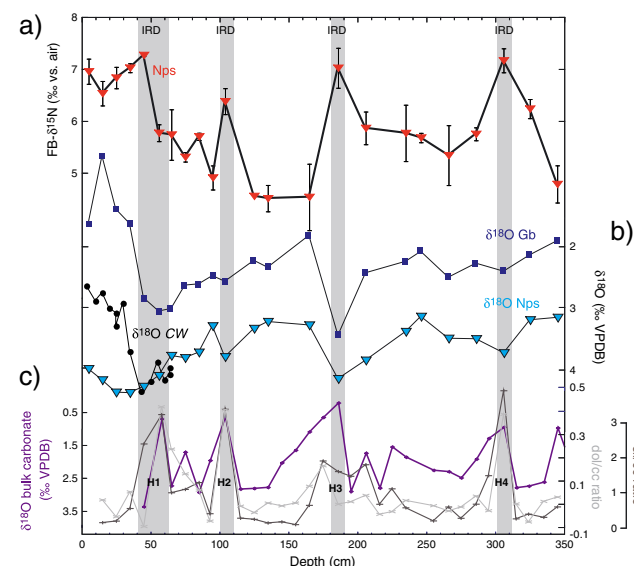


Figure 3. Down-core data from this study. (a) FB- $\delta^{15}\text{N}$ of *N. pachyderma s.*; (b) calcite $\delta^{18}\text{O}$ of *G. bulloides*, *N. pachyderma s.*, and *C. wuellerstorfi*; and (c) ratios of detrital dolomite (dol) and silicate (sil) to calcite (cc) based on FTIR spectra as well as bulk carbonate $\delta^{18}\text{O}$, an additional measure of the dolomite-to-calcite ratio. Gray bars identify the IRD rich intervals, based on visual analysis of the sieved coarse fractions ($> 63 \mu\text{m}$). Heinrich event layers typically include detrital carbonate with some dolomite, so the dol/cc and bulk carbonate $\delta^{18}\text{O}$ minima indicate that an IRD layer is associated with a Heinrich event, although dolomite does not typically pervade each Heinrich IRD layer, often occurring toward the top [Bond et al., 1992] (as in H3 here). Peaks in FB- $\delta^{15}\text{N}$ and weak maxima in the $\delta^{18}\text{O}$ of both planktonic foraminifera species coincide with the Heinrich event IRD layers. The $\delta^{18}\text{O}$ data of *C. wuellerstorfi* are from Oppo and Lehman [1993].

removing the liquid using a syringe, 200 μL methanol was added and the sample ultrasonicated again for 3–5 s; the liquid was then removed. The sample was rinsed with DW two to three times and dried in an oven at 60°C overnight.

[16] $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ for foraminifera and bulk sediment analysis were performed with a Thermo GasBench II coupled to a Thermo Delta V Plus mass spectrometer, following the protocol of Breitenbach and Bernasconi [2011]. The cleaned foraminifera samples were crushed and 35–80 μg weighed into 4.5 mL vials; for the bulk sediment, 80–130 μg were weighed in. The average of the standard deviation of single $\delta^{18}\text{O}$ measurements of Np and Gb is $\sim 0.04 \%$. Benthic foraminiferal $\delta^{18}\text{O}$ was measured previously on the species *Cibicides wuellerstorfi* down to 64 cm by Oppo and Lehman [1993].

2.3. Fourier Transform Infrared Spectrophotometry

[17] Fourier transform infrared (FTIR) spectrophotometry was used as a rapid approach for measuring down-core changes in detrital silicates and dolomite, to identify maxima in ice rafted detritus and Heinrich layers in particular [Ji et al., 2009]. The analyses were conducted in the lab of Prof. Satish Myneni at Princeton University, using a Bruker IFS 66 v/s FTIR spectrometer, in attenuated total reflectance (ATR) mode. Roughly 1 cc of sample was homogenized using a mortar and pestle, and 1 mm^2 of the powder was applied to the ATR crystal. Air was used as the background spectra. Samples were held against a single reflection diamond crystal ATR accessory. The signal was collected by a liquid nitrogen cooled mercury cadmium-telluride detector. Peak fitting was performed by GRAMS/AI (Thermo Electron software, Thermo Fisher Scientific, Waltham MA). The spectra from each sample were interpreted for ratios of dolomite/calcite and silicate/dolomite to identify samples with high IRD and high dolomite fractions.

3. Results

3.1. Foraminiferal Oxygen Isotopes and Ice Rafted Detritus

[18] Based on the $\delta^{18}\text{O}$ of Gb and the benthic species *C. wuellerstorfi* [Oppo and Lehman, 1993], we identify the last ice age at 45 cm and deeper (Figure 3). Remarkably, the $\delta^{18}\text{O}$ of Nps shows no decrease into the Holocene, suggesting that other effects on Nps $\delta^{18}\text{O}$ offset the effect of the deglacial decline in global ocean $\delta^{18}\text{O}$ (see discussion below).

