PALEOCEANOGRAPHY, VOL. 16, NO. 6, PAGES 617–626, DECEMBER 2001

A latitudinal productivity band in the central North Atlantic over the last 270 kyr: An alkenone perspective

J. Villanueva, E. Calvo, C. Pelejero, and J. O. Grimalt
Institute of Chemical and Environmental Research, Consejo Superior de Investigaciones Cientificas Barcelona, Spain

A. Boelaert and L. Labeyrie
Laboratoire des Sciences du Climat et de l'Environnement, CNRS, Gif-sur-Ivette, France

Abstract. Productivity changes in the central North Atlantic Ocean have been traced by means of the total C_{37} alkenone contents along two sediment cores located at 43°N and 37°N. Both alkenone signals revealed the occurrence of discrete productivity events every 23 kyr. Spectral analyses highlight the presence of a dominant 23-kyr periodicity in the alkenone signal, which is highly coherent to the precession index. However, a close comparison revealed small but relevant differences in the timing of several of the productivity events recorded at both locations. These asynchronies suggest that the alkenone maxima do not necessarily reflect a general increase of productivity over the North Atlantic. We propose that the events are related to a latitudinal band of productivity that moves northward and southward over time. Satellite-derived productivity estimates show that the present location of this band is 45°–55°N. To illustrate this hypothesis we have constructed a conceptual model that reconstructs the temporal changes of productivity at one given location by assuming a productivity band that evolutes latitudinally over time. The model is able to reconstruct the main features of the alkenone records, namely, (1) the occurrence of discrete and abrupt productivity events, (2) the asynchrony at different latitudes, and (3) the bimodal pattern of many of the productivity peaks.

1. Introduction

Marine productivity has been proposed to be one of the main factors controlling the CO_2 transport from the atmosphere to the intermediate and deep seawaters and sediments. Unfortunately, whereas the atmospheric CO_2 variations during the last four glacial-interglacial cycles have been well determined [*Petit et al.*, 1999], the changes in marine productivity are still far from being described with accuracy.

In the case of the North Atlantic Ocean, much controversy exists concerning estimates of past marine productivity. Studies based on total organic carbon (TOC) measurements in the northeastern Atlantic (50°–60°N) suggested enhanced or similar productivity during the Holocene and the Last Glacial Maximum (LGM) [*Manighetti and McCave*, 1995]. These conclusions were not confirmed by investigations based on benthic foraminiferal shell remains in similar cores, which indicated lower productivity during the LGM [*Thomas et al.*, 1995]. Moreover, distributions of diatom assemblages in core DSDP-609 suggested similar productivity in the central North Atlantic (50°N) during the LGM and Holocene periods [*Sancetta*, 1992]. On the other hand, studies covering one of several glacial cycles indicated higher productivity during glacial periods in the central Labrador Sea [*Stein*, 1991]. This temporal trend was inverted in the northern Labrador Sea [*Stein and Stax*, 1991]. Finally, the coccolithophorid-related productivity at 43°N was dominated by a 23-kyr cycle [*Villanueva et al.*, 1998b], a precessional control that was not apparent at 52°N [*Villanueva et al.*, 1997a]. All these contradicting results evidence a complex spatial and temporal behavior in the paleoproductivity history of the North Atlantic Ocean.

Copyright 2001 by the American Geophysical Union.

Paper number 2000PA000543.
0883-8305/01/2000PA000543$12.00

The evolution of the polar front in the North Atlantic Ocean during the last glacial-interglacial climatic cycles has been constrained by studies based on foraminiferal and coccolithophorid assemblages [*CLIMAP*, 1976; *Ruddiman and McIntyre*, 1976]. During glacial periods the polar front was located at intermediate positions between the present position north of Iceland and its southern location at 41°–46°N [*Ruddiman and McIntyre*, 1976]. *Ruddiman* [1977] showed that during the last glacial period a massive input of ice-rafted detrital matter accumulated north of the polar front. For this reason, glacial sediments accumulated north of 41°N in the North Atlantic received significant inputs of continental organic matter [*Manighetti and McCave*, 1995], which can account for more than 80% of the sedimentary organic carbon [*Villanueva et al.*, 1997a]. This fact limits substantially the traditional use of accumulation rates of organic carbon to trace paleoproductivity changes in the North Atlantic.

The long-chain alkenones are a series of C_{37}-C_{39} ketones with two, three, or four double bonds in the aliphatic chain that are specific markers of some Haptophyte algae [*Conte et al.*, 1995; *Marlowe et al.*, 1984]. These lipids occur in significant amounts in most marine sediments [*Marlowe et al.*, 1990] and represent a substantial fraction of the organic matter in the coccolithophorid *Emiliania huxleyi* (8.0 ± 2.9% [*Prahl et al.*, 1988]). A part from the well-established use of C_{37} alkenones for the assessment of paleotemperatures by means of the $U^{k'}_{37}$ index [e.g., *Brassell et al.*, 1986], the sedimentary content of these compounds was proposed as a tool to estimate changes in Haptophyceae productivity in the past [*Brassell*, 1993]. However, most studies performed on late Quaternary sediments have systematically shown that the downcore variabilities of the TOC and alkenone signals are virtually identical [*Müller et al.*, 1997; *Prahl et al.*, 1989; *Rostek et al.*, 1997; *Schubert et al.*, 1998; *Sicre et al.*, 2000]. The evidence collected by several studies indicates that the alkenone/TOC ratio in one given location remains constant over time [*Müller et al.*, 1997; *Sicre et al.*, 2000]. The implication is that the downcore alkenone and TOC variabilities are virtually the same because the alkenone content of the

