



## Elevated primary productivity of calcareous nannoplankton associated with ocean anoxic event 1b during the Aptian/Albian transition (Early Cretaceous)

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[1] Previous isotopic investigations of Aptian/Albian oceanic anoxic event (OAE) 1b from the western North Atlantic (Blake Nose) posited that increased sea surface temperatures and decreased salinity led to stratification of the upper water column, resulting in lowered dissolved oxygen and enhanced organic matter preservation. We examined calcareous nannofossils from the same site in the western North Atlantic (Blake Nose) to evaluate changes in surface water conditions prior to, during, and after the Aptian/Albian OAE1b. The results of our analysis conflict somewhat with the previous interpretation that OAE1b at Blake Nose was linked to water column stratification. The signal from calcareous nannofossils indicates that in the late Aptian, prior to OAE1b, oligotrophic conditions in the surface waters were replaced by mesotrophic conditions that persisted throughout the OAE event and into the early Albian. We speculate that increased surface water productivity facilitated to some degree the development of OAE1b at Blake Nose.

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### 1. Introduction

[2] Jurassic to Cretaceous marine sedimentary sequences are punctuated by several globally distributed lithologic and chronostratigraphic horizons which contain high amounts of organic carbon. These horizons are commonly called Ocean Anoxic Events, and they represent the enhanced preservation of organic matter throughout the world ocean [Schlanger and Jenkyns, 1976; Arthur *et al.*, 1990; Erbacher *et al.*, 1996; Leckie *et al.*, 2002]. The two most widespread events of the mid-Cretaceous are the early Aptian OAE1a (~120.5 Ma) and Cenomanian/Turonian boundary OAE2 (~93.5 Ma). The Aptian/Albian boundary OAE1b (~113–109 Ma) and the late Albian OAE1d (~99.5 Ma) were smaller events, typically with only regional occurrences.

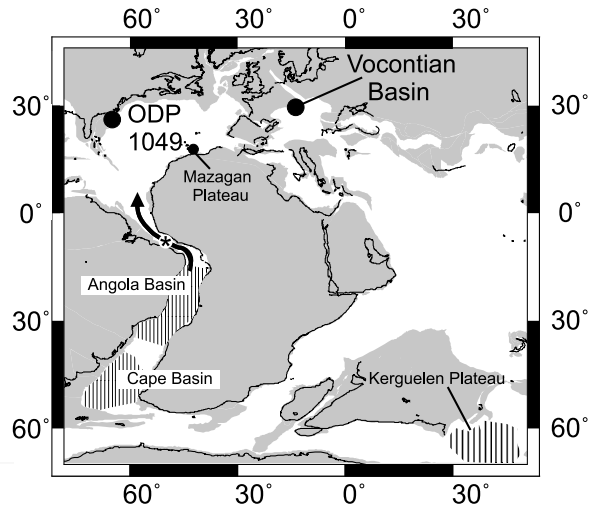
[3] Anoxic deep water and organic-rich sediments are found in several different environments today, and may provide an analog for these ancient events. As such there are two key hypotheses to account for the mid-Cretaceous OAEs: (1) an increase in primary productivity [Arthur *et al.*, 1987, 1990; Calvert and Pederson, 1992; Bralower *et al.*, 1994; Erba, 1994; Leckie *et al.*, 2002], and/or (2) the density driven stratification of the upper water column and enhanced preservation of organic matter [Bralower and Thierstein, 1984; Tribouillard and Gorin, 1991]. Evidence

from calcareous nannofossils, foraminifera, radiolarians, stable isotopes, organic matter composition, and trace metal concentrations suggests that surface water productivity was elevated during these mid-Cretaceous anoxic events: OAE1a [Erba, 1994; Erba, 2004; Kuypers *et al.*, 2004; Robinson *et al.*, 2004], OAE1b [Erbacher *et al.*, 1996; Leckie *et al.*, 2002], OAE1d [Watkins *et al.*, 2005], and OAE2 [Watkins, 1989; Leckie *et al.*, 2002; Erba, 2004; Kuypers *et al.*, 2004; Snow *et al.*, 2005]. Nevertheless, it has been difficult to assign productivity as the exclusive mechanism for anoxia in mid-Cretaceous OAEs because in some events inconsistent fertility, isotopic, and salinity signals are found in various localities [Leckie *et al.*, 2002; Bowman and Bralower, 2005].

[4] OAE1b has been attributed to density driven stratification of the upper water column as evidenced by a negative shift in planktonic foraminiferal oxygen isotope values at Blake Nose in the western North Atlantic (~1.5‰ [Erbacher *et al.*, 2001]), the Vocontian Basin in southeast France (~1.5‰ [Herrle *et al.*, 2004]), and Mazagan Plateau in the eastern North Atlantic (~1.2‰ [Herrle *et al.*, 2004]). The negative oxygen isotope shift and formation of OAE1b in the Vocontian Basin and Mazagan Plateau is explained by a monsoonally driven reduction in deep water formation and reduced deep water ventilation rates [Herrle *et al.*, 2004]. The negative oxygen isotope shift at Blake Nose is interpreted to reflect that a well mixed, well ventilated, upper water column characterized by high-salinity and low-temperature surface waters underwent both a moderate temperature increase and decrease in salinity leading to the initiation of OAE1b [Erbacher *et al.*, 2001]. The composition of the organic matter in OAE1b from Blake Nose [Kuypers *et al.*, 2001,

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**Figure 1.** Paleogeographic reconstruction for the late Aptian modified after *Erbacher et al.* [2001] showing the locations of ODP Hole 1049C on Blake Nose (western Tethys), the Vocontian Basin (eastern Tethys), and Mazagan Plateau. The arrow indicates a shallow to intermediate connection through the central Atlantic seaway (denoted by the star) based on studies from *Arthur and Natland* [1979] and *Moullade et al.* [1993].

2002], as well as the assemblage of benthic foraminifera [*Erbacher et al.*, 1999; *Holbourn and Kuhnt*, 2001] and carbon isotopic ratios of planktic foraminifera [*Erbacher et al.*, 1999], however, makes a case for elevated surface

water productivity, though to a lesser degree than in the other mid-Cretaceous OAEs.

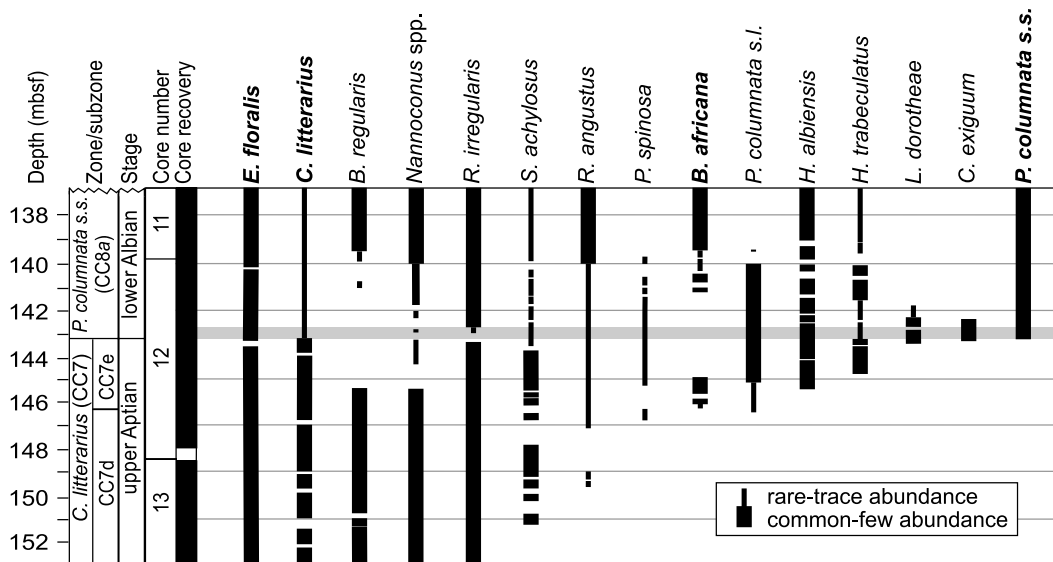
[5] The purpose of this study is to examine calcareous nannofossil assemblages deposited during Aptian/Albian boundary transition and OAE1b at Blake Nose (ODP Site 1049C) to evaluate evidence for density driven stratification or elevated primary productivity. We also compare the nannofossil fertility signal derived from OAE1b in an open ocean setting in western Tethys (e.g., this study, in the western North Atlantic) with a marginal setting in eastern Tethys [e.g., *Herrle*, 2002, 2003; *Herrle and Mutterlose*, 2003; *Herrle et al.*, 2003a, 2003b] (in the Vocontian Basin).

**2. Materials and Methods**

**2.1. Stratigraphic Framework**

[6] Ocean Drilling Program (ODP) Leg 171B to Blake Nose (Figure 1) recovered a shallowly buried Aptian-Albian sequence in Hole 1049C (30°8.5370'N, 76°06.7271'W; 2670.8 m present-day water depth). Benthic foraminiferal assemblages indicate that this interval of the Blake Nose accumulated at middle bathyal paleodepths (~800–1000 m) [*Norris et al.*, 1998]. During Aptian-Albian time, Site 1049 was situated in the tropical-subtropical western Tethys, just proximal to the eastern coast of the North American landmass and eastern margin of the Blake Plateau, a massive Jurassic-late Aptian rudist carbonate platform.