[19] Of the sampled sediments, four IRD peaks were recognized qualitatively from the sieved coarse fractions (vertical gray bars in Figure 3). At or near each visually identified IRD maximum, the FTIR data indicate a peak in silicate-to-calcite ratio. Moreover, these depths also correspond to FTIR-identified peaks in dolomite-to-calcite ratio and local minima in bulk carbonate $\delta^{18}\text{O}$, as expected for Heinrich layers [Hodell and Curtis, 2008; Ji et al., 2009]. Thus, we hereafter attribute these IRD-rich layers to Heinrich events (see H1 to H4 identifications in Figure 3). In the region of V28-73 (Figure 2), the appearance of Heinrich layers with detrital carbonate is not universal, and the layers are much less robust than to the south and the west [Bond et al., 1992]. This explains the very weak nature of the Heinrich-related dolomite-to-calcite maxima and bulk carbonate $\delta^{18}\text{O}$ minima in this core relative to cores from further south [Hodell and Curtis, 2008]. It also emphasizes

the potential power of $\text{FB-}\delta^{15}\text{N}$ to study these events: despite the weak sedimentological signature of the Heinrich events at this site, $\text{FB-}\delta^{15}\text{N}$ clearly responds to them (see below).

[20] Each of the IRD-rich layers coincides with a weak ($<0.5\%$) local maximum in the $\delta^{18}\text{O}$ of both Gb and Nps. Heinrich events as sampled in the glacial IRD belt at $42\text{--}52^\circ\text{N}$ [Grousset *et al.*, 1993; Ruddiman and McIntyre, 1977] and in the western North Atlantic are typically characterized by Nps $\delta^{18}\text{O}$ minima [Bond *et al.*, 1992; Bond and Lotti, 1995], the opposite sense of $\delta^{18}\text{O}$ change that we observe associated with our IRD peaks (Figure 2, core V23-81). However, various behaviors in Nps $\delta^{18}\text{O}$ have been observed in the eastern subpolar North Atlantic [Peck *et al.*, 2006]. In this region, Cortijo *et al.* [1997] identified a meridional gradient in the Nps $\delta^{18}\text{O}$ response to Heinrich event 4, with a Nps $\delta^{18}\text{O}$ decrease occurring in the IRD belt but a slight $\delta^{18}\text{O}$ increase in region of V28-73 to the North of the IRD belt, with which our data are consistent.

3.2. Foraminifera-Bound Nitrogen Isotopes

[21] Foraminifera-bound $\delta^{15}\text{N}$ is generally lower during the last glacial period (>45 cm depth) than during the Holocene (≤ 45 cm depth) (Figure 3a). The lowest $\delta^{15}\text{N}$ is observed between 125 and 175 cm, with $\delta^{15}\text{N}$ apparently slightly higher in the interval from 200 to 300 cm.

[22] Against this background of lower $\text{FB-}\delta^{15}\text{N}$ during the last ice age, three single-point maxima in $\text{FB-}\delta^{15}\text{N}$ are observed within the glacial section at 104, 186, and 306 cm, reaching similar to interglacial values. These depths coincide with the Heinrich layers as identified above. The apparent H1 IRD layer is also associated with a sharp $\text{FB-}\delta^{15}\text{N}$ increase, although not in its deeper half (which is rich in volcanic grains as well), and $\text{FB-}\delta^{15}\text{N}$ then remains high through the deglaciation and Holocene.

[23] Tentatively assigning Heinrich events to the observed IRD maxima, the IRD maximum at 45 cm is taken as H1 (~ 17 ka) (given its occurrence at the end of glacial interval), 110 cm is taken as H2 (~ 24 ka), 185 cm as H3 (~ 31 ka), and 310 cm as H4 (~ 38 ka) [Hemming, 2004]. With these assignments (or also if one Heinrich event has been missed), the $\text{FB-}\delta^{15}\text{N}$ decrease from 200 to 300 cm to the minimum between 125 and 175 cm coincides with the global climate cooling from marine isotope stage (MIS) 3 to MIS 2 (the Last Glacial Maximum, LGM). On the orbital time scale, this suggests a consistent correlation between climate and $\text{FB-}\delta^{15}\text{N}$ (and thus nitrate consumption) at V28-73. That is, just as MIS 3 is an intermediate climate state, so too is its $\delta^{15}\text{N}$ intermediate between MIS 1 (Holocene) and MIS 2 (LGM) values.

