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Key Points:
- A causal link between nutrient-rich deep oceans and nutrient-poor epicontinental seas during Oceanic Anoxic Event 2 (OAE2)
- Influence of abnormal oceanic nutrient cycling during Late Cretaceous OAE2 on shelf biota
- Response of benthic foraminifera and dinoflagellates to oligotrophy during OAE2

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Biotic and Isotopic Vestiges of Oligotrophy on Continental Shelves During Oceanic Anoxic Event 2

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Abstract The widespread expansion of the oxygen minimum zone onto shelves has been commonly regarded as a primary cause of benthos extinction in epicontinental sea ecosystems during the Cenomanian–Turonian boundary event (CTBE). However, neither lithology, geochemical proxies, nor micropaleontological data support this hypothesis. Instead, our integrated foraminiferal and dinoflagellate cyst study, corroborated by δ13Corg and δ15Norg data, indicate that the biota were impacted by an abrupt shift to well oxygenated oligotrophic conditions and a collapse of primary productivity in the epicontinental Central European Basin. Because the event was concurrent with the development of extensive and extreme oceanic bottom water anoxia that reached the photic zone in oceanic settings, we infer that the biotic crisis in the shelf seas during Oceanic Anoxic Event 2 (OAE2), and possibly during other OAEs, was triggered by this anomalous nutrient cycling in Earth’s oceans. This phenomenon was presumably associated with intensive denitrification combined with anammox activity in the deep “ammonium oceans,” which caused a significant loss of biologically reactive nitrogen from the ocean system. Impingement of ammonium-rich anoxic waters on the photic zone resulted in primary productivity based primarily on ammonium assimilation, as recorded by strongly 15N-depleted organic matter deposited in the oceans during the CTBE. We propose that, unlike in the oceanic settings, productivity in the well-oxygenated, oligotrophic epicontinental seas was nitrate-based, as evidenced by strongly 15N-enriched organic matter deposited in the contemporaneous epicontinental sea. These very high δ15Norg values (> +5‰) were related to the spreading of shallow oceanic waters carrying 15N-enriched nitrate onto epicontinental settings.

1. Introduction

The Cenomanian–Turonian boundary event (CTBE)—linked to Oceanic Anoxic Event 2 (OAE2, ca. 94.6 Ma [Bouilla et al., 2020])—is one of the most severe biotic crises of the Mesozoic, and resulted from significant paleoceanographic and paleoclimatic perturbations associated with large igneous province volcanic activity (e.g., Percival et al., 2018). A significant proportion of then-extant species (up to ca. 50%)—mainly marine invertebrates and microorganisms, including mollusks, bivalves, ostracods, calcareous nannoplankton, and dinoflagellates—became extinct in this interval (Jablonski, 1991; Jarvis et al., 1988; Harries, 1993). It was particularly deleterious to benthic foraminifera, of which more than 70% were wiped out (e.g., Peryt & Lamolda, 1996). The collapse of benthic foraminifera communities and the subsequent foraminiferal recovery across the CTBE has been extensively examined since the 1970s, with dozens of published manuscripts and papers (e.g., Arriaga et al., 2016; Hart, 1996; Jarvis et al., 1988; Koutsoukos & Hart, 1990; Pearce et al., 2009; Peryt & Wyrwicka, 1991; Tronchetti & Grosheny, 1991). Most of these studies linked the dramatic decline in foraminiferal diversity and abundance to widespread expansion of the oceanic oxygen minimum zone, specifically pointing toward the onset of anoxia/dysoxia in the ocean and the spread of unfavorable conditions onto continental shelves (Koutsoukos et al., 1990). However, in many cases these hypotheses contradict the foraminiferal TROX model (a conceptual model which explains benthic foraminiferal microhabitat preferences in terms of differences in the downward organic flux; Jorissen et al., 1995; Van der Zwaan et al., 2009; see also Kajho, 1991, 1994). For example, foraminiferal taxa such as large epifaunal calcareous rotaliids, which actually represent highly oxygenated and even nutrient-limited environments, have been erroneously regarded as a proxy for dysoxic environments. Therefore, in order to understand this foraminiferal redox condition paradox, we integrated qualitative and quantitative analyses of benthic foraminiferal and dinoflagellate assemblages with stable isotopic proxies (δ13Ccarb, δ13Corg, and δ15Norg) in a complete sedimentary
succession across the Cenomanian–Turonian boundary in the S-19 borehole (Lublin region, SE Poland), in the Central European Basin. Our study is a contribution to understanding the drivers of mass extinctions and ecological perturbations in marine ecosystems during oceanic anoxic events in general, which currently rank among the key questions in the Earth sciences.