[7] The record recovered between core 11–2, 120–121 cm through core 13–3, 90 cm (137.15–152.79 m below seafloor (mbsf) spans the upper Aptian to lower Albian (Figure 2). The upper Aptian is characterized by dm-scale alternations between red clay and white nannofossil



**Figure 2.** Biostratigraphy of selected taxa from ODP Site 1049C. OAE1b black shale is illustrated by gray horizontal shading. Calcareous nannofossil biostratigraphy is based on the zonation scheme of *Perch-Nielsen* [1985] with additional information regarding placement of the Aptian/Albian boundary from *Kennedy et al.* [2000]. The taxa in bold are age diagnostic.

chalk that grades into 1.90-m-thick greenish-gray clay at 145.29 mbsf in the uppermost Aptian. The deposition of the greenish-gray clay at 145.29 mbsf coincides with the termination of the Blake Platform [Norris *et al.*, 1998] in the latest Aptian. The greenish-gray claystone unit is interrupted at 143.19 mbsf by a 46-cm-thick black shale composed of well-preserved nannofossils and clay. This black shale is correlative to OAE1b and was deposited over 46 ka based on an estimated sedimentation rate of 1 cm/ka [Erbacher *et al.*, 2001]. High total organic carbon content (2–12% [Kuypers *et al.*, 2002]), distinct mm-scale laminae, and lack of bioturbation indicate an anoxic environment during deposition of the black shale [Norris *et al.*, 1998]. The basal Albian interval, above the black shale, is composed of cm-scale alternations between white chalk, red claystone, and green claystone. The rhythmic alternations of red clay and white chalk resume 1.95 m above the black shale at 141.69 mbsf.

## 2.2. Sample Preparation and Analysis

[8] One hundred and eighty-four samples from ODP Hole 1049C were examined for calcareous nannofossils in order to determine biostratigraphic ranges and quantitative species abundances. Samples were examined at 10 cm intervals from core 11–2, 120–121 cm through core 13–3, 89–90 cm (137.15–152.79 mbsf). High-resolution samples were taken at 1 cm intervals from 10 cm above the black shale to 10 cm below the black shale (core 12–3, 38–39 cm to core 12–3, 99–100 cm; 142.68–143.29 mbsf) to facilitate detailed biostratigraphic and paleoceanographic examination of OAE1b.

[9] Smear slides were prepared using a double slurry method shown to yield reproducible data at the 99% confidence level [Watkins and Bergen, 2003]. The percent abundances of nannofossil species were estimated by counting 456 specimens (this number assures 95% confidence interval [Chang, 1967]) in each sample using a Zeiss Universal Photomicroscope at X1250 magnification. Twenty-six samples exhibited multiple indications of significant diagenetic alteration including, sediment displaying brittle deformation, moderate to strong dissolution or overgrowth of the coccoliths and elevated (>40%) abundances of the most dissolution-resistant species, *Watznaueria barnesiae* [Thierstein, 1980; Roth, 1981; Roth and Bowdler, 1981]. These samples were examined for biostratigraphy but were not used for paleoecological analysis.

[10] A separate set of 27 samples was prepared using a suspension settling device [Geisen *et al.*, 1999] to estimate the total number of coccoliths in a unit mass of sediment (termed the absolute abundance). Suspension settling methods provide an accurate estimate (at the 95% confidence level) of the absolute abundance of coccoliths that settled to the seafloor at the time of deposition [Williams and Bralower, 1995; Geisen *et al.*, 1999]. Variations in absolute abundance were used to estimate fluctuations in the total carbonate produced by nannoplankton.

## 2.3. Paleoecological Data Analysis

[11] Several statistical and numerical analyses of the species census counts were used to estimate paleoproductivity and changes in the structure of the nannofossil

community before, during, and after OAE1b. The stratigraphic distributions of major taxa were plotted and smoothed with a 10-sample moving average. Relationships between the abundances of major taxa, with emphasis on fertility-indicating taxa, were analyzed by Pearson correlation and principal components analysis. Stratigraphic changes in community structure were analyzed by computing species richness (S), Shannon diversity (H), and evenness (E) from the species census counts. Richness (S) is the number of different species in an assemblage (also called simple diversity) and indicates the niche space within a nannofossil community [Watkins, 1989]. Shannon diversity (H) is an unbiased measure of both richness and evenness [Pielou, 1969]. Evenness (E) measures the degree of dominance by individual species in a paleocommunity [Watkins, 1989].

## 3. Results

[12] A total of 83 taxa were identified. In general, preservation within chalk intervals is moderate while preservation within the gray marl and black shale is good. Calcareous nannofossil biostratigraphy from this study suggests continuous sedimentation within the upper Aptian section of the studied interval (Figure 2), although foraminiferal biostratigraphy indicates a hiatus below the black shale interval at 145.29 mbsf, the interval corresponding to a lithologic change to greenish-gray clay (B.T. Huber, personal communication, 2007). There is an unconformity to the Upper Cretaceous between cores 11–2, 120–121 cm, and 11–2, 110–111 cm (137.05–137.15 mbsf) [Norris *et al.*, 1998; this study].

[13] Data are archived at the World Data Center-A for Paleoclimatology <http://www.ncdc.noaa.gov/paleo/data.html>.

[14] Five of the 83 taxa identified have abundances of more than 10% in at least one sample. Moreover, the combined abundance of these major taxa often exceeds 40% of the sample. The two most abundant species, *Zeughrabdotos erectus* (includes all zeughrabdotosids < 5  $\mu\text{m}$ ) and *Biscutum ellipticum*, exhibit broadly similar abundance trends and display a positive correlation ( $r = 0.60$ ;  $p < 4.65 \times 10^{-17}$ ). These taxa are found in relatively low abundances below 145.29 mbsf and both increase in abundance above 145.29 mbsf, a stratigraphic horizon that corresponds to a greenish-gray clay located 2.1 m below the base of the OAE1b black shale (Figure 3). Above 145.29 mbsf, the interval corresponding to increases in these taxa, *Z. erectus* increases from an average of 17% to 28% and *B. ellipticum* increases from an average of 5% to 14%. The abundance of *Z. erectus* decreases to near preevent averages of 17% and the abundance of *B. ellipticum* decreases somewhat to an average of 12% in the basal Albian starting at 141.24 mbsf (a stratigraphic horizon that corresponds to a white chalk and 1.5 m above the top of the OAE1b black shale) and continuing to the unconformity to the Upper Cretaceous at 137.15 mbsf.

[15] The abundance of the third major species, *Watznaueria barnesiae*, varies from 9% to 39%, and within the 145.29–152.79 mbsf interval maintains an average abundance of 27% (Figure 3). The abundance of *W. barnesiae* declines at