[24] Bulk sediment $\delta^{15}\text{N}$ appears to capture partially the higher $\delta^{15}\text{N}$ of Heinrich events, albeit as a weaker signal (Auxiliary Figure A1). However, there is no agreement with regard to the LGM/Holocene $\delta^{15}\text{N}$ difference, with bulk sediment $\delta^{15}\text{N}$ arguing for no clear change but a mid-Holocene decrease. Given the work documenting the importance of terrestrial organic matter in glacial North Atlantic sediments [Villanueva *et al.*, 1997], especially during Heinrich events [Huon *et al.*, 2002], we interpret the disagreements as deriving from the effect of allochthonous N on bulk sediment $\delta^{15}\text{N}$, and the bulk sediment $\delta^{15}\text{N}$ data are not discussed further.

4. Interpretation and Discussion

4.1. The Last Ice Age

[25] Today, productivity and nutrient conditions in the subpolar eastern North Atlantic are highly seasonal, dominated by the “North Atlantic Bloom,” which typically begins in April to May [Siegel *et al.*, 2002]. In subpolar and polar regions, the high-latitude North Atlantic included, the $\delta^{15}\text{N}$ of suspended and sinking particulate N (PN) is initially low as the seasonal bloom begins, due to preferential consumption of ^{14}N -nitrate [Altabet *et al.*, 1991]. As the residual nitrate pool increases in $\delta^{15}\text{N}$, so does the PN generated from it. In this and other polar regions, the spring-to-summer integrated, flux-weighted $\delta^{15}\text{N}$ of the sinking PN is similar to that of the nitrate that has been extracted from surface waters during this period [Altabet and Francois, 2001; Altabet *et al.*, 1991; Lourey *et al.*, 2003]. For our site, where summertime nitrate consumption is nearly complete today (Figure 2, see below), the sinking $\delta^{15}\text{N}$ should converge on the $\delta^{15}\text{N}$ of the wintertime nitrate supply.

[26] The N isotope dynamics associated with nitrate consumption are propagated to foraminifera by their feeding on phytoplankton, zooplankton, and/or detritus deriving from euphotic zone production. The measurements to date of net tow, sediment trap, and surface sediment foraminifera suggest that the $\text{FB-}\delta^{15}\text{N}$ of low latitude, spinose, symbiont bearing, euphotic zone dwelling species (*G. ruber*, *G. sacculifer*, *O. universa*) is similar to the $\delta^{15}\text{N}$ of nitrate consumed in the surface layer. In contrast, nonspinose, nonsymbiotic forms (the category into which Nps falls) tend to have a $\delta^{15}\text{N}$ $\sim 2\text{--}3\%$ higher than the nitrate supply to the surface [Ren *et al.*, 2012a]. Consistent with this expectation, Nps $\text{FB-}\delta^{15}\text{N}$ is found to be similar to the $\delta^{15}\text{N}$ of diatom frustule-bound organic N in the subarctic North Pacific, both of which appear to be elevated by $\sim 2\%$ relative to the expected sinking flux (H. Ren, in preparation). The tendency for $\text{FB-}\delta^{15}\text{N}$ to be similar to that of the nitrate supply likely derives from the feeding of foraminifera on zooplankton and large phytoplankton, the $\delta^{15}\text{N}$ of which is higher than bulk suspended PN but similar to the nitrate supply [Ren *et al.*, 2012a]. The $\delta^{15}\text{N}$ elevation of nonspinose forms (relative to spinose forms) may arise from their consumption of some deeper suspended particles and/or their lack of symbionts, the latter leading to full expression of the trophic ^{15}N enrichment [Ren *et al.*, 2012a; Uhle *et al.*, 1997].

[27] Globally, and especially in subpolar waters, the seasonal variation in planktonic foraminiferal production and flux is highly correlated with surface ocean productivity [Eguchi *et al.*, 2003; Thunell and Reynolds, 1984; Thunell and Honjo, 1987]. Temperature obviously plays a major role in global species patterns, and it also contributes to seasonal changes in species assemblage, especially in mid-latitude to low-latitude regions [Zaric *et al.*, 2005]. However, in polar and subpolar regions, species diversity is low, and the dominant dynamic is of Nps producing the greatest quantity of shells during the spring-to-summer bloom [Sautter and Thunell, 1989]. Since the foraminifera production peak roughly coincides with this bloom and the associated increase in sinking material, it is reasonable to expect that $\text{FB-}\delta^{15}\text{N}$ will track the seasonal nitrate drawdown in roughly the same way as it is recorded in the $\delta^{15}\text{N}$ of surface nitrate, suspended PN, and sinking N. In this context, the observations

from lower-latitude sites of a strong correlation between $\text{FB-}\delta^{15}\text{N}$ and the $\delta^{15}\text{N}$ of nitrate supply to the euphotic zone [Ren *et al.*, 2012a] represent the end-member case of complete nitrate consumption. In some data from the subarctic North Atlantic, there is the suggestion of a midsummer decrease in Nps flux, leading to the identification of a secondary flux peak in the late summer [Jonkers *et al.*, 2010]. While the N isotope dynamics associated with this secondary peak requires further study, a similar link between nitrate consumption and the N isotopes should apply.