2. Materials and Methods

The studied section was composed of chalk with some marly chalk intercalations, deposited in the relatively shallow epicontinental sea of the Central European Basin, and belongs to the southeastern part of a structural unit referred to as the Border Synclinorium (Pożaryski, 1997) or the Kościerzyna-Puławy Synclinorium (see Żelaźniewicz et al., 2011). The section encompasses a complete sedimentological record of the Cenomanian-Turonian transition. A biostratigraphic subdivision was performed using planktonic foraminifera: the studied interval includes the upper *Rotalipora cushmani*, *Whiteinella archaeocretacea*, and lower *Helvetoglobotruncana helvetica* Zones. This foraminiferal zonation was integrated with the $\delta^{13}$C_carb curve, which clearly displays the broad positive excursion of the Cenomanian–Turonian boundary interval (Jenkyns et al., 1994; Figure 1), thereby illustrating the CTBE in the studied section.

Fifty samples were taken from a 32 m thick interval of the S-19 borehole for micropaleontological and isotopic analyses. Washed residues for foraminiferal study were obtained by disaggregating the rocks via the Glauber’s salt method; the residues were subsequently cleaned in an ultrasonic bath. The $\geq 63$ μm fraction was used for foraminiferal counts, and contained 200–300 specimens per sample. The relative abundances of the most common species/genera are marked in Figure 1.

Thirteen samples, ranging between 22 and 110 g, were treated with 37% HCl and 40% HF to remove carbonate and silicate minerals. The residue was rinsed through a 15-μm sieve to neutralize the samples and remove fine particles; a heavy liquid separation was not performed due to the small amount of residue obtained. One slide from palynologically rich samples, and three slides from palynologically poor samples, were examined. Where possible, up to 300 dinoflagellate cyst specimens were counted per sample. Microphotographs were taken using a Nikon Eclipse E-600 microscope equipped with phase contrast.

Bulk-rock samples were powdered in an agate mortar prior to isotopic analyses. $\delta^{13}$C_carb values were measured using a dual inlet, triple collector mass spectrometer (a modified and modernized MI1305 IRMS) at the Mass Spectrometry Laboratory, Institute of Physics, Maria Curie-Skłodowska University, Lublin. Samples were reacted with 100% orthophosphoric acid in a vacuum line at 25°C directly connected to the mass spectrometer. The $\delta^{13}$C_carb values were normalized against the NBS-19 standard and reported relative to VPDB, with a standard uncertainty of 0.06‰.
After removing carbonates with 1 M HCl, samples were analyzed for $\delta^{13}$C$_{\text{org}}$ and $\delta^{15}$N$_{\text{org}}$ with a Thermo 1112HT Flash Elemental Analyzer coupled to a Thermo Delta V Advantage IRMS in continuous flow mode, at the Stable Isotope Laboratory, Institute of Geological Sciences, Polish Academy of Sciences, Warsaw. $\delta^{13}$C$_{\text{org}}$ and $\delta^{15}$N$_{\text{org}}$ values were normalized against USGS 40, USGS 41, and IAEA 600 standards and reported relative to VPDB and atmospheric nitrogen, respectively. The analytical error of the measurements was up to ±0.3‰ for $\delta^{13}$C$_{\text{org}}$ and ±0.2‰ for $\delta^{15}$N$_{\text{org}}$.