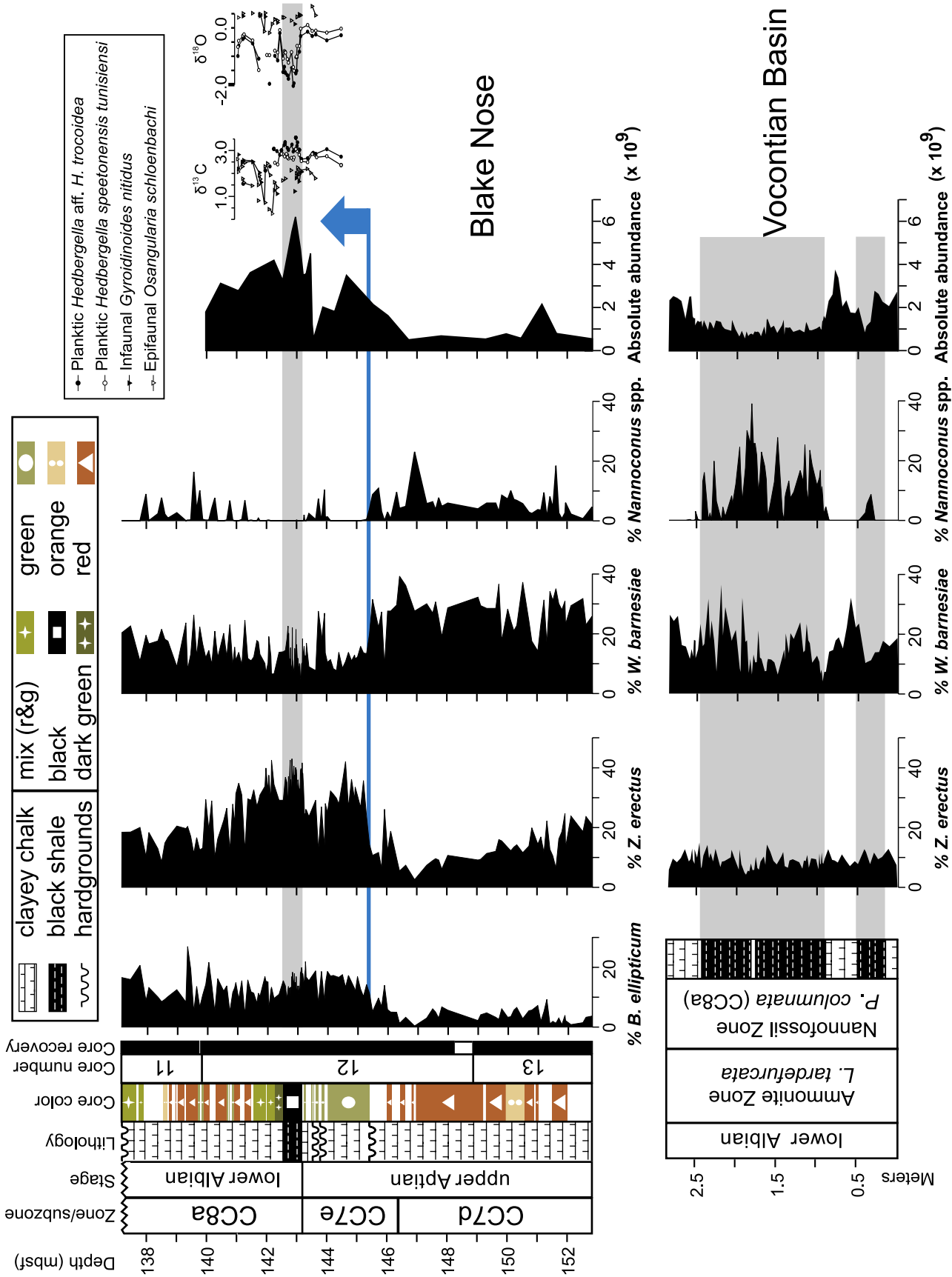
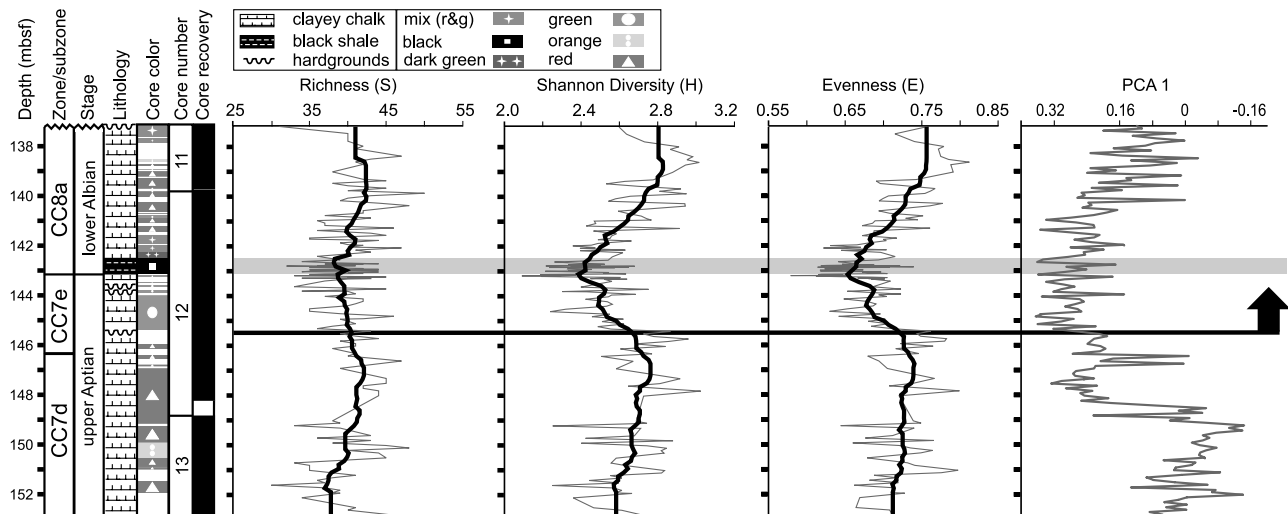


Figure 3



**Figure 4.** Values for richness (S), diversity (H), evenness (E), and PCA1 of calcareous nannofossils from the Aptian/Albian sequence in Hole 1049C. The level of OAE1b black shale is indicated by a dark gray horizontal bar. The horizontal black line and arrow indicates the interval (141.24–145.29 mbsf) of increased calcareous nannofossil fertility. Ten-member moving average for each index is shown by bold black lines.

145.29 mbsf and the average abundance for the overlying interval is 13.5%. *W. barnesiae* displays a negative correlation with *Z. erectus* ( $r = -0.78$ ;  $p < 7.03 \times 10^{-34}$ ) and *B. ellipticum* ( $r = -0.81$ ;  $p < 4.35 \times 10^{-39}$ ).

[16] *Nannoconus* spp. are common in lower portions of the section (145.29–152.79 mbsf) with an average abundance of 6.0%, with two abundance peaks that exceed 20%. Above 145.29 mbsf these taxa decline significantly in abundance and are rare in the remainder of the section (Figure 3). The abundance of *Nannoconus* spp. recovers partially at 141.24 mbsf, a stratigraphic horizon that corresponds to a white chalk and 1.5 m above the top of the OAE1b black shale. The average abundance of *Nannoconus* spp. above this interval (137.15–141.24 mbsf) is 3.0%. There is a positive correlation between *Nannoconus* spp. and *W. barnesiae* ( $r = 0.64$ ;  $p < 1.59 \times 10^{-19}$ ). *Nannoconus* spp. display a negative correlation to *Z. erectus* ( $r = -0.78$ ;  $p < 1.75 \times 10^{-28}$ ) and *B. ellipticum* ( $r = -0.63$ ;  $p < 4.81 \times 10^{-19}$ ).

[17] Species richness (S) varies from 30 to 50 species per sample. Shannon diversity (H) varies from 2.09 to 3.02 with a mean value of 2.58. Evenness (E) varies from 0.58 to 0.81 with an average of 0.70 (Figure 4). Species richness varies throughout the section but shows no clear trend. The 10-point moving average (Figure 4) indicates that richness was more variable below 145.29 mbsf than above, but the

significance of this change is difficult to assess. In general, species richness appears to have been relatively insensitive to the paleoceanographic changes associated with OAE1b. This insensitivity is similar to that observed with other Cretaceous OAEs [Watkins, 1989; Watkins et al., 2005]. Given the relative insensitivity of richness, the observed changes in Shannon diversity reflect variations in evenness. Evenness and diversity were highest in the interval prior to the onset of anoxic conditions and declined gradually from 148 to 150 mbsf to reach their minima corresponding precisely within the OAE (Figure 4). Following the OAE, evenness and diversity values increased to values comparable to the pre-OAE levels.

[18] Principle component analysis was performed using species that account for greater than 5% of the population in at least one sample. The first principle component (PCA1) explains approximately 69% of the variance in the assemblage. PCA1 has 4 important taxa as indicated by their high-component correlations and loadings. Two taxa have a strong positive correlation to PCA1: *Z. erectus* ( $r = 0.95$ ) and *B. ellipticum* ( $r = 0.79$ ) and two taxa have a strong negative correlation to PCA1: *W. barnesiae* ( $r = -0.93$ ) and *Nannoconus* spp. ( $r = -0.75$ ). PCA1 is negative in the interval 145.29–152.79 mbsf and positive in the interval 137.15–145.29 mbsf (Figure 4).

**Figure 3.** (top) Percent abundances of major calcareous nannofossil taxa (*B. ellipticum*, *Z. erectus*, *W. barnesiae*, and *Nannoconus* spp.) and absolute abundance of nannofossils from the Aptian/Albian sequence in Hole 1049C at Blake Nose. Oxygen and carbon isotope data are from Erbacher et al. [2001]. The level of OAE1b black shale is indicated by a gray horizontal bar. The horizontal blue line and blue arrow delineate the base of the interval (141.24–145.29 mbsf) of increased nannofossil fertility. (bottom) Percent abundances of nannofossil (*Z. erectus*, *W. barnesiae*, and *Nannoconus* spp.) and absolute abundance of nannofossils taxa from Herrle et al. [2003b] in the Aptian/lower Albian OAE1b in the Vocontian Basin. The level of OAE1b is indicated by a gray horizontal bar. Note the opposite trends in the abundance of calcareous nannofossils in the Vocontian Basin compared with Hole 1049C at Blake Nose.

[19] The absolute abundance of nannofossils has a mean value of approximately  $1.5 \times 10^9$  coccoliths per gram of sediment in the lower portion of the studied interval between 145.29 and 152.79 mbsf (Figure 3). At the top of the black shale, the absolute abundance increases to greater than  $6 \times 10^9$  coccoliths per gram of sediment, then gradually declines in the overlying section above the OAE.

## 4. Discussion

### 4.1. Surface Water Fertility

[20] During the Mesozoic, calcareous nanoplankton were an important part of the carbon cycle and likely the dominant primary producer [Falkowski et al., 2004]. Quantitative assessments of the nanoplankton communities can be used to estimate the level of fertility in ancient surface waters. Fertility reconstructions using nannofossils originate from the designation of calcareous nanoplankton as opportunist (“r-selected”) or specialist (“K-selected”) species, based on their presumed ecologic tolerances. Opportunist species show high environmental tolerance and dominate assemblages in high nutrient or harsh living conditions. Specialist species are intolerant of harsh environmental conditions and high-nutrient environments, and typify assemblages in oligotrophic environments [e.g., Hallock, 1987; Boersma et al., 1998].