[28] Over the course of the North Atlantic spring bloom, nitrate concentration is drawn down from $>10\ \mu\text{M}$ ($\sim 15\ \mu\text{M}$ at the site of V28-73) to levels of typically $1\ \mu\text{M}$ or lower by July/August (Figure 2a and b). Based on these values, by the end of the spring/summer bloom, nitrate consumption is $\geq 90\%$ at our site, such that the $\delta^{15}\text{N}$ of the organic N produced over the course of the spring and summer should be within $\sim 1\%$ of the wintertime nitrate supply. It is thus expected that the relationship between the nitrate supply and $\text{FB-}\delta^{15}\text{N}$ at this site in the North Atlantic would approximate the relationship observed in lower-latitude sites characterized by complete nitrate consumption. Indeed, the $\text{FB-}\delta^{15}\text{N}$ of Holocene Nps, $6.6\text{--}7.0\%$ (Figure 3), is $\sim 2\%$ higher than the $\delta^{15}\text{N}$ of $4.5\text{--}5.0\%$ in NADW [Sigman *et al.*, 2000; Sigman *et al.*, 2009] and shallow subsurface nitrate measured in the high-latitude North Atlantic (D.M. Sigman, unpublished results). This $\text{FB-}\delta^{15}\text{N}$ is consistent with expectations, given the previous observation from lower-latitude sites of a $\sim 2\text{--}3\%$ elevation of $\text{FB-}\delta^{15}\text{N}$ in nonsymbiotic foraminifera relative to the nitrate consumed in the euphotic zone.

[29] The generally lower $\text{FB-}\delta^{15}\text{N}$ of the last glacial period relative to the Holocene suggests that the $\delta^{15}\text{N}$ of organic N produced in the euphotic zone (and fed upon by Nps) was lower during the last ice age. If anything, tropical North

Atlantic $\text{FB-}\delta^{15}\text{N}$ records might allow for higher—not lower— $\delta^{15}\text{N}$ for deep and intermediate-depth nitrate in the North Atlantic during the last ice age, and N fixation changes in the North Atlantic are also of the opposite sign required to explain the glacial/interglacial $\delta^{15}\text{N}$ change at V28-73 via changes in thermocline nitrate $\delta^{15}\text{N}$ [Meckler *et al.*, 2011; Ren *et al.*, 2009].

[30] In general, it might seem possible for a given foraminifera species to shift its season of maximum growth, leading the shells to record the N isotopic composition of a different time of year and thus introduce a bias into the reconstruction of surface nitrate consumption. However, as described above, foraminifera production, especially for Nps, is observed to be tightly tied to the spring to summer bloom in polar and subpolar waters. Furthermore, if the timing of Nps production in the subpolar North Atlantic was different during the last ice age than during the Holocene, it would have involved a shift to closer to peak summer [Fraile *et al.*, 2009]. For a constant timing of the spring to summer bloom, this would tend to bias $\text{FB-}\delta^{15}\text{N}$ to be higher during the LGM than during the Holocene, in the opposite sense of the observations.

[31] Thus, short of unknown dynamics, the sole explanation for the lower $\text{FB-}\delta^{15}\text{N}$ during the last ice age is that summertime nitrate consumption was less complete (summertime surface nitrate concentration was higher), leading to a lower $\delta^{15}\text{N}$ for the nitrate assimilated into upper ocean organic N and thus a lower $\delta^{15}\text{N}$ in the surface PN pools (Figure 4). The amplitude of $\text{FB-}\delta^{15}\text{N}$ change provides some guidance as to the quantitative changes in surface nitrate, although with uncertainties exacerbated by the lack of specific ground-truthing data from the North Atlantic. If the isotope effect for nitrate assimilation is taken to be 8% in this region [Altabet *et al.*, 1991], the $\sim 2\%$ decrease in $\text{FB-}\delta^{15}\text{N}$ would