3. Results and Interpretation of Redox Conditions and Productivity in the Basin

3.1. Foraminiferal Assemblages

The benthic foraminiferal community before the extinction event (samples 9–21) was characterized by a high level of diversity, represented by calcareous and agglutinated epifaunal (e.g., Gavelinella), shallow infaunal (e.g., Gyroidinoides), and deep infaunal (e.g., Tritaxia) taxa, with a high percentage of agglutinated infaunal foraminifers (Figure 1). This type of community is characteristic of mesotrophic conditions with intermediate primary production and organic matter input to the sea floor (see discussion in Dubicka et al., 2014). Later, in the uppermost part of the R. cushmani Zone (samples 22–23), a dramatic decline in foraminiferal abundance and diversity occurred, including the extinction of many species (e.g., Gavelinella baltica, G. cenomanica, G. berthelini, G. lodziensis, Tritaxia macfadyeni). This extinction event was followed by a survival interval (placed in the lowermost part of the W. archaeocretacea Zone; samples 24–30) characterized by low-diversity assemblages dominated by a few survivors (Gavelinella belorussica, which is often regarded as synonymous with G. berthelini, as well as Lenticulina rotulata and Lingulogavelinella globosa) and an opportunistic dwarf species, Valvulinera lenticula. V. lenticula, a good example of a disaster taxon (Chen & Benton, 2012), has been documented as employing r-selected strategies (Bergamin et al., 1999; Tyszka, 2009). The two large surviving gavelinellid species are epifaunal forms, commonly interpreted as oxic (Kaiho, 1999), which prefer highly oxygenated environments with limited food availability. In contrast, the maximum abundance of lenticulinids is typically within the sediment, at depths of 2–4 cm (Corliss & Chen, 1988), suggesting demand for a somewhat greater food supply. Nevertheless, Lenticulina has been identified as a foraminifer capable of occupying the whole range of benthic microhabitats, from the sediment surface to a few centimeters within the sediment, depending on food availability (Koutsoukos & Hart, 1990; Tyszka, 1994). Moreover, Lenticulina exerts a strong vital effect on its $\delta^{13}$C and $\delta^{18}$O values, showing significantly depleted isotopic values in relation to other taxa (Friedrich et al., 2006; Wendler et al., 2013); this may be related to rapid metabolism, reproduction, and calcification on occasions when food was available, especially in oligotrophic environments (Wendler et al., 2013). Accordingly, the benthic foraminiferal assemblages in the extinction and survival intervals illustrate the collapse of primary productivity in the basin.

Following the extinction event, a benthic foraminiferal recovery is observed, albeit one that was rather slow in returning to the level of pre-extinction taxonomic diversity. Nevertheless, the first replacement species (Gavelinella vesca, Cibicides polyrraphes, Eponides belorussiensis) appear rapidly within 100 kyr of the mass extinction (sample 27), much faster relative to benthic foraminiferal recoveries in the aftermath of other mass extinctions (Song et al., 2011). Complex foraminiferal communities did not re-emerge until the middle Turonian, ca. 2 Myr after the crisis. The recovery interval is still characterized by a low level of specific diversity dominated by opportunistic taxa: Lenticulina, Valvulinera, Gyroidinodes, and Praebulimina (Tyszka, 2009; Wendler et al., 2013). Furthermore, the early and middle Turonian foraminiferal community rebuilt stepwise, with the emergence of entirely new lineages such as Gavelinella vesca–G. vombensis, Globorotalites hangensis–G. hiltermanni, and Gavelinella ammonoides–G. costulata, which evolved continuously until the Campanian or Maastrichtian.