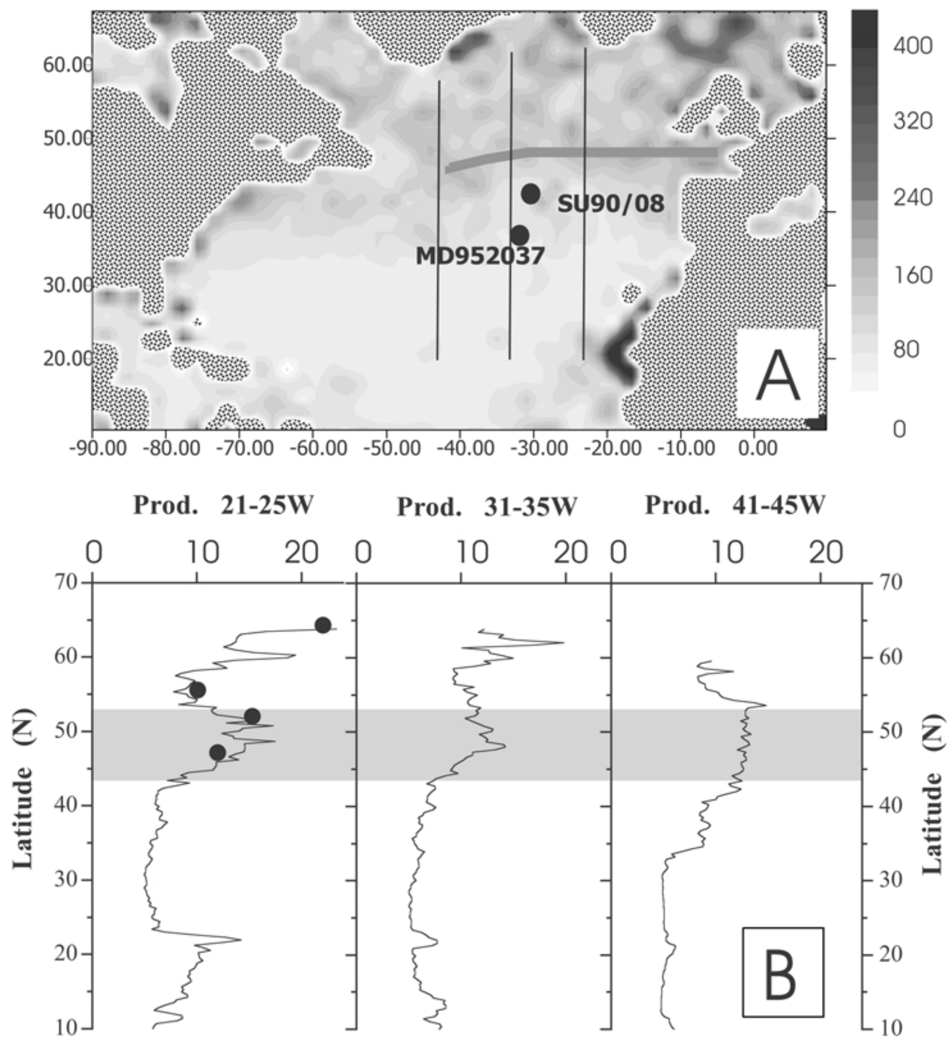

Figure 1. (a) Map showing the spatial distribution of marine productivity (in gC m^{-2}) during the month of June over the North Atlantic Ocean (adapted from *Antoine et al.* [1996]). The location of cores SU90/08 and MD952037 are included for reference. The thick gray line reflects the presence of a latitudinal area with high productivity. (b) Latitudinal transects of satellite-derived productivity at three different longitudes (see vertical lines in Figure 1a). The shaded area highlights the presence of a distinct latitudinal band of high productivity. The data used to construct the map and to calculate the latitudinal transects have been kindly provided by David Antoine. The satellite data are compared to the productivity estimates measured by *Weeks et al.* [1993] in June 1989 over a transect at ~20°W (see dots at the 21°–25°W transect).

sedimentary organic matter is a constant feature in one given sedimentary setting.

Schubert et al. [1998] suggested that the relative constancy of the biomarker composition of the organic matter was probably an indicator of a relatively stable phytoplankton community in the past. However, the role of diagenetic processes in uniformizing the sedimentary alkenone/TOC ratio is not well constrained. One remarkable result is the marked difference in the alkenone/TOC ratio measured in sediments younger and older than 74 kyrs B.P. [*Müller et al.*, 1997; *Sicre et al.*, 2000] that indicates a drastic change in the alkenone content of the sedimentary organic matter associated with a major reversal in the coccolithophorid populations (the main alkenone producers) from the dominance of *Gephyrocapsaceae* spp. to *Emiliania huxleyi* [*Müller et al.*, 1997]. This shift in the alkenone/TOC ratio is a clear indication that changes in the photic zone are reflected in the sediments and that diagenesis is not the only controlling factor of this ratio.

The downcore alkenone and TOC profiles from intermediate and high latitudes of the North Atlantic Ocean usually display distinct trends [*Madureira et al.*, 1997; *Rosell-Melé*, 1994; *Villanueva et al.*, 1997a]. These differences are related to significant contributions of continentally derived organic matter associated with ice-rafted detritus. *Villanueva et al.* [1997a] reconstructed the marine fraction of the TOC in two North Atlantic cores assuming a linear relationship alkenone/TOC. In the present study we have used the alkenone profiles to overcome the interference of terrigenous inputs in paleoproductivity studies based on the sedimentary organic matter content in North Atlantic sediments.

In the present study an assessment of the North Atlantic paleoproductivity is obtained from the study of the sedimentary alkenones in a new core located at 37°N. The results are directly

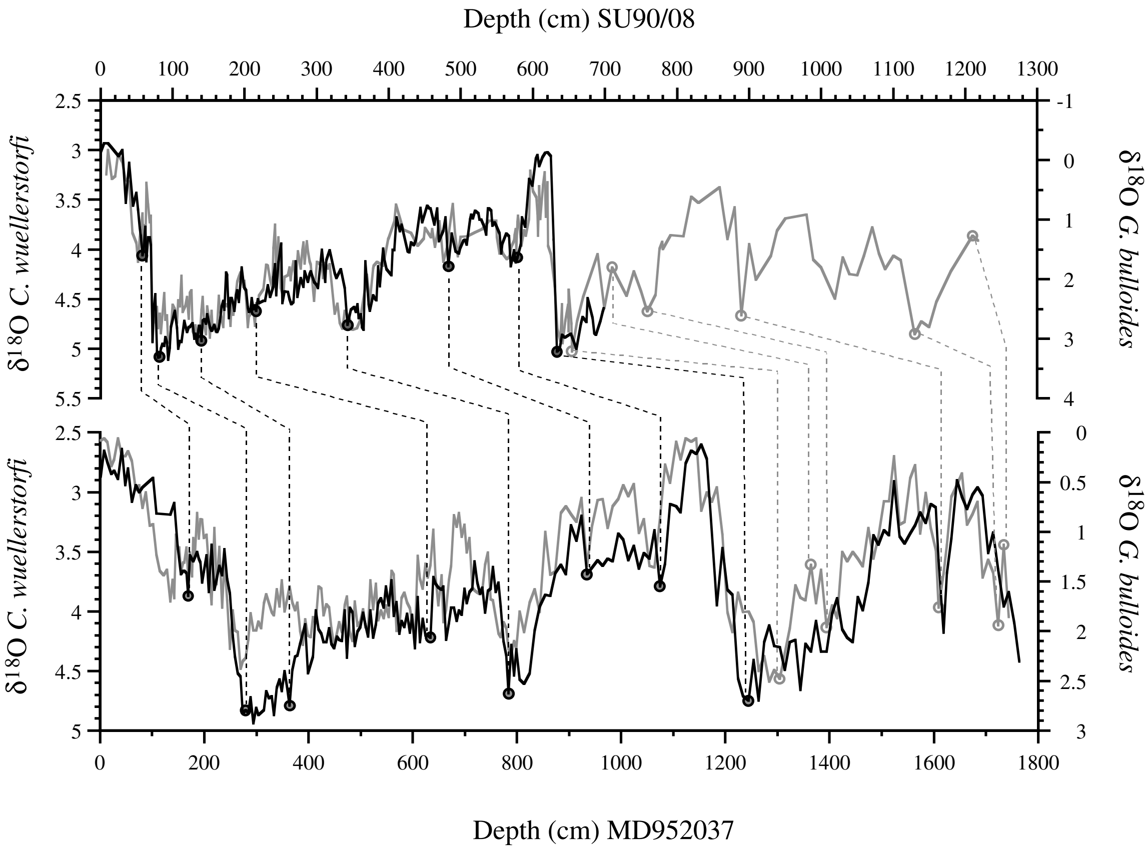

Figure 2. Detailed chronostratigraphy of core MD952037 performed by comparison with the well-studied core SU90/08. Dashed lines connecting circles mark all control points used. The ages of the upper 13 m are based on comparison between both *C. wuellerstorfi* δ^{18}O lines (thick lines). For deeper sections the *Globigerina bulloides* δ^{18}O data were used, since there was no SU90/08 *C. wuellerstorfi* δ^{18}O data available for this period (dotted lines).

compared to a previous biomarker study performed at 43°N [*Villanueva et al.*, 1998b]. The spectral analyses of these two records reveal a precessional control of marine productivity, which is inferred by the occurrence of discrete events occurring approximately every 23 kyr. However, a detailed comparison of both records reveals significant temporal offsets which can be interpreted from latitudinal oscillations of an area of increased productivity over the central North Atlantic.

2. Relevant Oceanographic and Ecological Features

Studies based on sediment accumulation rates and incubation experiments have suggested a latitudinal gradient of primary productivity in the North Atlantic between 30° and 65°N. More intense seasonal algal blooms and a higher flux of biogenic particles to the sediments have been reported north of 40°–50°N [*Shimmield et al.*, 1995; *Weeks*, 1993]. Between 15° and 40°N, productivity is generally low, owing to the presence of a deep and well-established thermocline associated with the Eckman pumping in the central gyre.