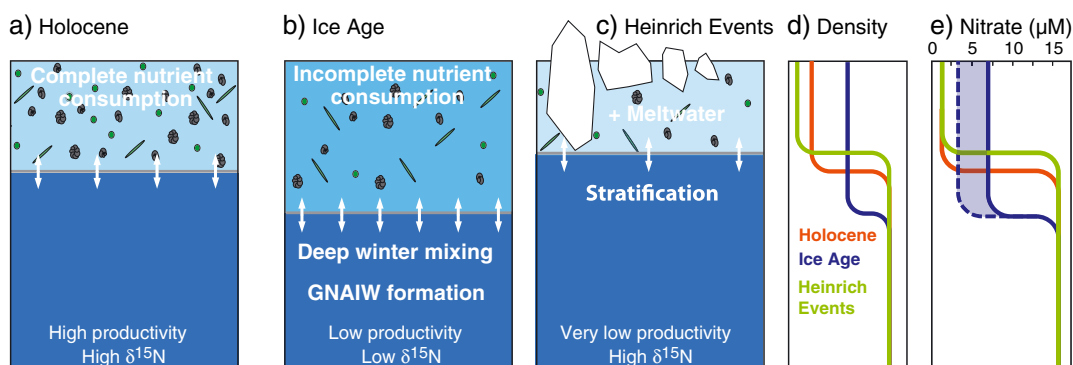


Figure 4. Interpretation of conditions at the North Atlantic site of V28-73 during the Holocene (a), LGM (b), and Heinrich events (c), with schematic depth profiles of proposed changes in mixed-layer depth, surface density, and nitrate concentration (d, e). The Holocene (a) is characterized by wintertime nitrate supply followed by a shallow summer mixed layer, leading to high productivity and nearly complete nitrate consumption. The LGM (b) is interpreted as having a deeper summertime mixed layer, with light limitation leading to lower productivity and less complete nitrate consumption (lower $\delta^{15}\text{N}$). The deeper mixed layer of the LGM may have been related to GNAIW formation in this region. The two alternatives for LGM surface nitrate concentration relate to different choices for the isotope effect of nitrate assimilation (8% for dashed line, 5% for the solid line; see text). During Heinrich events (c), an apparent further decline in productivity from background glacial conditions coupled with more complete nitrate consumption (higher $\delta^{15}\text{N}$) suggest a strong reduction in nitrate supply. This is consistent with previous suggestions of stronger stratification due to iceberg-associated meltwater and an extreme shoaling of the mixed layer. One uncertainty in panel e is the nitrate concentration of the deep waters through time.

yield LGM nitrate consumption 20% less than in the Holocene. If the isotope effect were instead assumed to be 5%, a rough lower bound for field estimates [DiFiore *et al.*, 2010], the FB- $\delta^{15}\text{N}$ decrease would translate to 35% less consumption during the LGM. In either case, the reconstructed decrease in the degree of nitrate consumption is modest. If the minimum summertime nitrate concentration at our site is taken to be $\sim 1\ \mu\text{M}$ during the Holocene, assuming a constant wintertime nitrate concentration of $15\ \mu\text{M}$, the summertime concentration would have been $< 7\ \mu\text{M}$ during the LGM (Figure 4). This is similar to what can be found in midsummer today at the regional nitrate concentration maximum $\sim 15^\circ$ west of V28-73 (Figure 2b). Thus, the changes suggested by the FB- $\delta^{15}\text{N}$ data do not appear to require LGM nutrient conditions radically different from those of the modern North Atlantic. Furthermore, even if the reconstructed nutrient concentration change applied directly to the preformed nutrient content of NADW/GNAIW, the change would not be adequately large to substantially alter the role of the North Atlantic as a region where water with low preformed nutrients enters the ocean interior because the Antarctic end-member has a much higher preformed nitrate concentration, $> 32\ \mu\text{M}$ [Toggweiler *et al.*, 2003].

[32] Nevertheless, we are left with the important mechanistic question of why nitrate consumption would be less complete during the last ice age. As described above, the preponderance of data argues for reduced ice age productivity in this region (Figure 1) [Francois and Bacon, 1994; Manighetti and McCave, 1995; Thomas *et al.*, 1995; van Weering and de Rijk, 1991], and this has been associated with the classic observation of a shift in the polar front from a position well to the north of our site today to an ice age position well south of V28-73 [McIntyre *et al.*, 1976]. The existing temperature reconstructions do not suggest that spring and summer sea ice cover would have been adequate to reduce ice age productivity near our site [de Vernal and Hillaire-Marcel, 2000; Sarnthein *et al.*, 2003]. Neither does stronger iron limitation seem plausible for the ice age North Atlantic conditions [Fuhrer *et al.*, 1999]. Thus, the coupled decreases in productivity and nutrient consumption would seem to call for a hydrographically driven reduction in light availability, that is, a deeper spring-to-summer wind-mixed layer [Siegel *et al.*, 2002] (Figure 4).