[21] Observations of modern nannofossil assemblages have shown that small-sized (3–5  $\mu\text{m}$ ) placoliths, from coccolithophorids that inhabit the uppermost photic zone, dominate assemblages in high-nutrient conditions [e.g., Okada and Honjo, 1973, Takahashi and Okada, 2000]. *Zeugrhabdotus erectus* and *Biscutum ellipticum* are small-sized mid-Cretaceous nannofossil species which display characteristics of opportunist species. These taxa dominate nannofossil communities with low diversity and have been designated as high-fertility indicators based on their abundance in paleoupwelling areas [Roth and Bowdler, 1981; Roth and Krumbach, 1986; Erba, 1992] and in rocks with high organic carbon contents [Watkins, 1986, 1989; Premoli Silva et al., 1989; Erba et al., 1992]. Accordingly, the dominance of *Z. erectus* and *B. ellipticum* in nannofossil assemblages is considered indicative of mesotrophic to eutrophic surface waters [Roth, 1981, 1986, 1989; Roth and Bowdler, 1981, Roth and Krumbach, 1986; Premoli Silva et al., 1989]. The sharp increase in abundances of *Z. erectus* and *B. ellipticum* at Blake Nose approximately 2.1 m below the black shale interval (OAE1b) and continued dominance of these taxa upward into the lower Albian (141.24–145.29 mbsf; Figure 3) suggests that mesotrophic to eutrophic conditions became established in surface waters prior to the onset of OAE1b, peaked during deposition of the OAE1b black shale, and then persisted for some time after OAE1b. The decline in the abundance of *Z. erectus* and *B. ellipticum* in the lower Albian (141.24 mbsf) signifies a gradual return to oligotrophic conditions in the upper surface waters.

[22] *Watznaueria barnesiae* and *Nannoconus* spp. are common in diverse Cretaceous nannofossil assemblages that inhabited oligotrophic surface waters [Roth and Krumbach, 1986; Erba et al., 1992; Williams and Bralower, 1995].

*W. barnesiae* however was often the first nannofossil to appear in abundance during marine invasion of a continental basin [e.g., Watkins, 1986; Mutterlose, 1993] or foundering of an oceanic plateau [Watkins, 1992], and it survived across the Cretaceous-Tertiary boundary, suggesting it had a high tolerance for unstable environmental conditions [Bown, 2005]. Given these factors, it is likely that *W. barnesiae* was abundant in oligotrophic settings only because the abundances of fertility-sensitive species decreased.

[23] *Nannoconus* spp. were likely adapted to the dimly lit but nutrient rich conditions at the base of the photic zone (60–200 m); for further details on *Nannoconus* spp. morphology and adaptation, see Molfino and McIntyre [1990a, 1990b], Coccioni et al. [1992], and Erba [1994]. This adaptation has provided a method, based on changes in the abundance of *Nannoconus* spp., for reconstructing the relative position of the nutricline during the mid-Cretaceous [e.g., Erba, 1994]. Accordingly, a decrease in *Nannoconus* spp. indicates a shallow nutricline due to upwelling and high surface water fertility, and visa versa. The observed decrease in *Nannoconus* spp. to very rare abundances prior to and during the deposition of the OAE1b black shale (141.24–145.29 mbsf) is indicative of a shallow nutricline and elevated surface water fertility, as further suggested by the relative increased abundances of *Z. erectus* and *B. ellipticum* (Figure 3).

[24] Nanoplankton communities characterized by low S, H, and E values can result from the dominance by a few opportunist species in high-nutrient environments [Watkins, 1989]. On the contrary, high H and E values reflect a more equitable distribution of resources among a large number of specialist species in low nutrient environments [Watkins, 1989]. The gradual decline in diversity (H) and evenness (E) values beginning 2.1 m below OAE1b at Blake Nose (Figure 4) coincides with the increase of high-fertility taxa (Figure 3) and is indicative of a nanoplankton community adapted to an environment with elevated nutrient abundances. The shift to the lowest diversity values during OAE1b (Figure 4) signifies that at the peak of anoxia the community of surface dwelling phytoplankton was operating in unstable environmental conditions, likely associated with elevated nutrient availability.

[25] Three of the taxa with a strong correlation to PCA1 have well-documented paleoecologic affinities. As noted above, *Z. erectus* and *B. ellipticum* are abundant in mesotrophic-eutrophic conditions, and *Nannoconus* spp. are more common in oligotrophic conditions. The eigenvalue (approximately 69% of variance) of PCA1 indicates that most of the assemblage variance can be explained by this factor, which is interpreted as a measure of surface water fertility.

[26] The increase in absolute abundance of calcareous nannofossils approximately 2.1 m below the OAE interval coincides with the sharp increase of high-fertility taxa (Figure 3) and decrease in the nannofossil assemblage diversity (H) and evenness (E) (Figure 4). These trends suggest that the onset of nutrient rich surface waters prior to OAE1b cultivated an increase in the coccolithophorid biomass. *Z. erectus* and *B. ellipticum* are the dominant taxa within the interval of increased absolute abundance. These

tiny placoliths contain a relatively low amount of calcite, compared with large taxa such as *Nannoconus* spp., likely explaining why an increase in carbonate export production [e.g., Watkins, 1989] does not coincide with the increase in absolute abundance of carbonate.

[27] Other studies from Blake Nose support our finding of elevated surface water fertility prior to and during OAE1b. There is a slight increase in the vertical carbon isotopic gradient (e.g., 0.9% increase of  $\delta^{13}\text{C}$  values of planktic foraminifera) just below OAE1b at Blake Nose at ~143.40 mbsf (Figure 3). This slight increase occurs synchronous to the replacement of a diverse benthic foraminiferal assemblage with a low-diversity assemblage dominated by opportunistic phytodetritus feeders that were likely subsisting on elevated carbon flux to the seafloor and tolerating some degree of oxygen depletion [Erbacher et al., 1996; Holbourn and Kuhnt, 2001]. This increase in carbon isotopic values and change in the benthic foraminiferal assemblage structure implies that surface water productivity was elevated to some degree prior to the onset of anoxia [Erbacher et al., 1999, 2001; Holbourn and Kuhnt, 2001].

[28] A majority (approximately 80%) of the organic matter (OM) in OAE1b at Blake Nose is composed of chemoautotrophic nonthermophilic marine archaea (Crenarchaeota) [Kuypers et al., 2001, 2002]. Kuypers et al. [2001] speculate that compounds originating from the peak in ocean crust production at the Aptian-Albian boundary transition [Bralower et al., 1997] and/or the prolonged period of hydrothermal activity during the mid-Cretaceous may have been one mechanism able to sustain the large populations of marine archaea found in the OM of OAE1b at Blake Nose. However, this assertion is rather cautionary as the ecologic niche of archaea during the Mesozoic is still uncertain [Kuypers et al., 2001].

#### 4.2. Comparison With the Vocontian Basin

[29] Nannofossil fertility during OAE1b has been previously reconstructed for the Vocontian Basin [Herrle, 2002, 2003; Herrle and Mutterlose, 2003; Herrle et al., 2003a, 2003b]. There is evidence to suggest that surface water conditions were markedly different during OAE1b at Blake Nose and in the Vocontian Basin. The nannofossil assemblage in the Vocontian Basin is dominated by the oligotrophic taxon *Nannoconus* spp. below and within OAE1b, while the maximum abundance of the mesotrophic-eutrophic taxon *Z. erectus* is less than 14.8% within this interval (Figure 3) [from Herrle et al., 2003a, 2003b]. *Nannoconus* spp. are the most abundant nannofossil taxa within the OAE interval, with an average abundance of ~25% and peak abundances exceeding ~38%. The prevalence of *Nannoconus* spp. points to oligotrophic surface waters and a deep nutricline during OAE1b in the Vocontian Basin [Herrle et al., 2003a, 2003b].

[30] The absolute abundance of nannofossils in Vocontian Basin never exceeds  $4 \times 10^9$  specimens/gram in the upper Aptian-Albian interval, and the absolute abundance is highest in sediments below and above the OAE interval (Figure 3) [from Herrle et al., 2003b]. The lowest absolute

abundances occur within OAE1b and on average remain below  $1.5 \times 10^9$  specimens/gram within the OAE interval [Herrle et al., 2003b]. This is opposite of what is observed at Blake Nose (Figure 3), with peaks in absolute abundance exceeding  $6.0 \times 10^9$  within OAE1b, and the lowest average abundances (approximately  $1.5 \times 10^9$ ) occurring in the upper Aptian sediment, and corresponding to a nannofossil assemblage dominated by oligotrophic taxa.

[31] These contrasting nannofossil trends from OAE1b at Blake Nose and the OAE1b in the Vocontian Basin signify that paleoecologic conditions were vastly different in the open ocean region of western Tethys (Blake Nose) and in the restricted embayment of eastern Tethys (Vocontian Basin) prior to and during OAE1b. Moreover, the OM composition is quite different at each site. At the onset of OAE1b in the Vocontian Basin, there is a dramatic increase in the palynomorph: terrigenous marine ratio (TMR), showing a freshwater influence during formation of OAE1b at this location [Herrle et al., 2003b]. The composition of the OM in OAE1b Blake Nose has a marine archaeal lipid origin [Kuypers et al., 2001, 2002], a further indication of dissimilar surface water conditions during OAE1b at Blake Nose.