More recently, modeling of satellite-derived chlorophyll fields has been used to predict primary production in the global oceans [*Antoine et al.*, 1996; *Antoine and Morel*, 1996; *Morel et al.*, 1996; *Platt et al.*, 1995]. This newly developed tool allows the possibility of examining spatial gradients of primary production, their seasonal variation, and their fluctuation between years. Concerning the central North Atlantic, the oligotrophic character of the subtropical gyre is well represented between 15° and 40°N by such satellite-derived estimations [*Antoine et al.*, 1996; *Platt et al.*, 1995]. Productivity increases latitudinally north of the subtropical gyre (Figures 1a and 1b). One remarkable feature revealed by the satellite estimates is the existence of a distinct latitudinal band of high primary productivity that extends from 45° to 55°N (Figure 1), which is well developed during spring and summer [*Antoine et al.*, 1996; *Platt et al.*, 1995]. The occurrence of a band of high productivity is better observed at the 21°–25°W transect than farther west. The latitudinal trend reconstructed by satellite data coincides remarkably well with the productivity estimates measured in situ in June 1989 [*Weeks*, 1993].

3. Materials and Methods

3.1. Stratigraphy

Gravity core SU90/08 (43°30′N, 30°24′W, 3100 m deep, 12 m long) and piston core MD952037 (37°05′N, 32°02′W, 2630 m deep, 36 m long) were retrieved in the North Atlantic during PALEOCINAT I (1990); *Le Suroît* vessel) and IMAGES 101 (1995; *Marion Dufresne II* vessel) cruises, respectively. Both cores are located in the western side of the Mid-Atlantic Ridge. Core SU90/08 and core MD952037 are located at the northern edge and within the subtropical North Atlantic Gyre, respectively.

In order to put both records into the same age scale, the age model published for core SU9008 [*Villanueva et al.*, 1998b] has been taken as a reference. This core has already been extensively

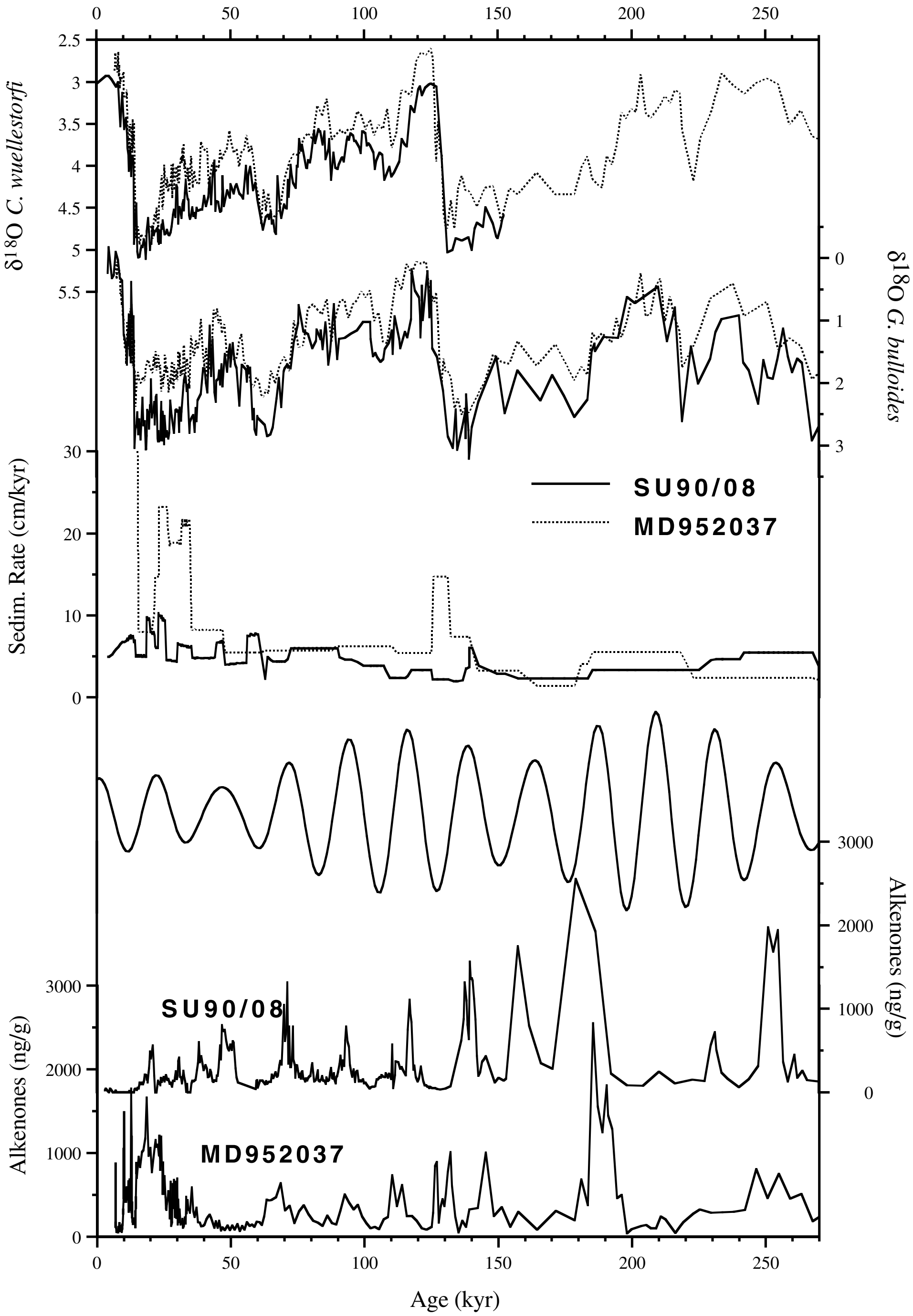

Figure 3. Comparison of time profiles of cores SU90/08 and MD952037 of *C. wuellerstorfi* $\delta^{18}O$, *G. bulloides* $\delta^{18}O$, sedimentation rate, and C_{37} alkenone concentration. The precessional index is also plotted for comparison [*Laskar*, 1990].

studied [*Cortijo et al.*, 1997; *Elliot et al.*, 1998; *Grousset et al.*, 1993; *Vidal et al.*, 1997], and its age model is based on 10 accelerator mass spectrometry (AMS) ^{14}C measurements and correlation between $\delta^{18}O$ records of *Cibicides wuellerstorfi* and *Globigerina bulloides* with the SPECMAP-normalized isotope curve [*Imbrie et al.*, 1984; *Martinson et al.*, 1987]. Core MD952037 has been correlated with SU90/08 on the basis of comparison between parallel features on both *C. wuellerstorfi* $\delta^{18}O$ curves for the period from which they are available (Figure 2; 150 kyr B.P. till present). For the rest of the record (270–150 kyr B.P.) the age model was determined relying on planktic *G. bulloides* $\delta^{18}O$ data (Figure 2).

Both planktonic and benthic foraminifera oxygen isotope records are plotted versus ages in Figure 3, evidencing a clear concordance and thus inferring the same response to the major ice volume changes for these two close locations. Sedimentation rates for both cores range between 2 and 10 cm kyr^{-1} (Figure 3). According to our sampling intervals, the temporal resolution ranges from.4 to 2 kyr in the northernmost core and from 0.05 to 4 kyr in the southern one, the period from 150 kyr till the present being the one examined