3.2. Dinoflagellate Cyst Assemblages

The lower part of the section (samples up to 15) yielded rich and well diversified dinoflagellate cyst assemblages consisting of about 30 taxa, including a few abundant multispecies groups of Achomosphaera/Spinitereis spp., Sentusidinium spp., and Pterodinium/Impagidinium spp. (Figure 2), indicative of a nutrient rich
environment (Egerton et al., 2014). The subordinate occurrence of land derived elements—in particular, terrestrial palynomorphs and plant tissue—in the lower part of the section is also observed. The middle part of the section, which encompasses the extinction and survival events (samples 20–33), is barren of dinoflagellate cysts and depleted in OM, which here is only comprised of sparse terrestrial palynomorphs, amorphous organic matter (AOM), and plant tissue. As dinoflagellates are among the most important primary producers in modern marine ecosystems, which are generally impoverished when nutrient levels are low (Bonnet et al., 2008), the dramatic decrease in dinoflagellate abundance in this interval seems to be linked to a significant drop in vital nutrients in the basin. The upper part of the section (samples 38 and 41) contains impoverished, undiversified dinoflagellate cyst assemblages represented by a few specimens of *Odontochitina operculata* per slide, with subordinate proportions of *Sentusidinium* spp. and *Achomosphaera/Spiniferites* spp. This slow increase in the number and diversity of dinoflagellate assemblages above the OAE2 level is indicative of a partial reconstruction of the nutrient distribution system in the basin. Accordingly, the relative increase in the abundance of *Odontochitina operculata*, a widely tolerant taxon (Lebedeva, 2010; Pearce et al., 2009) also considered indicative of eutrophic environments (Coccioni et al., 1993), confirms the presumably slow restoration of the nutrient distribution system. The distinguishing feature of these dinoflagellate cyst assemblages from those in the lower part of the section is the occurrence (although in low number) of *Palaeohystrichophora infusoroides*, assigned to the order Peridiniales, which is usually treated as heterotrophic (Olde et al., 2015). In oceanic conditions, it is widely accepted that the dominance of heterotrophic dinoflagellate cyst assemblages can be indicative of active upwelling (Pospelova et al., 2006; Reichart & Brinkhuis, 2003), which is rather ambiguous in shelf environments (Aytan et al., 2018). The absence of heterotrophic dinoflagellate cysts in the lower part of the section and their insignificant contribution in the upper part is in clear contrast with previous studies from England, France, and Spain (Clarke & Verdier, 1967; Foucher, 1979; Dodsworth, 2000; Peyrot et al., 2011; Robaszynski et al., 1980; Tocher & Jarvis, 1995) where dinoflagellate assemblages in the Cenomanian-Turonian boundary interval were conspicuously dominated by these forms. This may be related to differences in the characteristics of these basins, such as the depth and palaeogeographic location, and in particular the distance to the continental slope where upwelling could have been a substantial driver of nutrient availability. A significant number of *Spiniferites* spp., belonging to the order Gonyaulacales, through the entire section support our observation concerning the absence of an oxygen deficiency, as this genus has been reported from various open marine and well-oxygenated basins from Europe (Marshall & Batten, 1988), Tunisia (Brinkhuis & Zachariasse, 1988), and North America (Harker et al., 1990; Harris & Tocher, 2003).
3.3. Isotopic Proxies

The $\delta^{13}C_{\text{carb}}$ curve in the section rises gradually from $+1.5\%$ before OAE2, with a sharp increase from $+2.5\%$ to $+3.5\%$ at the onset of the event (Figure 1). In the aftermath of OAE2, the $\delta^{13}C_{\text{carb}}$ curve does not revert to the pre-event values, instead stabilizing at ca. $+3\%$. The $\delta^{13}C_{\text{org}}$ values vary between $-28.0$ and $-25.6\%$ with a zig-zag pattern before the OAE2 (avg. $-26.5\%$; sd = $0.8\%$; n = 7) and become strikingly uniform ($-26.9$ to $-26.1\%$) during and after the event, with the same average value ($-26.5\%$; sd = $0.3\%$; n = 8) as in the pre-event interval (Figure 1; Table 1). The $\delta^{15}N_{\text{org}}$ values (Table 1) are significantly lower before ($+2.0\%$ on average; sd = $1.2\%$; n = 5) than during and after the OAE2 ($+5.5\%$ on average; sd = $0.4\%$; n = 4) with a sharp increase from 0.8 to 5.9\% at the onset of the event. Nitrogen isotope measurements were unsuccessful for six samples, due to insufficient concentrations of nitrogen in the HCl-insoluble residue related to very low organic matter content (see section 2 for details of the protocol), particularly in the interval encompassing OAE2. The low abundance of the HCl-insoluble residue (<1.8\% in all samples, avg. 1.0%; sd = 0.5%; n = 15; Table 1) is also reflective of a scarcity of siliciclastic material across the entire section. The residue abundance does not change across the CTBE, as the average (1.0\%) and sd (0.5\%) are the same below and above the CTBE. Only the $\delta^{13}C_{\text{carb}}$ curve follows the global pattern observed across OAE2 in oceanic sections; the $\delta^{13}C_{\text{org}}$ curve does not vary significantly, and $\delta^{15}N_{\text{org}}$ exhibits an opposite trend to that observed in deep oceanic settings.