#### 4.3. Comparison to Other Mid-Cretaceous OAEs

[32] The absence of a large positive carbon isotope excursion in OAE1b, as has been observed in the large productivity events of OAE1a (>2‰) [Sliter, 1989; Bralower et al., 1994; Jones and Jenkyns, 2001] and OAE2 (>2‰) [Scholle and Arthur, 1980; Summerhayes, 1981, 1987; Pratt and Threlkeld, 1984; Arthur et al., 1987, 1990; Schlanger et al., 1987], makes it difficult to assert that productivity alone was responsible for the formation of OAE1b at Blake Nose. However, the sharp increase in the abundance of mesotrophic-eutrophic nannofossils and the parallel decline in nannofossil community evenness observed in OAE1b at Blake Nose are similar to those documented in mid-Cretaceous OAEs associated with elevated surface water fertility (Table 1, e.g.; OAE1a, OAE1d, and OAE2). An increase in the abundance of mesotrophic taxa *Z. erectus* approximately 40 ka prior to and during the early Aptian OAE1a at ODP Site 641 on the Galicia Margin in the Atlantic Ocean (Table 1) [from Tremolada et al., 2006] and decrease in the nannofossil diversity and approximately 40 ka prior to and during OAE1a at the Ontong Java and Manihiki Plateaus [Erba, 1994; Larson and Erba, 1999] suggest an increase in surface water fertility [Erba, 1994; Larson and Erba, 1999; Tremolada et al., 2006]. An increase in the abundance of mesotrophic taxa *Z. erectus* and *B. ellipticum* approximately 1 Ma before the onset of latest Albian OAE1d in Hole 1052E from the Blake Nose (Table 1) [from Watkins et al., 2005] and decline in nannofossil community evenness within the OAE interval suggest that the collapse of water column stratification associated with OAE1d [Norris and Wilson, 1998; Wilson and Norris, 2001] was preceded by increased surface water fertility and water column instability [Watkins et al., 2005]. Elevated abundances of *Z. erectus* and *B. ellipticum* during the Cenomanian-Turonian OAE2 from the Western Interior

**Table 1.** Calcareous Nannofossil Assemblage Data From Mid-Cretaceous OAE1a, OAE1b, OAE1d, and OAE2<sup>a</sup>

Ocean Anoxic Events	<i>Biscutum ellipticum</i> <sup>b</sup>	<i>Zeugrhabdotus erectus</i> <sup>b</sup>	<i>Nannoconus</i> spp. <sup>c</sup>	Organic Matter Composition
OAE2, C/T boundary	Average abundance (~14%) within the black shale (1). Peaks (>22%) within the black shale (1). Average abundance increases ~1 Ma before anoxia (from <10% to >15%) (3). Peaks (~23%) at top of the black shale (3).	Average abundance (~20%) within the black shale (1). Peaks (>28%) within the black shale (1). Average abundance increases slightly ~1 Ma before anoxia (3). Peaks (>20%) within the black shale (3).	N/A	marine cyanobacteria (2)
OAE1d, late Albian	Average abundance increases ~1 Ma before anoxia (from <10% to >15%) (3). Peaks (~23%) at top of the black shale (3).	Average abundance increases ~2.1 m below the black shale (from 5% to 14%) (4). Peaks (>20%) within the black shale (4).	Average abundance decreases ~1 Ma before anoxia (from ~10% to ~5%) (3). Disappearance at the top of the black shale (3).	N/A
OAE1b, Aptian/Albian boundary	Average abundance increases ~2.1 m below the black shale (from 5% to 14%) (4). Peaks (>20%) within the black shale (4).	Average abundance increases ~2.1 m below the black shale (from 17% to 28%) (4). Peaks (>40%) within the black shale (4).	Average abundance decreases ~2.1 m below the black shale (from 6% to <1%) (4). Disappearance within the black shale (4).	marine chemoautotrophic nonthermophilic archaea (5)
OAE1a, early Aptian	Average abundance (~30%) within the black shale (6). Peaks (>40%) ~10 m below the black shale (6).	Average abundance decreases ~0.4 Ma before anoxia (from 20 to 60% to <1%) (7). Disappearance within the black shale (7).	Average abundance decreases ~0.4 Ma before anoxia (from 20 to 60% to <1%) (7). Disappearance within the black shale (7).	marine cyanobacteria (2)

<sup>a</sup>N/A, not available. References 1, *Watkins* [1989]; 2, *Kuypers et al.* [2004]; 3, *Watkins et al.* [2005]; 4, this study; 5, *Kuypers et al.* [2001, 2002]; 6, *Tremolada et al.* [2006]; 7, *Erba* [1994].

<sup>b</sup>High fertility nannofossil taxon.

<sup>c</sup>Oligotrophic nannofossil taxon.

Seaway (Table 1) [from *Watkins*, 1989] and a decline in nannofossil assemblage diversity during OAE2 at the same site [*Watkins*, 1989] and in OAE2 from Eastbourne, England [*Jarvis et al.*, 1988; *Lamolda et al.*, 1994; *Paul et al.*, 1999; *Erba*, 2004] indicate mesotrophic surface water conditions and increased productivity at the time of anoxia.

[33] The decline in the abundance of the oligotrophic taxa *Nannoconus* spp. prior to and during OAE1b at Blake Nose resembles similar trends of this taxon observed in other mid-Cretaceous OAEs. *Nannoconus* spp. are abundant (20–60%) in the lower Aptian nannofossil assemblage below OAE1a at the Ontong Java and Manihiki Plateaus (Table 1) [from *Erba*, 1994]. The abundance of *Nannoconus* spp. declines markedly approximately 40 ka prior to OAE1a, decreases to near zero levels during the OAE, and then recovers only partially after OAE1a (Table 1) [from *Erba*, 1994]. Numerous studies have documented similar decreases in the abundance of *Nannoconus* spp. prior to OAE1a, and this is considered a worldwide event [*Erba*, 2004]. The disappearance of *Nannoconus* spp. prior to and during OAE1a has been attributed to a shallow nutricline position and high surface water fertility [*Erba*, 1994]. *Nannoconus* spp. are abundant (2–10%) in the upper Albian nannofossil assemblage below OAE1d from Blake Nose, but approximately 1 m below OAE1d declines gradually in abundance, and rapidly disappear at the top of the OAE interval (Table 1) [from *Watkins et al.*, 2005]. The decline in the abundance and disappearance of *Nannoconus* spp. has been attributed to the collapse of water column stratification and elevated surface water fertility associated with OAE1d [*Watkins et al.*, 2005]. During the Cenomanian-Turonian and OAE2 *Nannoconus* spp. were no longer common members of nannofossil assemblages.

#### 4.4. Mechanisms for OAE1b Formation

[34] The large negative  $\delta^{18}\text{O}$  shift within the OAE1b black shale in the Vocontian Basin (~1.5‰ [*Herrle et al.*, 2004]) and Mazagan Plateau (~1.2‰ [*Herrle et al.*, 2004]) is interpreted as a monsoon-driven reduction in deep water formation [*Herrle et al.*, 2004], which eventually lead to stratification of the upper water column and enhanced preservation of organic matter. Nannofossil and benthic foraminiferal assemblages from OAE1b at Blake Nose, however, advocate for major biotic changes and ecologic disturbances throughout the entire water column at the time of anoxia; therefore reduced deep water ventilation may have only been a partial factor controlling formation of OAE1b at Blake Nose. Undoubtedly the near opposite nannofossil fertility reconstruction from Blake Nose (mesotrophic-eutrophic association) and in the Vocontian Basin (oligotrophic association) elucidate that surface water conditions at these sites were different leading up to and during the inception of OAE1b.

[35] The negative  $\delta^{18}\text{O}$  shift during OAE1b at Blake Nose (~1.5‰; Figure 2) has been attributed to a moderate warming and freshening of the upper water column that cultivated “super sapropel” conditions across western Tethys analogous to the Quaternary sapropels of the Mediterranean [*Emeis*, 1998, *Erbacher et al.*, 2001]. Given the close proximity of Blake Nose to the North American



landmass during the Aptian-Albian it is plausible that there could have been a significant freshwater influence to this area of Tethys during the mid-Cretaceous and during OAE1b. But the question remains whether the magnitude of this freshening was large enough to form a super sapropel across the entire western Tethys [Herrle *et al.*, 2003b].

[36] Since changes in the nannofossil assemblage prior to and during OAE1b at Blake Nose closely resembles those found in mid-Cretaceous OAEs associated with elevated surface water fertility (Table 1, e.g., OAE1a, OAE1d, and OAE2) we propose that this event too was associated with an increase in productivity. An enhanced hydrologic cycle and weathering of the North America landmass may have provided a nutrient source to Blake Nose, but the marine composition of the OM implies that perhaps another mechanism accounts for OAE1b at Blake Nose. The nutrient source necessary to fuel the increased productivity in the mid-Cretaceous OAEs is widely debated, but the “iron fertility hypothesis” has been suggested as a triggering mechanism for OAE1a, OAE1b, and OAE2 [Sinton and Duncan, 1997; Leckie *et al.*, 1998; Larson and Erba, 1999; Leckie *et al.*, 2002; Snow *et al.*, 2005]. Increased productivity across vast areas of the world ocean during OAE1a and OAE2 may have been facilitated from hydrothermal micronutrients (namely iron) originating from the emplacement of Ontong-Java (and Manihiki) (~125–118 Ma and ~96–84 Ma [Larson, 1991a, 1991b; Larson and Kincaid, 1996; Bralower *et al.*, 1997; Jones and Jenkyns, 2001]) and Caribbean Plateaus (~96–87 Ma [Ingram *et al.*, 1994; Bralower *et al.*, 1997; Jones and Jenkyns, 2001]).