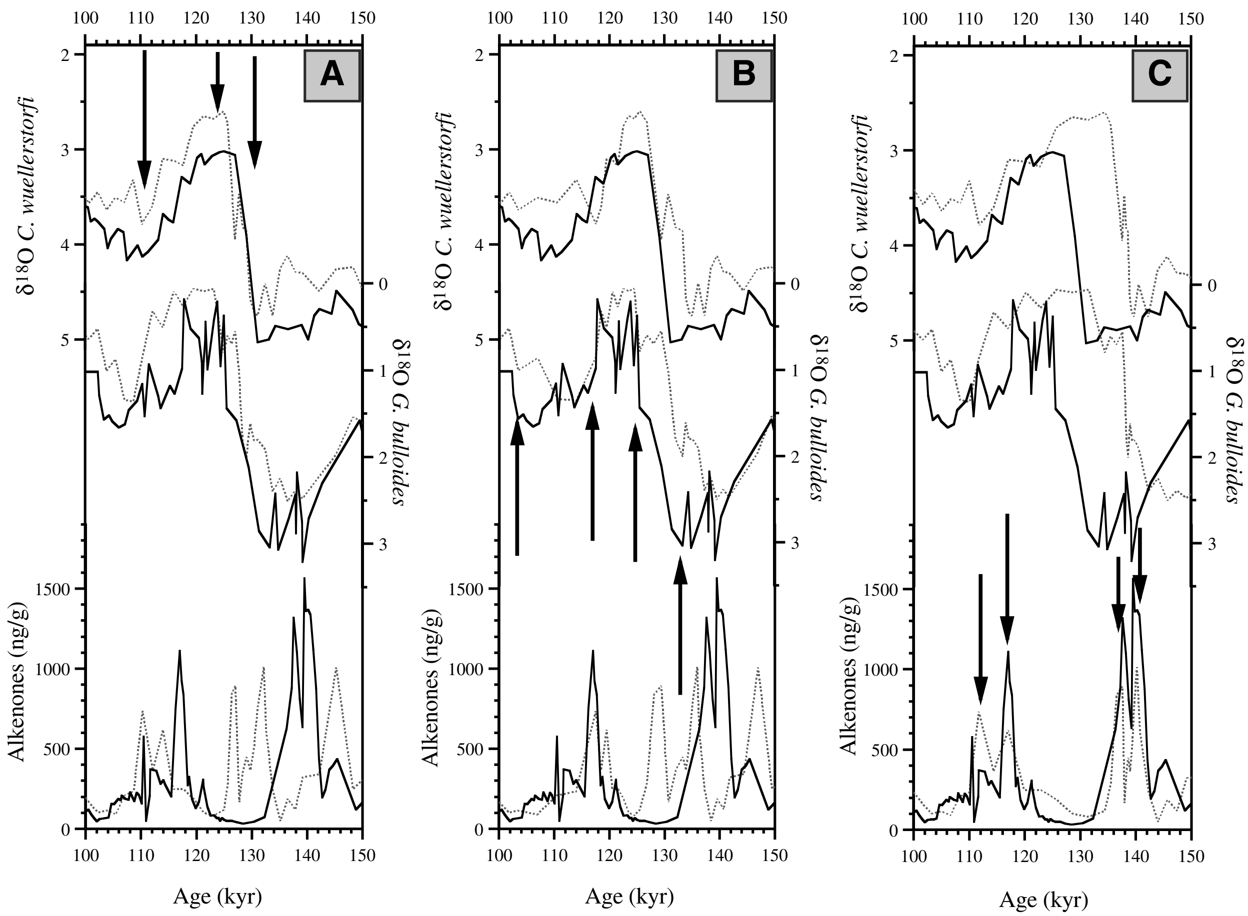

Figure 4. A comparison of three dating methods used to evaluate the existence or not of significant temporal shifts in the occurrence of alkenone peaks at 37°N and 43°N. (a) A comparison of the benthic $\delta^{18}O$, planktonic $\delta^{18}O$, and alkenone profiles that result from the age model described in Figure 2, which is based on the pointers described with the arrows. While the $\delta^{18}O$ show concordant features (as imposed by the age model based on the benthic record), the alkenone peaks in both cores occur at completely different times, with temporal offsets of ~10 kyr. (b) An artificial age model produced with the planktic $\delta^{18}O$ profiles. The pointers used to construct this age model are represented with arrows. Using this method, one pair of the alkenone peaks coincide in time, but significant shifts in the other peaks still exist. (c) An artificial model based on the hypothesis that the alkenone peaks at both core locations are coeval. This assumption clearly leads to significant shifts in the timing of termination II observed in both cores, which are not realistic. Therefore the alkenone peaks recorded at both core locations are not synchronous.

at a higher resolution in both cases. The unusually high sedimentation rates of the top 6 m of core MD952037 (50–10 cm kyr^{-1}) are probably related to stretching processes associated to the Calypso coring device and do not represent the "true" sedimentation rate in this location.

3.2. Analysis

The procedures and equipment used for C_{37} alkenones in deep-sea sediments are described elsewhere [*Villanueva et al.*, 1997b]. Briefly, sediment samples were freeze-dried and manually grounded to ensure sample homogeneity. After the addition of an internal standard containing *n*-nonadecan-1-ol, *n*-hexatriacontane, and *n*-tetracontane, dry subsamples (~3 g) were extracted with dichloromethane in an ultrasonic bath. The extracts were hydrolyzed with 6% potassium hydroxide in methanol for the elimination of wax ester interferences. The *n*-hexane extracts were then evaporated under a N_2 stream, derivatized with bis(trimethylsilyl)trifluoroacetamide, and analyzed by gas chromatography with flame ionization detection. The $C_{37:2}$ and $C_{37:3}$ alkenones were identified by coelution with synthetic standards kindly provided by J. R. Maxwell (University of Bristol, England, UK). Selected samples were examined by gas chromatography; mass spectrometry was used for the confirmation of compound identification and the evaluation of possible coelutions. The concentration of each compound was determined using hexatriacontane as the internal standard and expressed as ng g^{-1} of dry weight sediment (ng gdw^{-1}). Absolute concentration errors of C_{37} alkenones were below 10%.

4. Results

4.1. Description of Alkenone Profiles

The alkenone concentration patterns obtained along cores SU90/08 and MD952037, which are situated only 700 km apart, show the same general features (Figure 3). First, the concentration range is the same in both cores, with values lying between 10 and 2800 ng gdw^{-1}. Second, both cores show similar temporal evolutions in the alkenone signal, which is not dominated by a glacial-interglacial pattern. Third, some of the alkenone peaks display a bimodal pattern, presenting a clear interruption at the middle of the event.