4. Discussion

Our study of changes in foraminiferal and dinoflagellate assemblages, as well as in C and N isotope proxies, across the CTBE strongly suggests that continuously well oxygenated conditions prevailed in the Polish portion of the Central European Basin, and that a switch to oligotrophy occurred concomitant with the start of OAE2. We believe that the ecological and taxonomic collapse of both benthic and planktonic organisms in shelf seas occurred in response to the onset of oligotrophy, which supports the findings of Gale et al. (2000). These emergent oligotrophic conditions appeared to support life only for selected opportunistic taxa, apparently resulting from a decline in primary productivity leading to a decrease in food supply, a consequence of reduced nutrient supply to the epicontinental sea. Gale et al. (2000) interpreted this phenomenon as resulting from normal oceanographic processes, specifically "the collapse of the shelf break front and the spread of oligotrophic, stratified oceanic waters onto the shelves, as a consequence of Late Cenomanian sea-level rise."
rise”. While this hypothesis seems feasible, we infer that a causal link existed between the exceptional shelf oligotrophy and bottom-water anoxia in the deep oceans across the CTBE. We further propose a scenario elucidating this linkage based on isotopic indices.

### 4.1. Post-Depositional Alteration of $\delta^{13}C_{\text{org}}$ and $\delta^{15}N_{\text{org}}$

In the section studied, neither a positive $\delta^{13}C_{\text{org}}$ excursion nor enhanced organic deposition, both characteristic for deep ocean settings with anoxic bottom waters during OAE2 (Kuyper et al., 2002; Tsikos et al., 2004), are observed across the CTBE. The abundance of marine microfossils and scarcity of siliciclastic material indicate that marine organic matter (OM) must have dominated in the basin. Yet, land-derived palynomorphs occur in the section and the $\delta^{13}C_{\text{org}}$ values plot in the range typical for terrestrial sources (Lamb et al., 2006). Moreover, the OM content is very low, especially in the interval encompassing the OAE2, where it was even insufficient for $\delta^{15}N_{\text{org}}$ analysis in many samples (Table 1). All these seemingly contrasting data can be explained by secondary oxidation of OM affecting the preservation and C isotopic composition of OM. C isotope composition differs considerably between organic compounds. In general, more refractory organic compounds, for example, lignin, are enriched in $^{13}C$ relative to more labile ones, for example, lipids and proteins (Tyson, 1995). Since marine OM is enriched in easily degradable organic compounds relative to the terrestrial OM, oxic degradation of OM in surface sediments often leads to an increase in the relative content of the refractory OM and in the bulk $\delta^{13}C_{\text{org}}$ composition approaching that of the refractory fraction (Lamb et al., 2006 and references therein). We believe that the intensive post-depositional degradation of OM underoxic conditions lead to the depleted OM content and the relatively low bulk $\delta^{13}C_{\text{org}}$ values in the section studied, which is in line with the well-oxygenated water column in the epicontinental sea before, during and after the event.