[37] The Aptian/Albian boundary OAE1b occurs at the height of oceanic crust production during the mid-Cretaceous (e.g., Sr record of Bralower *et al.* [1997] and Jones and Jenkyns [2001]) and synchronous to the emplacement of the Kerguelen Plateau (~116–110 Ma [Whitechurch *et al.*, 1992; Coffin and Eldholm, 1994; Frey *et al.*, 1999]). It is possible that micronutrients originating from the emplacement of the Kerguelen Plateau stimulated an increased productivity prior to and during OAE1b at Blake Nose [Leckie *et al.*, 2002; this study]. Hardgrounds in Aptian-Albian sediment in sites located across southern alpine Tethys [Weissert and Lini, 1991], the North Atlantic [Arthur and Natland, 1979], at Blake Nose [Norris *et al.*, 1998], and along the Mazagan Plateau margin [Leckie, 1984] signify a reorganization of Tethyan shallow to intermediate circulation during the Aptian-Albian, suggesting that the breach of the Central Atlantic seaway may have provided a shallow conduit to the proto-North Atlantic (Figure 1, for a detailed discussion on the paleoceanographic consequences of the mid-Cretaceous central Atlantic seaway breach, see Arthur and Natland [1979]) through which nutrients that had built up in the Cape and Angola Basins during emplacement of

the Kerguelen Plateau could have been delivered to Blake Nose prior to the onset of OAE1b.

## 5. Conclusions

[38] Prior to this study it was suggested that Aptian/Albian boundary OAE1b at Blake Nose resulted from a moderate warming and freshening of the upper water column that culminated in super sapropel conditions throughout western Tethys [Erbacher *et al.*, 2001]. The calcareous nannofossil evidence from OAE1b (Blake Nose) however indicates that elevated primary productivity was associated with enhanced organic carbon burial and that increased productivity began well before the OAE1b black shale. Four lines of evidence suggest that the nannoplankton community was living under mesotrophic to eutrophic conditions prior to and during the onset of anoxia in OAE1b: (1) Below OAE1b there is a sharp increase in the abundance of nannofossil species that flourish in high-nutrient conditions, which intensifies within OAE1b, and continues above OAE1b into the early Albian; (2) nannofossil assemblage diversity declined prior to OAE1b and, at the onset of the event, diversity values showed a considerable drop in diversity; (3) a marked decrease in the abundance of the oligotrophic taxon *Nannoconus* spp. prior to OAE1b indicates a shallow nutricline and elevated surface water fertility; and (4) the absolute abundance of calcareous nannofossils, a measure of the nannofossil biomass, increased gradually prior to the onset of OAE1b and reached high levels within the OAE interval.

[39] Previous reconstructions of nannoplankton paleoproductivity in OAE1b were derived from plankton assemblages located in the Vocontian Basin, a marginal basin of eastern Tethys, where the initiation of OAE1b resulted from monsoonally driven reduction bottom water ventilation. This study maintains that the phytoplankton signal from Vocontian Basin represents local paleoceanographic conditions in eastern Tethys, and does not traverse to the open ocean site at Blake Nose in western Tethys, where elevated nannofossil productivity was associated with OAE1b.

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## References

- Arthur, M. A., and J. H. Natland (1979), Carbonaceous sediments in the North and South Atlantic: The role of salinity in stable stratification of Early Cretaceous basins, in *Deep Drilling Results in the Atlantic Ocean: Continental Margins and Paleoenvironment*, Maurice Ewing Ser., vol. 3, edited by M. Talwani, pp. 375–401, AGU, Washington, D.C.
- Arthur, M. A., S. O. Schlanger, and H. C. Jenkyns (1987), The Cenomanian-Turonian oceanic anoxic event II, Paleocceanographic controls on organic matter production and preservation, in *Marine Petroleum Source Rocks*, edited by J. Brooks and A. Fleet, *Geol. Soc. Spec. Publ.*, 26, 399–418.
- Arthur, M. A., H. J. Brumstack, H. C. Jenkyns, and S. O. Schlanger (1990), Stratigraphy, geochemistry, and paleoceanography of organic carbon-