[33] It is unclear whether our interpretation of a deeper LGM summer mixed layer fits with other observations from the region. A changing $\delta^{18}\text{O}$ difference between Gb and Nps in the North Atlantic has been interpreted as an index of upper ocean stratification over glacial cycles, based on evidence that Nps records submixed layer conditions in the modern North Atlantic while Gb at least partially records summer mixed layer conditions [de Vernal *et al.*, 2002; Jonkers *et al.*, 2010; Peck *et al.*, 2006]. As in our study, in a nearby core to the southeast, Peck *et al.* [2006] observe a reduced Gb-Nps $\delta^{18}\text{O}$ difference during the last ice age, which they interpret as indicating weaker upper ocean stratification (Figure 2, core MD01-2461). We argue that this change might be better described in terms of mixed-layer depth. While Gb shows the expected $\delta^{18}\text{O}$ rise during the ice age (due to whole ocean $\delta^{18}\text{O}$ change), Nps does not. This implies that Nps $\delta^{18}\text{O}$ is declining relative to regional waters. This is consistent with a mixed-layer deepening that would have moved the base of mixed layer below the common

depth of Nps during the LGM, such that both Gb and Nps recorded mixed-layer $\delta^{18}\text{O}$. As a deeper mixed layer is typically associated with weaker upper ocean stratification in polar regions, this view is consistent with that of Peck *et al.* [2006].

[34] In contrast, in the northwestern North Atlantic south of the Labrador Sea, Hillaire-Marcel and Bilodeau [2000] observe a greater difference $\delta^{18}\text{O}$ difference between Gb and Nps during the last ice age (Figure 2, core P-013). The same logic as Peck *et al.* [2006] leads Hillaire-Marcel and Bilodeau [2000] to propose generally stronger stratification in that region during the last ice age. While these findings would seem contradictory, de Vernal *et al.* [2002] deduce from dinoflagellate cyst species a stronger spatial variation in upper ocean stratification during the last ice age, with a strengthening of the halocline in the western subpolar North Atlantic but a weakening of the halocline toward the east. The FB- $\delta^{15}\text{N}$ data would seem to agree with the interpretation of a deeper mixed layer in the eastern than western North Atlantic, suggesting in addition that the LGM summer mixed layer in the east was deeper than during the Holocene.

[35] Physical arguments can be made either way as to whether summer mixed layer should have been deeper in the LGM subpolar North Atlantic. A southward migration of the winds may have left the subpolar North Atlantic far north of the path of the westerly winds. Such a shift would have tended to reduce local wind-driven upwelling. It might have also exported less freshwater from the region due to Ekman transport, potentially allowing salinity-driven stratification to strengthen (an analogous scenario has been described for the glacial Antarctic [de Boer *et al.*, 2008; Toggweiler *et al.*, 2006]). However, countering these effects, a decrease in Ekman transport might have reduced the import of low-salinity, coastal water into the region. More importantly, integrated westerly wind strength over the North Atlantic may have intensified [Brauer *et al.*, 2008], which would have added turbulence to the upper water column and thus deepened the mixed layer (Figure 4).

[36] The ice age deepening of the summer mixed layer inferred from the $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ data may be related to the shift from NADW to GNAIW during ice ages and the associated southward shift in the locus of wintertime convection to the region of our core site [Oppo and Lehman, 1993]. Using planktonic foraminiferal $\delta^{18}\text{O}$, Duplessy *et al.* [1991] and Labeyrie *et al.* [1992] argue for lower salinity during the LGM in the subpolar and polar North Atlantic except for an incursion of higher salinity into the region at $\sim 50\text{--}54^\circ\text{N}$ and $\sim 30^\circ\text{W}$, and they suggest that this region hosted GNAIW formation. These results are roughly supported by the dinoflagellate reconstruction of de Vernal *et al.* [2002], although there is a mismatch in the exact regions that the two studies identify as having greatest surface density. This mismatch aside, the reconstructed high surface density region in the eastern subpolar North Atlantic might be interpreted as resulting from the influx of Gulf Stream-derived warm and salty water, which was then quickly cooled under the subpolar atmosphere. Our site is at the outer margin of the salty (high-density) region reconstructed by Duplessy *et al.* [1991]; given the sites sampled by de Vernal *et al.* [2002], which are just to the southwest of V28-73, our results might be related to their reconstructed region of higher surface density.

[37] The combined paleoproductivity and N isotope data contrast with data from the Antarctic and Subarctic North Pacific, where productivity was also reduced during the LGM but nutrient consumption was apparently more complete [Brunelle *et al.*, 2007; Francois *et al.*, 1997; Jaccard *et al.*, 2005; Robinson and Sigman, 2008]. These changes have been argued to indicate reduced nutrient supply from below, providing the central evidence for reduced surface/subsurface communication in the polar regions during ice ages, “polar stratification” [Sigman *et al.*, 2010]. In this scenario for the Antarctic and North Pacific, the shift to higher nutrient consumption might have derived either from iron inputs from above and/or a shoaling of the spring/summer mixed layer. In this context, the apparently opposite response of subpolar North Atlantic nutrient consumption to LGM conditions begs for an explanation.