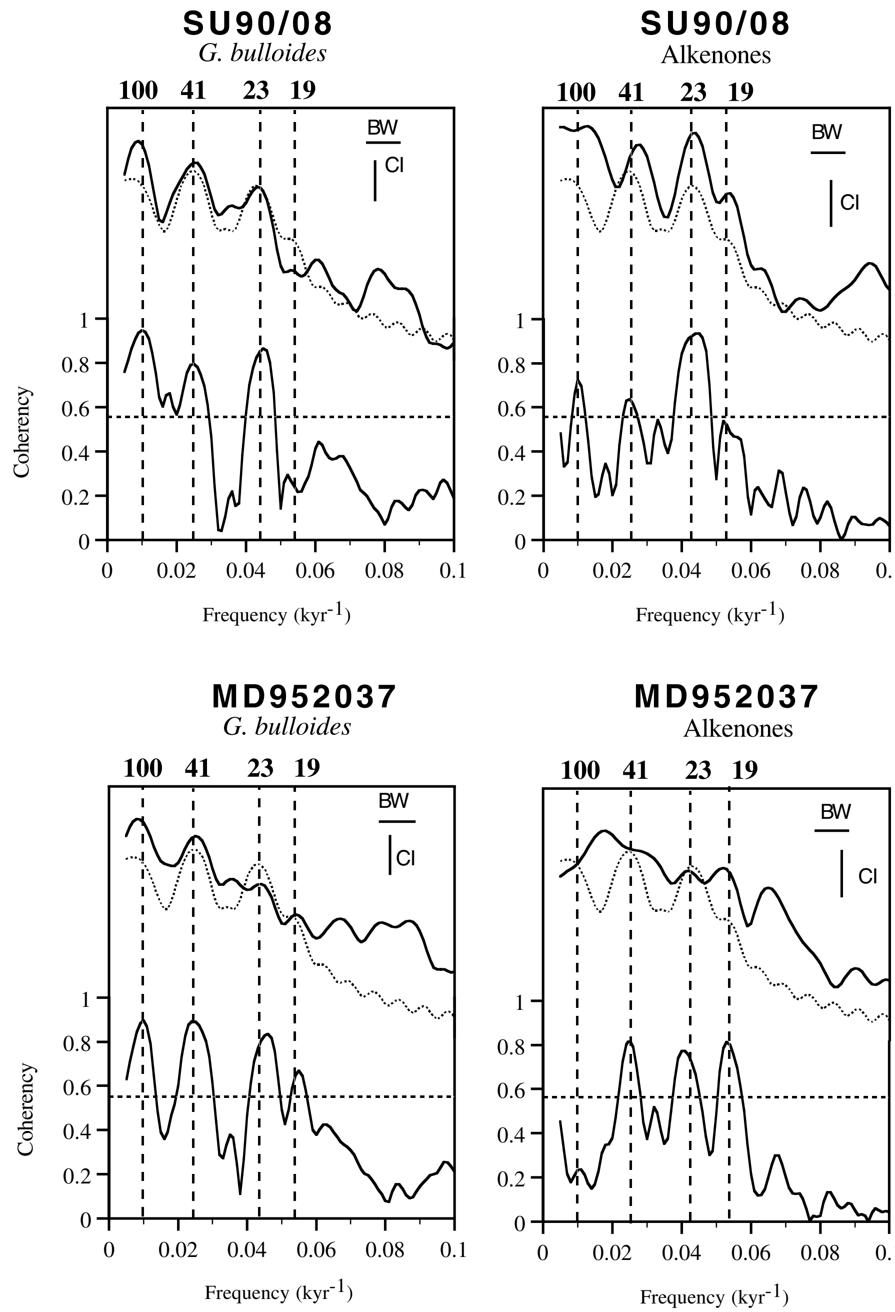

Figure 5. Variance spectra of *G. bulloides* $\delta^{18}O$ and C_{37} alkenone abundances for both cores (expressed as the logarithm of spectral power density versus frequency in cycles kyr^{-1}). Solid lines were obtained using the Blackman-Tuckey method and cross-correlated with a combination of the three main orbital parameters, the ETP curve (dotted lines) [*Imbrie et al.*, 1984]. CI and BW stand for confidence interval at 80%, and bandwidth, respectively. The vertical and horizontal solid lines represent their magnitudes, respectively. Vertical dashed lines mark the main orbital periods of eccentricity (100 kyr), obliquity (41 kyr), and precession (23 and 19 kyr). The coherency spectra between core profiles and ETP are shown at the bottom of each profile. The horizontal dashed line indicates the level of nonzero coherence at the 80% confidence interval. We used the Analyseries software [*Paillard et al.*, 1996] to perform the spectral analyses.

Finally, both records coincide in the regular appearance of discrete concentration maxima, suggesting a cyclic pattern. However, a closer inspection reveals discrepancies in the timing of some of the events between both cores. Although some of the maxima are synchronous, some of them show some dephasing, especially between 150 and 100 kyr B.P. In order to assess whether the differences in the timing of some events are significative or are simply associated with uncertainties in the age model, we generated an artificial age model by matching the alkenone peaks observed in both cores (Figure 4). This exercise resulted in serious biases in the oxygen isotope records for both cores, with differences of ~10 kyr in the ages of some well-defined events such as the termination II and the transition 5e–5d. Such discrepancies are well beyond the uncertainties of the dating method. Thus we conclude that the temporal biases observed between the two alkenone records represent true differences in productivity maxima between the two locations.

4.2. Spectral Analysis

Simple visual comparison evidences a significant relationship between alkenone maxima and high values in the precession index (Figure 3). In order to evaluate the response of the alkenone signal to the precessional orbital forcing, cross-spectral analyses of both records with the eccentricity-tilt-precession (ETP) curve [*Imbrie et al.*, 1984] have been performed. The alkenone signal of core SU90/08 shows a very high coherency (k = 0.93) at the precessional 23-kyr cyclicity (Figure 5). This mathematical tool also suggests a minor response to the eccentricity and obliquity orbital components that are not visually observed in the original record (Figure 3). Core MD952037 also presents a strong response to the precessional 23- and 19-kyr periodicities with a coherency of 0.77 and 0.80, respectively. In contrast to core SU90/08, in this case the spectral analysis reveals significant variance at the obliquity cycle (41 kyr) with a coherency of 0.82. Overall, the spectral analyses highlight the relevance of the precessional forcing in the accumulation of alkenones in the central North Atlantic.

The downcore variability of the alkenone signals could be attributed to paleoproductivity changes over time or to a changing degree of preservation of the organic matter, which are associated with sedimentary conditions, especially sedimentation rate and the redox conditions of the bottom waters. In previous North Atlantic studies the possible dominance of preservation effects in the alkenone pattern was discarded on the basis of distinct downcore patterns between the alkenones and other lipids such as the *n*-alkanes and the fatty acids unsaturation index. In the two cores studied, *n*-alkanes display a glacial-interglacial pattern that is very similar to the pattern of other tracers of terrigenous components, such as the magnetic susceptibility and the noncarbonate fraction (see *Villanueva et al.* [1997a] and *Calvo et al.* [2001] for a detailed discussion). In contrast, the profiles of concentration and accumulation rates of alkenones display a different pattern dominated by a precessional cyclicity [*Villanueva et al.*, 1998a, 1998b]. Moreover, none of the alkenone peaks did coincide with any detectable increase in the abundance of the *n*-alkanes. Accordingly, diagenesis alone cannot account for the large differences observed in the downcore profiles of alkenones and *n*-alkanes, which have similar diagenetic stability but a different origin.

On the other hand, there is no evidence for changing sedimentary conditions associated with the alkenone peaks. For example, sedimentation rates in both cores are relatively uniform over the whole sedimentary column (Figure 3), and there is no hint of high sedimentation rates during the alkenone peaks. The possibility of changing bottom redox conditions in the North Atlantic Ocean linked to a precessional forcing is highly unlikely. Other studies have found evidence of a precessional control on surface processes in this oceanographic region [*Bout-Roumazeilles et al.*, 1997; *Imbrie et al.*, 1989]. *Imbrie et al.* [1989] described a precessional control in the sea surface temperature (SST) evolution in core V3097 (41°N) and hypothesized a direct link between low-latitude processes and surface or atmospheric processes in this region. In this sense, the alkenone accumulation rate in core SU90/08 has been correlated with surface processes of low-latitude areas typically dominated by a strong precessional forcing, such as the trade wind intensity in the equatorial Atlantic [*Villanueva et al.*, 1998b]. Accordingly, the precessional forcing in the alkenone signal observed in cores MD952037 and SU90/08 reflects the temporal variability in surface productivity.

5. Discussion

By considering core SU90/08 by its own, *Villanueva et al.* [1998b] concluded that productivity changes in the central North Atlantic were precessionally related. The incorporation of the new alkenone profile of core MD952037 provides a unique opportunity to further understand the causes and mechanisms of this precessional control. Clear similarities between the pulsating behaviors of both cores as well as between the alkenone magnitudes of individual productivity peaks are evident, thus confirming a similar response to the climatic system in both records. However, a detailed comparison of both alkenone records indicates several discrepancies in the timing of some of the alkenone maxima. Clear examples of this situation are the productivity event at ~130 kyr B.P. observed only in core MD952037 and the peaks recorded at 260 and 50 kyr B.P., only present at core SU90/08 (Figure 3). These examples represent periods when productivity estimations were higher in the southern location and periods when this trend was reversed, respectively. According to the alkenone records, productivity decreased northward at 10, 65, 130, 145, and 190 kyr B.P., a situation opposed to the general trend observed in the modern ocean. In order to explain this in principle unexpected result, we have examined the spatial distribution of productivity in the modern ocean. Satellite-derived productivity maps of the North Atlantic reveal the occurrence of a high-productivity latitudinal band centered at ′50°N [*Antoine*, 1996] (Figures 1a and 1b). From 45° to 55°N there is a clear decreasing trend northward that is related to the existence of this area of high productivity. We suggest that the past episodes of reversed latitudinal gradient could be explained by the displacement of the productivity band south of 43°N, causing higher productivity estimates at 37°N. Accordingly, we suggest that the productivity band observed in the modern ocean existed in the past and that its latitudinal position changed over time.

This hypothesis is able to account for the main features observed in the alkenone data. The first feature is the pulsating character of the alkenone profiles in both cores can be explained by the latitudinal displacement of this productivity band. High-productivity events are related to the passage of this latitudinal band over the core location, and low-productivity periods are recorded during the absence of this band at the given latitude. The second feature successfully explained by this hypothesis is the asynchrony observed in some productivity events at different latitudes.