- rich Cretaceous sequences, in *Cretaceous Resources, Events, and Rhythms*, edited by R. N. Ginsburg and B. Beaudoin, pp. 75–119, Kluwer Acad., Norwell, Mass.
- Boersma, A., I. Premoli Silva, and P. Hallock (1998), Trophic models for well-mixed and poorly mixed warm oceans across the Paleocene/Eocene epoch boundary, in *Late Paleocene-Early Eocene Climatic and Biotic Events in Marine and Terrestrial Records*, edited by M. P. Aubry, S. G. Lucas, and W. A. Berggren, pp. 204–213, Columbia Univ. Press, New York.
- Bowman, A. R., and T. J. Bralower (2005), Paleocceanographic significance of high resolution carbon isotope records across the Cenomanian-Turonian boundary in the Western Interior and New Jersey coastal plain, USA, *Mar. Geol.*, *217*, 305–321, doi:10.1016/j.margeo.2005.02.010.
- Bown, P. (2005), Selective calcareous nannoplankton survivorship at the Cretaceous-Tertiary boundary, *Geology*, *33*, 653–656, doi:10.1130/G21566.1.
- Bralower, T. J., and H. R. Thierstein (1984), Low productivity and slow deep-water circulation in mid-Cretaceous oceans, *Geology*, *12*, 614–618, doi:10.1130/0091-7613 [1984]12<614:LPASDC>2.0.CO;2.
- Bralower, T. J., M. A. Arthur, R. M. Leckie, W. V. Slitter, D. Allard, and S. O. Schlanger (1994), Timing and paleoceanography of oceanic dysoxia/anoxia in the late Barremian and early Aptian, *Palaiois*, *9*, 335–369, doi:10.2307/3515055.
- Bralower, T. J., P. D. Fullagar, C. K. Paull, G. S. Dwyer, and R. M. Leckie (1997), Mid-Cretaceous strontium-isotope stratigraphy of deep-sea sections, *Geol. Soc. Am. Bull.*, *109*, 1421–1442, doi:10.1130/0016-7606 [1997]109<1421:MCSISO>2.3.CO;2.
- Calvert, S. E., and T. F. Pederson (1992), Organic carbon accumulation and preservation in marine sediments: How important is anoxia? in *Organic Matter: Productivity, Accumulation, and Preservation in Recent and Ancient Sediments*, edited by J. K. Whelan and J. W. Farrington, pp. 231–263, Columbia Univ. Press, New York.
- Chang, Y. M. (1967), Accuracy of fossil percentage estimation, *J. Paleontol.*, *41*, 500–502.
- Coccioni, R., E. Erba, and I. Premoli Silva (1992), Barremian-Aptian calcareous plankton biostratigraphy from the Gorgo Cerbara section (Marche, central Italy) and implications for plankton evolution, *Cretaceous Res.*, *13*, 517–537, doi:10.1016/0195-6671(92)90015-1.
- Coffin, M. F., and O. Eldholm (1994), Large igneous provinces: Crustal structure, dimensions, and external consequences, *Rev. Geophys.*, *32*, 1–36, doi:10.1029/93RG02508.
- Emeis, K. C. (1998), Stable isotope and alkenone temperature records of sapropels from sites 964 and 967: Constraining the physical environment of sapropel formation in the eastern Mediterranean Sea, *Proc. Ocean Drill. Program Sci. Results*, *160*, 309–331.
- Erba, E. (1992), Mid-Cretaceous calcareous nannofossils from the western tropical Pacific (ODP Leg 129): Evidence for paleoequatorial crossings, *Proc. Ocean Drill. Program Sci. Results*, *129*, 189–201.
- Erba, E. (1994), Nannofossils and superplumes: The early Aptian “nannocoid crisis”, *Paleoceanography*, *9*(3), 483–501.
- Erba, E. (2004), Calcareous nannofossils and Mesozoic oceanic anoxic events, *Mar. Micropaleontol.*, *52*, 85–106, doi:10.1016/j.marmicro.2004.04.007.
- Erba, E., D. Castradori, G. Guasti, and M. Rippepe (1992), Calcareous nannofossils and Milankovitch cycles: The example of the Albian Gault Clay Formation (southern England), *Palaeoogeogr. Palaoclimatol. Palaeoecol.*, *93*, 47–69, doi:10.1016/0031-0182(92)90183-6.
- Erbacher, J. O., J. Thurov, and R. Littke (1996), Evolution patterns of radiolarian and organic matter variations: A new approach to identifying sea-level changes in mid-Cretaceous pelagic environments, *Geology*, *24*, 499–502, doi:10.1130/0091-7613 [1996]024<0499:EPORAO>2.3.CO;2.
- Erbacher, J., C. Hemleben, B. T. Huber, and M. Markey (1999), Correlating environmental changes during early Albian oceanic anoxic event 1B using benthic foraminiferal paleoecology, *Mar. Micropaleontol.*, *38*, 7–28, doi:10.1016/S0377-8398(99)00036-5.
- Erbacher, J. O., B. T. Huber, R. D. Norris, and M. Markey (2001), Increased thermohaline stratification as a possible cause for an ocean anoxic event in the Cretaceous Period, *Nature*, *409*, 325–327, doi:10.1038/35053041.
- Falkowski, P. G., M. E. Paul, A. H. Katz, A. Knoll, J. A. Quigg, J. A. Raven, O. Schofield, and F. J. R. Taylor (2004), The evolution of modern eukaryotic phytoplankton, *Science*, *305*, 354–360, doi:10.1126/science.1095964.
- Frey, F. A., M. F. Coffin, and P. J. Wallace (1999), Origin and evolution of a submarine large igneous province: The Kerguelen Plateau and Broken Ridge, southern Indian Ocean, *Eos Trans. AGU*, *80*(46), Fall Meet. Suppl., 1103.
- Geisen, M. A., J. Bollman, J. Herrle, J. Mutterlose, and J. R. Young (1999), Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton, *Micropaleontology*, *45*, 437–442, doi:10.2307/1486125.
- Hallock, P. (1987), Fluctuations in the trophic resource continuum: A factor in global diversity cycles?, *Paleoceanography*, *2*, 457–471, doi:10.1029/PA002i005p0457.
- Herrle, J. O. (2002), Paleocceanographic and paleoclimatic implications on mid-Cretaceous black shale formation in the Vocontian Basin and the Atlantic: Evidence from calcareous nannofossils and stable isotopes, *Tub. Mikropalaontol. Mitteil.*, *27*, 1–114.
- Herrle, J. O. (2003), Reconstructing nutricline dynamics of mid-Cretaceous oceans: evidence from calcareous nannofossils from the Niveau Paquier black shale (SE France), *Mar. Micropaleontol.*, *47*, 307–321, doi:10.1016/S0377-8398(02)00133-0.
- Herrle, J. O., and J. Mutterlose (2003), Calcareous nannofossils from the Aptian and lower Albian of southeast France: Paleocceanological and biostratigraphic implications, *Cretaceous Res.*, *24*, 1–22, doi:10.1016/S0195-6671(03)00023-5.
- Herrle, J. O., J. Pross, O. Friedrich, P. Koessler, and C. Hemleben (2003a), Forcing mechanisms for mid-Cretaceous black shale formation: evidence from the upper Aptian and lower Albian of the Vocontian Basin (SE France), *Palaeoogeogr. Palaoclimatol. Palaeoecol.*, *190*, 399–426, doi:10.1016/S0031-0182(02)00616-8.
- Herrle, J. O., J. Pross, O. Friedrich, and C. Hemleben (2003b), Short-term environmental changes in the Cretaceous Tethyan ocean: Micropaleontological evidence from the early Albian ocean anoxic event 1b, *Terra Nova*, *15*, 14–19, doi:10.1046/j.1365-3121.2003.00448.x.
- Herrle, J. O., P. Köbber, O. Friedrich, H. Erlenkeuser, and C. Hemleben (2004), High resolution carbon isotope records of the Aptian to lower Albian from SE France and the Mazagan Plateau (DSDP Site 545): A stratigraphic tool for paleoceanographic and paleobiologic reconstruction, *Earth Planet. Sci. Lett.*, *218*, 149–161, doi:10.1016/S0012-821X(03)00646-0.
- Holbourn, A., and W. Kuhnt (2001), No extinctions during ocean anoxic event 1b: The Aptian-Albian benthic foraminiferal record of ODP Leg 171, in *Western North Atlantic Paleogene and Cretaceous Paleocceanography*, edited by D. Kroon, R. D. Norris, and A. Klaus, *Geol. Soc. Spec. Publ.*, *183*, 73–92.
- Ingram, B. L., A. Montanari, and F. M. Richter (1994), Strontium isotopic composition of Mid-Cretaceous seawater, *Science*, *264*, 546–550, doi:10.1126/science.264.5158.546.
- Jarvis, I., G. A. Carlson, M. K. E. Cooper, M. B. Hart, P. N. Leary, B. A. Tocher, D. Horne, and A. Rosenfield (1988), Microfossil assemblages and the Cenomanian-Turonian (Late Cretaceous) oceanic anoxic event, *Cretaceous Res.*, *9*, 3–103, doi:10.1016/0195-6671(88)90003-1.
- Jones, C. E., and H. C. Jenkyns (2001), Seawater strontium isotopes, oceanic anoxic events, and seafloor hydrothermal activity in the Jurassic and Cretaceous, *Am. J. Sci.*, *301*, 112–149, doi:10.2475/ajs.301.2.112.
- Kennedy, W. J., A. S. Gale, P. R. Bown, M. Caron, R. J. Davey, and D. S. Wray (2000), Integrated stratigraphy across the Aptian-Albian boundary in the Marnes Blues, at the Col de Pre-Guittard, Arayon (Drome), and at Tartonne (Alpes-de-Haute-Provence), France: A candidate global boundary stratotype section and boundary point for the base of the Albian stage, *Cretaceous Res.*, *21*, 591–720, doi:10.1006/cres.2000.0223.
- Kuypers, M. M., P. Blokker, J. Erbacher, H. Kinkel, R. D. Pancost, S. Schouten, and J. S. Sinninghe Damste (2001), Massive expansion of marine Archaea during a mid-Cretaceous oceanic anoxic event, *Science*, *293*, 92–94, doi:10.1126/science.1058424.
- Kuypers, M. M., P. Blokker, E. C. Hopmans, H. Kinkel, R. D. Pancost, S. Schouten, and J. S. Sinninghe Damste (2002), Archaeal remains dominate marine organic matter from the early Albian oceanic anoxic event 1b, *Palaeoogeogr. Palaoclimatol. Palaeoecol.*, *185*, 211–234, doi:10.1016/S0031-0182(02)00301-2.
- Kuypers, M. M., Y. van Breugel, S. Schouten, E. Erba, and J. S. Sinninghe Damste (2004), N<sub>2</sub>-fixing cyanobacteria supplied nutrient N for Cretaceous oceanic anoxic events, *Geology*, *32*, 853–856, doi:10.1130/G20458.1.
- Lamolda, M. A., A. Gorostidi, and C. R. C. Paul (1994), Quantitative estimates of calcareous nannofossil changes across the Plenus Marls (latest Cenomanian), Dover, England: Implications for the generation of the Cenomanian-Turonian boundary event, *Cretaceous Res.*, *14*, 143–164.
- Larson, R. L. (1991a), Latest pulse of Earth: Evidence for a Mid-Cretaceous super plume, *Geology*, *19*, 547–550, doi:10.1130/0091-7613[1991]019<0547:LPOEEF>2.3.CO;2.
- Larson, R. L. (1991b), Geological consequences of superplumes, *Geology*, *19*, 963–966, doi:10.1130/0091-7613 [1991]019<0963:GCOS>2.3.CO;2.
- Larson, R. L., and E. Erba (1999), Onset of the Mid-Cretaceous greenhouse in the Barremian-Aptian: Igneous events and the biological, sedimentary, and geochemical responses, *Paleoceanography*, *14*, 663–678, doi:10.1029/1999PA900040.