[38] In ocean model experiments, convection and deep water formation tend to show anticorrelation between the North Atlantic and Southern Ocean [Kuhlbrodt *et al.*, 2007]. de Boer *et al.* [2008] argue that, for a global ocean state in which salinity is proportionally more important for deep convection, convection will be higher in North Atlantic but lower in the Antarctic and North Pacific; furthermore, they argue that the last ice age represents such a state. In ocean model experiments, this inverse behavior between the North Atlantic and Southern Ocean is typically part of a global compensation for regional changes in deep water formation. The compensation arises because, with a decrease in deep water formation in one region, the ocean interior gains buoyancy until convection in another polar region becomes favorable [Broecker, 1998; de Boer *et al.*, 2007, 2008]. From this perspective, our findings of a deeper summer mixed layer in the ice age subpolar North Atlantic, to the degree that it is associated with winter mixed-layer deepening and GNAIW formation, might not simply be driven by local forcing but might rather be a part of a global ocean teleconnection that leads to inverse behavior in the North Atlantic and Antarctic, that is, the “bipolar seesaw” [Broecker, 1998].

4.2. Heinrich Events

[39] In the Heinrich layers, FB- $\delta^{15}\text{N}$ is similar to that of the Holocene and thus suggests comparably complete nitrate consumption as observed today. Data on biogenic material and assemblages of planktonic and benthic foraminifera suggest that North Atlantic productivity was notably reduced, even relative to LGM productivity, which was in turn apparently lower than Holocene productivity (Figure 1) [Bond *et al.*, 1992; Broecker *et al.*, 1992; Nave *et al.*, 2007; Thomas *et al.*, 1995]. Combining this constraint with the FB- $\delta^{15}\text{N}$ data suggests that increased stratification in the high-latitude North Atlantic during Heinrich events sharply reduced the flux of deep nutrients to the euphotic zone. This enhanced perennial stratification, with a shallower winter mixed layer, would also have yielded a shallower summer mixed layer (Figure 4). Given the evidence for reduced productivity, these periods cannot be described as conducive to phytoplankton growth; nevertheless, the environmental conditions apparently allowed phytoplankton to completely consume the weak nutrient supply.

[40] It would seem straightforward to argue for stronger surface layer freshening during Heinrich events as the cause for the increased upper ocean stratification that the

paleoproductivity and FB- $\delta^{15}\text{N}$ data together suggest. Indeed, the existence of Nps $\delta^{18}\text{O}$ minima during Heinrich events suggests the melting of iceberg derived freshwater [Bond *et al.*, 1993; Bond *et al.*, 1992]. However, at V28-73, we observe no such $\delta^{18}\text{O}$ minima in either Nps or Gb but rather a slight rise in $\delta^{18}\text{O}$ (Figure 3b), and this is consistent with much more exhaustive studies of Nps $\delta^{18}\text{O}$ in the region [Cortijo *et al.*, 1997], which suggest that the Heinrich $\delta^{18}\text{O}$ decrease is largely a feature of sediment cores further south, which are centered over the ice age IRD belt [Ruddiman, 1977] (Figure 2). Sea ice melt provides a possible mechanism for freshening the upper ocean without lowering $\delta^{18}\text{O}$ (in fact, it can cause complex signals [Hillaire-Marcel and de Vernal, 2008]), while cooling could also work against the effect of water $\delta^{18}\text{O}$ decline in determining the $\delta^{18}\text{O}$ of foraminifera. Thus, the $\delta^{18}\text{O}$ data do not seem to rule out freshening-driven water column stratification. Nevertheless, they do not provide any support for this interpretation. Adding further nuance to these considerations, Peck *et al.* [2006] observe declines in $\delta^{18}\text{O}$ of Gb but not Nps in IRD layers in their site west of Ireland (Figure 2, core MD01-2461), which they interpret as freshening-driven upper ocean stratification, but their IRD layers typically are not the same as the Heinrich layers.

[41] For a site at the southern margin of the glacial IRD belt (Figure 2, CHN82-20, 43.3°N, 29.5°W), Rashid and Boyle [2007] find that the $\delta^{18}\text{O}$ of different foraminifera species converge during at least some Heinrich events, which they interpret as a sign of mixed-layer deepening. There might be mechanisms for reducing the nutrient supply to the subpolar North Atlantic without shoaling the mixed layer, so as to allow for consistency between the interpretation of Rashid and Boyle [2007] with our N isotope observations. However, there are also different viewpoints as to how to interpret the observed interspecies foraminiferal $\delta^{18}\text{O}$ differences [Rashid and Boyle, 2008]. Hillaire-Marcel and de Vernal [2008] tentatively link the $\delta^{18}\text{O}$ convergence of species to the subduction of low- $\delta^{18}\text{O}$ brines from sea ice formation. Arguably the most likely explanation is that CHN82-20 is almost 15° south of V28-73, such that the findings of Rashid and Boyle [2007] do not apply to our region.