5.1. Description of the Productivity Band Model

In order to illustrate and evaluate this hypothesis, a simple conceptual model has been constructed that assumes a latitudinal productivity band that moves northward and southward over time. The model has been designed to reconstruct the temporal changes of productivity at one given latitude, which are caused by the movement of the productivity band. In this case the productivity variations at 37° and 43°N computed by the model have been compared to the alkenone data in cores MD952037 and SU90/08, respectively.

The simplest method for modeling the occurrence of a productivity band similar to that observed in the modern North Atlantic is by describing it as a Gaussian function:

$$Pi = e^{-\frac{1}{2}F^2(Li-Lx)^2} \qquad (1)$$

where Pi are the calculated productivity values at a given latitude Li, F is related to the amplitude of the Gaussian function and thus to the productivity band (Figure 6a), and Lx represents the latitude coordinate of the maximum of the Gaussian curve (approximately the productivity band) at a given time. We used a value of F = 2 (representing 4°–6° in latitude) as a realistic amplitude of the productivity band, according to the satellite-derived primary production values for present times (Figure 1b). The movement of the productivity band over time has been traced by using the

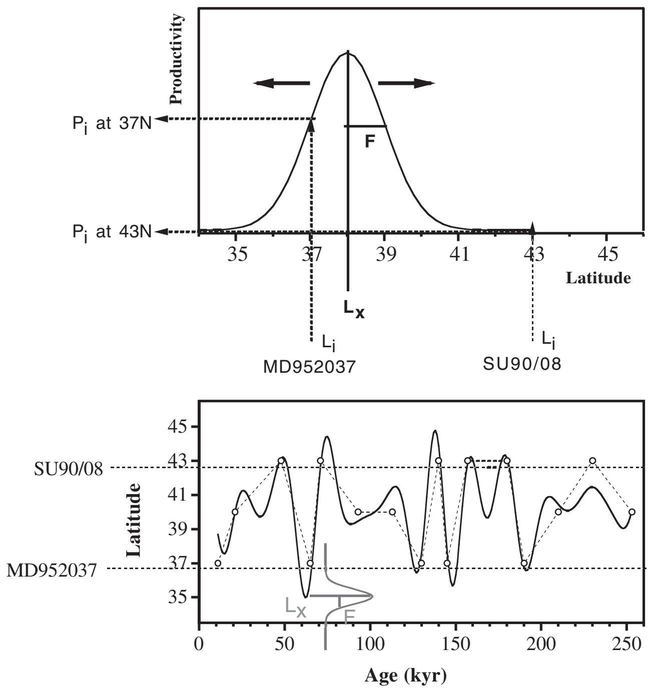

Figure 6. Description of the productivity band model. The top panel depicts the Gaussian curve used to represent the productivity band (see equation (1) for a description of the parameters). In this situation, high productivity values would be observed in the location of core MD952037, whereas core SU90/08 would record very low values (dashed arrows). Solid thick arrows represent the latitudinal displacement of the productivity band. The bottom panel shows the proposed trajectory followed by the band over time. Circles represent all selected snapshots, dashed line represents the staircased pathway, and the solid line represents the trajectory after filtering by a 23-kyr filter (see text).

following procedure. First, the periods where the productivity band overpassed the latitudes 43° and 37°N were determined by locating the alkenone maxima in cores SU90/08 and MD952037, respectively. In the cases where the alkenone maxima were synchronous at both locations, we assumed that the productivity band was located between 37° and 43°N, and a latitude of 40°N was arbitrarily chosen. The selected list of known positions of the productivity band is represented in Figure 6 (bottom) as circles. In order to obtain a continuous trajectory of the productivity band, we interpolated the staircased pathway every 1 kyr, and the resulting trajectory was smoothed by using a band-pass Gaussian filter. The best fitting to all known band locations was obtained by using a filter centered at 23 kyr. Tests performed after filtering at 41 and 100 kyr gave poor results. This finding is not surprising, since the alkenone records show a marked response to the precessional 23-kyr cyclicity.

5.2. Modeled Productivity at Both Locations

A comparison of the productivity reconstructed by the model at 37° and 43°N with the alkenone records in cores MD952037 and SU90/08 is shown in Figure 7. By using this simple conceptual model, several of the main features observed in the alkenone profiles have been simulated successfully. First, the pulsating character of the productivity events is explained by assuming a latitudinal motion of the productivity band. Second, the model is able to reconstruct the asynchrony of the productivity events observed at the two sites. Third, the model reproduces the bimodal pattern of some of the productivity events. The model computes such a peculiar feature every time that after migration from one core latitude to the other, the productivity band slightly overpasses the core location. A clear example of this situation is the maximum observed around 140 kyr in core SU90/08 (Figure 6, bottom, and Figure 7). In contrast, the finding of synchronous alkenone events at both locations implies the occurrence of periods of a general increase of productivity between 37° and 43°N. Within the context of the proposed model, these particular events can be explained by assuming a band wide enough to comprise both latitudes at the same time. Such a possibility has not been considered in this model, and therefore it is not able to reconstruct these features (see the period between 90 and 120 kyr B.P. in Figure 7). In the context of the hypothesis proposed here, the periods of increased productivity at both locations can be explained by assuming an increase in the geographical extent of the productivity band. Accordingly, in our mathematical model those discrepancies could be solved by assuming a variable width of the productivity band ("*F*" of the Gaussian function).

Thus the main features of the alkenone records have been reconstructed by using an extremely simple mathematical model, providing further support to the hypothesis of a moving productivity band as a control of productivity changes in the past. However, this raises the question on the causes and mechanisms governing the temporal evolution of this productivity band. Remarkably, the alkenone profiles in cores SU90/08 and MD952037 do not follow a glacial-interglacial pattern. Consequently, the controls on productivity are independent of the global climatic changes. This result is unexpected since the evolution of the water masses in the North Atlantic is linked to the growth and decay of the northern ice sheets [*CLIMAP*, 1976]. For example, the polar front migrated as far south as 43°N during the last glacial period, involving a transition from intermediate to polar conditions at the location of core SU90/08. In contrast, the alkenone records at both locations show a strong response to the precessional orbital forcing and suggest that the controls on the latitudinal evolution of the productivity band are related to low-latitude processes. *Villanueva et al.* [1998b] correlated the periods of increased productivity in the North Atlantic with enhanced trade wind intensity in the equatorial Atlantic. This temporal coincidence suggested the idea that productivity in the North Atlantic could be modulated by the strength of the westerlies, and it proposed the idea of a coupling in the dynamics of the Ferrell and Hadley cells. However, this simple explanation does not explain successfully the observed asynchronies observed between 37° and 43°N and cannot account for the hypothesis of a moving productivity band. The understanding of the mechanisms controlling the history of this paleoproductivity band in the past requires a better knowledge of the causes of its existence in the modern ocean.

6. Conclusions

The paleoproductivity history of the central North Atlantic has been studied by means of the alkenone abundances along two sediment cores located at 43°N and 37°N. A simple visual inspection of the alkenone records has revealed that discrete events of high productivity dominated the temporal productivity evolution. The timing of the productivity peaks in the northern location presented a strong response to the precessional cycle. Such a precessional control is not so evident at the 37°N site, where spectral analysis suggests a response to both the obliquity and the precessional cycles. On the other hand, a detailed comparison of the productivity peaks in the two records has revealed some slight but significant discrepancies in the timing of the productivity events at the two latitudes. We suggest that this asynchrony can be explained by a latitudinal productivity band that migrated northward and southward over time. Satellite-derived productivity estimates indeed