- Larson, R. L., and C. Kincaid (1996), Onset of Mid-Cretaceous volcanism by elevation of the 670 km thermal boundary layer, *Geology*, *24*, 551–554, doi:10.1130/0091-7613[1996]024<0551:OOCVVB>2.3.CO;2.
- Leckie, R. M. (1984), Mid-Cretaceous planktonic foraminiferal biostratigraphy off central Morocco, Deep Sea Drilling Project Leg 79, sites 545 and 547, *Initial Rep. Deep Sea Drill. Proj.*, *79*, 579–620.
- Leckie, R. M., R. F. Yuretich, O. L. O. West, D. Finkelstein, and M. Schmidt (1998), Paleocyanography of the southwestern Western Interior Sea during the time of the Cenomanian-Turonian boundary (Late Cretaceous), in *Stratigraphy and Paleoenvironments of the Cretaceous Western Interior Seaway, USA, SEPM Concepts Sedimentol. Paleontol.*, vol. 6, edited by W. E. Dean and M. A. Arthur, pp. 101–126, Soc. for Sediment. Geol., Tulsa, Okla.
- Leckie, R. M., T. J. Bralower, and R. Cashman (2002), Oceanic anoxic events and plankton evolution: Biotic response to tectonic forcing during the mid-Cretaceous, *Paleoceanography*, *17*(3), 1041, doi:10.1029/2001PA000623.
- Molfini, B. R., and A. McIntyre (1990a), Precessional forcing of nutrient dynamics in the equatorial Atlantic, *Science*, *249*, 766–769, doi:10.1126/science.249.4970.766.
- Molfini, B. R., and A. McIntyre (1990b), Nutrient variation in the equatorial Atlantic in the equatorial coincident with the Younger Dryas, *Paleoceanography*, *5*, 997–1008, doi:10.1029/PA005i006p00997.
- Moullade, M., J. Mascle, J. Benkhelil, M. Cousin, and P. Tricart (1993), Occurrence of marine mid-Cretaceous sediments along the Guinean slope (Equamarge II cruise): Their significance for the evolution of the central Atlantic African margin, *Mar. Geol.*, *110*, 63–72, doi:10.1016/0025-3227(93)90105-5.
- Mutterlose, J. (1993), Late Valanginian calcareous nannofossils from central Europe and their biogeographic significance, *Zitteliana*, *20*, 15–24.
- Norris, R. D., and P. A. Wilson (1998), Low-latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktic foraminifera, *Geology*, *26*, 823–826, doi:10.1130/0091-7613[1998]026<0823:LLSSTF>2.3.CO;2.
- Norris, R. D., D. Kroon, and A. Klaus (1998), *Proceedings of the Ocean Drilling Program Initial Results*, vol. 171B, Ocean Drill. Program, College Station, Tex.
- Okada, H., and S. Honjo (1973), The distribution of oceanic coccolithophorids in the Pacific Ocean, *Deep Sea Res.*, *20*, 355–374.
- Paul, C. R. C., M. A. Lamolda, S. F. Mitchell, M. R. Vaziri, A. Gorostidi, and J. D. Marshall (1999), The Cenomanian-Turonian boundary at Eastbourne (Sussex, UK): A proposed European reference section, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *150*, 83–121, doi:10.1016/S0031-0182(99)00009-7.
- Perch-Nielsen, K. (1985), Mesozoic calcareous nannofossils, in *Plankton Stratigraphy*, edited by H. M. Bolli, J. B. Saunders, and K. Perch-Nielsen, pp. 329–426, Cambridge Univ. Press, Cambridge, U.K.
- Pielou, E. C. (1969), *An Introduction to Mathematical Ecology*, 286 pp., John Wiley, New York.
- Pratt, L. M., and C. N. Threlkeld (1984), Stratigraphic significance of (super 13) C/(super 12) C ratios in Mid-Cretaceous rocks on the Western Interior, U.S.A., in *The Mesozoic of middle North America*, 9, edited by D. F. Stott and D. J. Glass, pp. 305–312, Can. Soc. of Pet. Geol., Calgary, Alberta.
- Premoli Silva, I., E. Erba, and M. E. Tornaghi (1989), Paleoenvironmental signals and changes in surface fertility in Mid Cretaceous corg-rich pelagic facies of the Fucooid Marls (central Italy), *Geobios*, *22*, 225–236, doi:10.1016/S0016-6995(89)80059-2.
- Robinson, S. A., T. Williams, and P. R. Bown (2004), Fluctuations in biosiliceous production and the generation of Early Cretaceous oceanic anoxic events in the Pacific Ocean (Shatsky Rise, Ocean Drilling Program Leg 198), *Paleoceanography*, *19*, PA4024, doi:10.1029/2004PA001010.
- Roth, P. H. (1981), Mid-Cretaceous calcareous nannoplankton from the central Pacific: Implications for paleoceanography, *Initial Rep. Deep Sea Drill. Proj.*, *62*, 471–489.
- Roth, P. H. (1986), Mesozoic paleoceanography of the North Atlantic Tethys oceans, in *North Atlantic Paleocyanography*, edited by C. P. Summerhayes and N. J. Shackelton, *Geol. Soc. Spec. Publ.*, *21*, 299–320.
- Roth, P. H. (1989), Ocean circulation and calcareous nannoplankton evolution during the Jurassic and Cretaceous, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *74*, 111–126, doi:10.1016/0031-0182(89)90022-9.
- Roth, P. H., and J. L. Bowdler (1981), Middle-Cretaceous calcareous nannoplankton biostratigraphy and oceanography of the Atlantic Ocean, *Spec. Publ. Soc. Econ. Paleontol. Mineral.*, *32*, 517–546.
- Roth, P. H., and K. R. Krumbach (1986), Middle-Cretaceous calcareous nannofossil biogeography and preservation in the Atlantic and Indian oceans: Implications for paleoceanography, *Mar. Micropaleontol.*, *10*, 235–266, doi:10.1016/0377-8398(86)90031-9.
- Schlanger, S. O., and H. C. Jenkyns (1976), Cretaceous oceanic anoxic events: Causes and consequences, *Geol. Mijnbouw*, *55*, 179–184.
- Schlanger, S. O., M. A. Arthur, H. C. Jenkyns, and P. A. Scholle (1987), The Cenomanian-Turonian oceanic anoxic event; I, Stratigraphy and distribution of organic carbon-rich beds and the marine delta <sup>13</sup>C excursion, in *Marine Petroleum Source Rocks*, edited by J. Brooks and A. J. Fleet, *Geol. Soc. Spec. Publ.*, *26*, 371–399.
- Scholle, P. A., and M. A. Arthur (1980), Carbon isotope fluctuations in Cretaceous pelagic limestones: Potential stratigraphic and petroleum exploration tool, *AAPG Bull.*, *64*, 67–87.
- Sinton, C. W., and R. A. Duncan (1997), Potential links between ocean plateau volcanism and global ocean anoxia at the Cenomanian-Turonian boundary, *Econ. Geol.*, *93*, 836–842.
- Sliter, W. V. (1989), Biostratigraphic zonation for Cretaceous planktonic foraminifers examined in thin section, *J. Foraminiferal Res.*, *19*, 1–19.
- Snow, L. J., R. A. Duncan, and T. J. Bralower (2005), Trace element abundances in the Rock Canyon Anticline, Pueblo, Colorado, marine sedimentary section and their relationship to Caribbean plateau construction and oxygen anoxic event 2, *Paleoceanography*, *20*, PA3005, doi:10.1029/2004PA001093.
- Summerhayes, C. P. (1981), Organic facies of mid-Cretaceous black shales in the deep North Atlantic, *AAPG Bull.*, *65*, 2364–2380, doi:10.1306/2F91A345-16CE-11D7-8645000102C1865D.
- Summerhayes, C. P. (1987), Organic-rich Cretaceous sediments from the North Atlantic, in *Marine Petroleum Source Rocks*, edited by J. Brooks and A. J. Fleet, *Geol. Soc. Spec. Publ.*, *26*, 301–316.
- Takahashi, K., and H. Okada (2000), The paleoceanography for the last 30,000 years in the southeastern Indian Ocean by means of calcareous nannofossils, *Mar. Micropaleontol.*, *40*, 83–103, doi:10.1016/S0377-8398(00)00033-5.
- Thierstein, H. R. (1980), Selective dissolution of late Cretaceous and earliest Tertiary calcareous nannofossils; experimental evidence, *Cretaceous Res.*, *1*, 165–176, doi:10.1016/0195-6671(80)90023-3.
- Tremolada, F., E. Erba, and T. J. Bralower (2006), Late Barremian to Early Aptian calcareous nannofossil paleoceanography and paleoecology from the Ocean Drilling Program Hole 641C (Galicia Margin), *Cretaceous Res.*, *27*, 887–897.
- Tribovillard, N. P., and G. E. Gorin (1991), Organic facies of the early Albian Niveau Paquier, a key black shales horizon of the Marnes Bleues Formation in the Vocontian Basin (Subalpine Ranges, SE France), *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *85*, 227–237, doi:10.1016/0031-0182(91)90162-K.
- Watkins, D. K. (1986), Calcareous nannofossil paleoceanography of the Cretaceous Greenhorn Sea, *Geol. Soc. Am. Bull.*, *97*, 1239–1249, doi:10.1130/0016-7606[1986]97<1239:CNPOTC>2.0.CO;2.
- Watkins, D. K. (1989), Nannoplankton productivity fluctuations and rhythmically-bedded pelagic carbonates of the Greenhorn Limestone (Upper Cretaceous), *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *74*, 75–86, doi:10.1016/0031-0182(89)90020-5.
- Watkins, D. K. (1992), Upper Cretaceous nannofossils from ODP Leg 120, Kerguelen Plateau, Southern Ocean, *Ocean Drill. Proj. Initial Rep.*, *120*, 343–370.
- Watkins, D. K., and J. A. Bergen (2003), Late Albian adaptive radiation in the calcareous nannofossil genus *Eiffellithus*, *Micropaleontology*, *49*, 231–252.
- Watkins, D. K., M. J. Cooper, and P. A. Wilson (2005), Calcareous nannoplankton response to late Albian ocean anoxic event in the western North Atlantic, *Paleoceanography*, *20*, PA2010, doi:10.1029/2004PA001097.
- Weissert, H., and A. Lini (1991), Ice Age interglades during the time of Cretaceous greenhouse climate?, in *Controversies in Modern Geology: Evolution of Geological Theories Sedimentology, Earth History, and Tectonics*, edited by D. W. Muller, J. A. McKenzie, and H. Weissert, pp. 173–191, Harcourt, London.
- Whitechurch, H., R. Montigny, J. H. Sevigny, M. Storey, and V. J. Salters (1992), K-Ar and <sup>40</sup>Ar/<sup>39</sup>Ar ages of central Kerguelen Plateau basalts, *Proc. Ocean Drill. Program Sci. Results*, *120*, 71–77.
- Williams, J. R., and T. J. Bralower (1995), Nannofossil assemblages, fine fraction stable isotopes, and the paleoceanography of the Valanginian-Barremian (Early Cretaceous) North Sea Basin, *Paleoceanography*, *10*, 815–839, doi:10.1029/95PA00977.
- Wilson, P. A., and R. D. Norris (2001), Warm tropical ocean surface and global anoxia during the Mid-Cretaceous period, *Nature*, *412*, 425–428, doi:10.1038/35086553.

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