[42] Here, we suggest an interpretation of the slight $\delta^{18}\text{O}$ rises in both Gb and Nps during Heinrich events that appears to fit with the N isotope data. We have proposed above that the more similar $\delta^{18}\text{O}$ of Gb and Nps during the ice age was caused by a deep base to the summer mixed layer (Figure 4d, blue line), such that it sat below the common depths of both species. For both species to remain similar in $\delta^{18}\text{O}$ during the Heinrich events, we would then need to argue that they remained in the same water, either below or above the mixed layer. As a $\delta^{18}\text{O}$ decline would have been expected with freshening of the mixed layer during Heinrich events, the tendency for slight $\delta^{18}\text{O}$ rises suggests that the mixed layer may have shoaled above the common depths of both species (Figure 4d). Given that the $\delta^{18}\text{O}$ data suggest that the two species are separated by the summer mixed-layer base in the Holocene, the implication is that the Heinrich event mixed layer was even shallower than that of the Holocene. In this scenario, the mixed layer was shallowest during the Heinrich events and deepest during the background LGM, with the Holocene having an intermediate summer mixed-layer depth (Figure 4). Of course, we recognize the

speculative nature of this very literal interpretation of Gb and Nps $\delta^{18}\text{O}$ changes, and our interpretation of the N isotope data does not rely on it.

[43] The inferred H1 IRD layer is possibly different from the other Heinrich events in its relatively late onset of the FB- $\delta^{15}\text{N}$ increase (Figure 3). As noted above, the IRD layer itself seems to undergo some depth changes in mineralogy. Further work will be needed to resolve whether this difference from the other IRD layers is robust.

[44] Taking a broader view, the contrasting behavior of this subpolar North Atlantic site and the Southern Ocean, raised previously in the context of the LGM background conditions, is also apparent in association with the Heinrich events. Antarctic opal flux data are taken to indicate higher nutrient supply during Heinrich events, presumably due to increased upwelling and/or vertical mixing [Anderson *et al.*, 2009]. In contrast, the FB- $\delta^{15}\text{N}$ and biogenic flux data for the subpolar North Atlantic together indicate reduced nutrient supply in this region, apparently associated with the development of strong upper water column stratification (Figure 4). During Heinrich events, the North Atlantic changes were likely driven by the external factor of accelerated ice discharge. The Antarctic changes, in contrast, are thought to represent a response to the North Atlantic changes, be it by an atmospheric connection [Toggweiler and Lea, 2010] or a feedback through the ocean interior [Broecker, 1998; Schmittner and Galbraith, 2008; Sigman *et al.*, 2007]. This inverse behavior between regions fits with the expectations of North Atlantic/Antarctic compensation in maintaining deep ocean ventilation.

4.3. Conclusions

[45] Based on the foraminifera bound- $\delta^{15}\text{N}$ in planktonic foraminifera *Neogloboquadrina pachyderma* (sinistral) from the eastern subpolar North Atlantic, we infer that summer-time nutrient consumption was less complete during the last ice age (Figure 4b). Coupling this with the evidence for reduced productivity in the ice age subpolar North Atlantic, we infer that light conditions were less favorable due to a deeper summer mixed layer in this eastern region of the subpolar North Atlantic, consistent with other findings from the region [Peck *et al.*, 2006]. Across most of the polar/subpolar ocean, deep summer mixed layers reflect weak year-round density stratification. Thus, our results imply that the ice age eastern subarctic North Atlantic was less well stratified, and this may be related to the suggestion that this region was a locus of GNAIW formation [Duplessy *et al.*, 1991; Labeyrie *et al.*, 1992; Oppo and Lehman, 1993; Peck *et al.*, 2007]. In contrast, the FB- $\delta^{15}\text{N}$ peaks in the Heinrich layers call for less nitrate supply and thus stronger upper water column stratification during these events, due to the previously reconstructed freshwater inputs during Heinrich events (Figure 4c). This is consistent with observations of sharply reduced GNAIW formation during Heinrich events [Maslin *et al.*, 1995; Zahn *et al.*, 1997; McManus *et al.*, 2004; Willamowski and Zahn, 2000]. However, given the suggestions from foraminiferal $\delta^{18}\text{O}$ and dinoflagellate cysts for extreme spatial variability in surface ocean salinity and density across the subpolar North Atlantic during the last ice age [de Vernal *et al.*, 2002; Duplessy *et al.*, 1991] and in Heinrich events [Cortijo *et al.*, 1997], these changes in upper ocean conditions and their connections to North

Atlantic overturning must be investigated in other sites across the region.

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