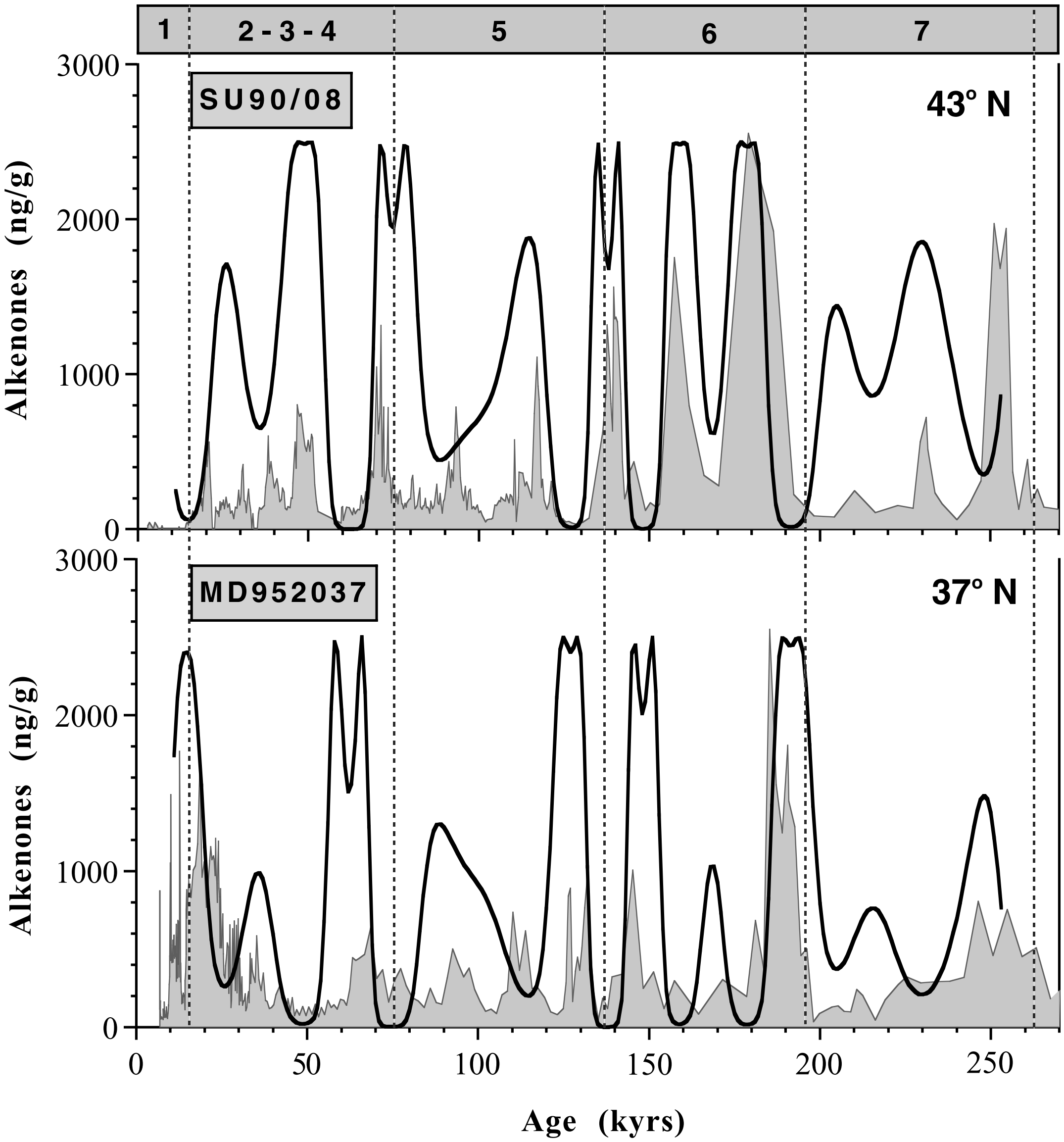

Figure 7. Modeled productivity at sites SU90/08 and MD952037. Comparison of the reconstructed paleoproductivity (solid thick line) to the alkenone-derived productivity records (shaded area) for each location. Numbers above the plot refer to the oxygen isotopic stages, and vertical dashed lines refer to the transition between them.

show the existence of a productivity band in the modern North Atlantic between 45° and 55°N. We have illustrated our hypothesis by modeling the latitudinal movement of this band over time. Both the timing of the productivity events at the two locations and their bimodal pattern have been reconstructed using this conceptual model. The relevance of the precessional forcing in the alkenone records suggests that the mechanism controlling the migration of this productivity band is controlled by low-latitude processes.

Acknowledgments. Thanks are due to the French MENRT, TAAF, CNRS/INSU, and IFRTP for support to the Marion Dufresne and the IMAGES program. C. P. and J. V. thank a Ph.D. grant and a postdoctoral contract from C.I.R.I.T (Generalitat de Catalunya), respectively. Financial support from the TEMPUS EU project (ENV4-CT97-0564) is acknowledged. We are grateful to David Antoine (Laboratoire de Physique et Chimie Marines, Villefranche-sur-Mer, France) and to Ramon Crehuet (C.I.D.-C.S.I.C., Barcelona, Spain) for useful comments and for computer assistance, respectively.

References

Antoine, D., and A. Morel, Oceanic primary production, 1, Adaptation of a spectral light-photosynthesis model in view of application to satellite chlorophyll observations, *Global Biogeochem. Cycles*, *10*(1), 43–55, 1996.

Antoine, D., J. M. André, and A. Morel, Oceanic primary production, 2, Estimation at global scale from satellite (coastal zone color scanner) chlorophyll, *Global Biogeochem. Cycles*, *10*(1), 57–69, 1996.

Bout-Roumazeilles, V., P. Debrabant, L. Labeyrie, H. Chamley, and E. Cortijo, Latitudinal control of astronomical forcing parameters on the high-resolution clay mineral distribution in the 45°–60°N range in the North Atlantic Ocean during the past 300,000 years, *Paleoceanography*, *12*(5), 671–686, 1997.

Brassell, S. C., Applications of biomarkers for delineating marine paleoclimatic fluctuations during the Pleistocene, in *Organic Geochem-*

istry: Principles and Applications, edited by M. H. Engel and S. A. Macko, pp. 699–738, Plenum, New York, 1993.

Brassell, S. C., G. Eglinton, I. T. Marlowe, U. Pflaumann, and M. Sarnthein, Molecular stratigraphy: A new tool for climatic assessment, *Nature*, *320*, 129–133, 1986.

Calvo, E., J. Villanueva, J. O. Grimalt, A. Boelaert, and L. Labeyrie, New insights into the glacial latitudinal temperature gradients in the North Atlantic: Results from UK'37 — sea surface temperatures and terrigenous inputs, *Earth Planet. Sci. Lett.*, *188*, 509–519, 2001.

CLIMAP, The surface of the ice-age Earth, *Science*, *191*, 1131–1137, 1976.

Conte, M. H., A. Thompson, G. Eglinton, and J. C. Green, Lipid biomarker diversity in the coccolithophorid *Emiliania huxleyi* (Prymnesiophyceae) and the related species *Gephyrocapsa oceanica*, *J. Phycol.*, *31*, 272–282, 1995.

Cortijo, E., et al., Changes in sea surface hydrology associated with Heinrich event 4 in the North Atlantic Ocean between 40°and 60°N, *Earth Planet. Sci. Lett.*, *146*, 29–45, 1997.

Elliot, M., L. Labeyrie, G. Bond, E. Cortijo, J.-L. Turon, N. Tisnerat, and J.-C. Duplessy, Millenial-scale iceberg discharges in the Irminger Basin during the last glacial period: Relationship with the Heinrich events and environmental settings, *Paleoceanography*, *13*(5), 433–446, 1998.

Grousset, F., L. Labeyrie, J. Sinko, G. Bond, J. Duprat, M. Cremer, and S. Huon, Patterns of ice rafted detritus in the Glacial North Atlantic (40–55°N), *Paleoceanography*, *8*(2), 175–192, 1993.

Imbrie, J., J. D. Hays, D. G. Martinson, A. McIntyre, A. C. Mix, J. J. Morley, N. G. Pisias, W. L. Prell, and N. J. Shackleton, The orbital theory of Pleistocene climate: Support from a revised chronology of the marine $d^{18}O$ record, in *Milankovitch and Climate: Part 1*, edited by A. L. Berger et al., pp. 269–305, D. Reidel, Norwell, Mass., 1984.

Imbrie, J., A. McIntyre, and A. Mix, Oceanic response to orbital forcing in the late Quaternary: Observational and experimental strategies, in *Climate and Geosciences*, edited by A. Berger, S. Schneider, and J.-C. Duplessy, *NATO ASI Ser.*, *285*, 121–164, 1989.

Laskar, J., The chaotic motion of the solar system: A numerical estimate of the chaotic zones, *Icarus*, *88*, 266–291, 1990.

Madureira, L. A. S., S. A. van Kreveld, G. Eglinton, M. H. Conte, G. Ganssen, J. E. van Hinte, and J. J. Ottens, Late Quaternary high-resolution biomarker and other sedimentary climate proxies in a northeast Atlantic core, *Paleoceanography*, *12*(2), 255–269, 1997.

Manighetti, B., and I. N. McCave, Depositional fluxes, palaeoproductivity, and ice rafting in the NE Atlantic over the past 30 ka, *Paleoceanography*, *10*(3), 579–592, 1995.

Marlowe, I. T., J. C. Green, A. C. Neal, S. C. Brassell, G. Eglinton, and P. A. Course, Long chain (n-C_{37}-C_{39}) alkenones in the Prymnesiophyceae: Distribution of alkenones and other lipids and their taxonomic significance, *Br. Phycol. J.*, *19*, 203–216, 1984.

Marlowe, I. T., S. C. Brassell, G. Eglinton, and J. C. Green, Long-chain alkenones and alkyl alkenoates and the fossil coccolith record of marine sediments, *Chem. Geol.*, *88*, 349–375, 1990.

Martinson, D. G., N. G. Pisias, J. D. Hays, J. J. Imbrie, T. C. Moore, and N. J. Shackleton, Age dating and the orbital theory of the ice ages: Development of a high-resolution 0 to 300,000 year chronostratigraphy, *Quat. Res.*, *27*, 1–29, 1987.

Morel, A., D. Antoine, M. Babin, and Y. Dandonneau, Measured and modeled primary production in the northeast Atlantic (EUMELI JGOFS program): The impact of natural variations in photosynthetic parameters on model predictive skill, *Deep Sea Res., Part I*, *43*(8), 1273–1304, 1996.

Müller, P. J., M. Cepek, G. Ruhland, and R. Schneider, Alkenone and coccolithophorid species changes in late Quaternary sediments from the Walvis Ridge: Implications for the alkenone paleotemperature method, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *135*, 71–96, 1997.

Paillard, D., L. Labeyrie, and P. Yiou, Macintosh program performs time-series analysis, *Eos Trans. AGU*, *7*, 379, 1996.

Petit, J. R., et al., Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica, *Nature*, *399*, 429–436, 1999.

Platt, T., S. Sathyendranath, and A. Longhurst, Remote sensing of primary production in the ocean: Promise and fulfilment, *Philos. Trans. R. Soc. London., Ser. B*, *348*, 191–202, 1995.

Prahl, F. G., L. A. Muehlhausen, and D. L. Zahnle, Further evaluation of long-chain alkenones as indicators of palaoceanographic conditions, *Geochim. Cosmochim. Acta*, *52*, 2303–2310, 1988.

Prahl, F. G., L. A. Muehlhausen, and M. Lyle, An organic geochemical assessment of oceanographic conditions at MANOP Site C over the past 26,000 years, *Paleoceanography*, *4*(5), 495–510, 1989.

Rosell-Melé, A., Long-chain alkenone and alkyl alkenoate, and total pigment abundances as climatic proxy-indicators in the northeastern Atlantic: Analytical methods, calibration, and stratigraphy, Ph.D. thesis, Univ. of Bristol, Bristol, England, 164 pp., 1994.

Rostek, F., E. Bard, L. Beaufort, C. Sonzogni, and G. Ganssen, Sea surface temperature and productivity records for the past 240 kyr in the Arabian Sea, *Deep Sea Res., Part II*, *44*(6–7), 1461–1480, 1997.

Ruddiman, W. F., Late Quaternary deposition of ice-rafted sand in the subpolar North Atlantic (lat 40 to 60 N), *Geol. Soc. Am. Bull.*, *88*, 1813–1827, 1977.

Ruddiman, W. F., and A. McIntyre, Northeast Atlantic paleoclimatic changes over the past 600,000 years, *Mem. Geol. Soc. Am.*, *145*, 111–146, 1976.

Sancetta, C., Primary production in the glacial North Atlantic and North Pacific oceans, *Nature*, *360*, 249–250, 1992.

Schubert, C. J., J. Villanueva, S. E. Calvert, G. L. Cowie, U. von Rad, H. Schulz, and U. Berner, Stable phytoplankton community in the Arabian Sea over the last 200,000 years, *Nature*, *394*(6), 563–566, 1998.

Shimmield, G. B., T. D. Brand, and G. Ritchie, The benthic geochemical record of late Holocene carbon flux in the northeast Atlantic, in *The Role of the North Atlantic in the Global Carbon Cycle*, edited by G. Eglinton et al., *Philos. Trans. R. Soc. London, Ser. B*, *348*, 153–160, 1995.

Sicre, M.-A., Y. Ternois, M. Paterne, A. Boireau, L. Beaufort, P. Martinez, and P. Bertrand, Biomarker stratigraphic records over the last 150 kyears off the NW African coast at 25°N, *Org. Geochem.*, *31*, 577–588, 2000.

Stein, R., Accumulation of organic carbon in marine sediments, *Lect. Notes Earth Sci.*, *34*, 217 pp., 1991.

Stein, R., and R. Stax, Late Quaternary organic carbon cycles and paleoproductivity in the Labrador Sea, *Geo Mar. Lett.*, *11*, 90–95, 1991.

Thomas, E., L. Booth, M. Maslin, and N. J. Shackleton, Northeastern Atlantic benthic foraminifera during the last 45,000 years: Changes in productivity seen from the bottom up, *Paleoceanography*, *10*(3), 545–562, 1995.

Vidal, L., L. Labeyrie, E. Cortijo, M. Arnold, J. C. Duplessy, E. Michel, S. Becqué, and T. C. E. van Weering, Evidence for changes in the North Atlantic Deep Water linked to meltwater surges during the Heinrich events, *Earth Planet. Sci. Lett.*, *146*, 13–27, 1997.

Villanueva, J., J. O. Grimalt, E. Cortijo, L. Vidal, and L. Labeyrie, A biomarker approach to the organic matter deposited in the North Atlantic during the Last Climatic Cycle, *Geochim. Cosmochim. Acta*, *61*(21), 4633–4646, 1997a.

Villanueva, J., C. Pelejero, and J. O. Grimalt, Clean-up procedures for the unbiassed estimation of C_{37}-C_{39} alkenones sea surface temperatures and terrigenous n-alkane inputs in paleoceanography, *J. Chromatogr.*, *757*, 145–151, 1997b.

Villanueva, J., J. O. Grimalt, E. Cortijo, L. Vidal, and L. Labeyrie, Assessment of sea surface temperature variations in the central North Atlantic using the alkenone unsaturation index (Uk'37), *Geochim. Cosmochim. Acta*, *62*(14), 2421–2427, 1998a.

Villanueva, J., J. O. Grimalt, L. D. Labeyrie, E. Cortijo, L. Vidal, and J.-L. Turon, Precessional forcing of productivity in the North Atlantic Ocean, *Paleoceanography*, *13*(6), 561–571, 1998b.

Weeks, A. E. A., The physical and chemical environment and changes in community structure associated with bloom evolution: The Joint Global Flux Study North Atlantic Bloom Experiment, *Deep Sea Res., Part II*, *40*, 347–368, 1993.

A. Boelaert and L. Labeyrie, Laboratoire des Sciences du Climat et de l'Environnement, Domaine du CNRS, Av. De la Terrasse, 91191 Gif-sur-Ivette, Cedes, France.

E. Calvo, J. O. Grimalt, C. Pelejero, and J. Villanueva, Institute of Chemical and Environmental Research, Consejo Superior de Investigaciones Cientificas, Jordi Girona, 18, 08024 Barcelona, Catalonia, Spain. (jvrqam@cid.csic.es)

(Received May 19, 2000;
revised May 2, 2001;
accepted May 25, 2001.)