While mesotrophic conditions in the sediment related to intermediate primary production in the water column are indicated by the characteristic benthic foraminiferal community in the pre-event interval, the rest of the section is characterized by oligotrophic conditions related to a breakdown (during OAE2) and modest restoration (after OAE2) of primary productivity. It is attested to by the drastic decrease of foraminiferal abundance and disappearance of dinoflagellate assemblages across the CTBE. Higher OM flux before the event must have resulted in lower effective OM removal (Pedersen & Calvert, 1990), and so a lesser impact on the bulk isotope composition of OM, as relatively less labile OM was removed. The $\delta^{13}C_{\text{org}}$ values in the pre-OAE2 interval vary erratically between −28.0 and −25.6‰ (Figure 1), which can be chiefly assigned to local fluctuations in OM flux and burial, regulated, for instance, by the rates of primary productivity and deposition. The $\delta^{13}C_{\text{org}}$ values in the middle and top of the section are strikingly uniform, and identical to the average value for the lower part (Figure 1). Given the very low OM flux during and after OAE2, the $^{13}C$ depletion in OM associated with the oxidation of OM may have been larger than before the event. Consequently, it is very likely that the autochthonous OM recorded the positive $\delta^{13}C_{\text{org}}$ excursion during OAE2, although the amplitude of the excursion must have been much lower than in the very productive anoxic basinal settings with higher OM preservation potential, but the excursion was subsequently obliterated by the intensive OM oxidation affecting preferentially the more labile autochthonous biomass than the refractory terrestrial OM (see Middelburg & Nieuwenhuize, 1998). Conversely, the positive $\delta^{13}C_{\text{carb}}$ excursion in the CTBE is preserved due to the absence of significant post-depositional carbonate alteration.

Analogously, the nitrogen isotope ratio may have also been affected by OM oxidation. The oxidation of OM liberates nitrate with depleted $\delta^{15}N$, causing complementary $^{15}N$ enrichment in the remaining OM; these processes are thought to mostly occur in the water column (Altabet & Francois, 1994; Möbius et al., 2010; Robinson et al., 2012). Given the shallow water depth in the epicontinental sea examined in this study, the impact of OM oxidation on bulk $\delta^{15}N_{\text{org}}$ during settling was probably insignificant, and surely not higher than in the open ocean, where the residence time of OM in oxygenated water must have been similar, if not longer. On the other hand, post-depositional decomposition of OM in the well-oxygenated epicontinental basin was surely higher than in the deep oceanic settings with anoxic bottom waters. Still, early diagenetic oxidation of OM oxidation is not capable of significant modification of bulk $\delta^{15}N_{\text{org}}$, even in well-oxygenated basins with low OM fluxes (Algeo et al., 2014 and references therein); modeling based on downcore data shows that the maximum $^{15}N$ depletion of organic N is ca. 2‰ (Freudenthal et al., 2001). Another important factor is the assimilative uptake of nitrate by phytoplankton, which leads to a slight $^{15}N$ depletion in the
biomass produced and a residual enrichment in the remaining nitrate pool (Altabet & Francois, 1994; Waser et al., 1998). As coccoliths are the dominant component of the chalk studied, diagenetic 15N enrichment was likely compromised by 15N depletion related to phytoplankton production. Last, but not least, at the onset of the CTBE δ15NOrg values rise dramatically by 5‰ in the examined section (Table 1), although neither redox nor sedimentary conditions changed during this transition. As the pre-event interval was also affected by OM oxidation, this isotopic rise cannot be accounted for by diagenetic alteration in any way. Therefore, although internal cycling of N species likely did take place, it did not significantly impact bulk δ15NOrg in this epicontinental setting; the observed abrupt increase of δ15NOrg at the CTBE should be interpreted in terms of paleoceanographic processes.

4.2. Significance of 15N Enrichment in OM

The positive δ15NOrg shift, together with abrupt changes in foraminiferal and dinoflagellate assemblages, were apparently related to a shift in OM production and nitrogen cycling across the CTBE, despite unchanged lithology and pelagic sedimentary conditions in the section. Evidently, this switch was related to dramatic perturbations at the onset of OAE2, when anoxia spread globally in deep oceanic settings, causing increased organic deposition. Depleted δ15NOrg values (<−2‰) in these deep oceanic settings are only partly attributed to intensive N fixation by diazotrophs, mainly cyanobacteria (Junium & Arthur, 2007; Kuypers et al., 2004). Instead, they are thought to be chiefly driven by the assimilation of recycled ammonium by primary producers, mainly phytoplankton, on a global scale (Higgins et al., 2012; Junium & Arthur, 2007). It has been shown that exceptionally large quantities of ammonium were delivered to the surface layer by upwelling and impingement of anoxic bottom waters on the photic zone, and that ammonium, not nitrate, was the main source of fixed N during OAE2 (Higgins et al., 2012; Naafs et al., 2019). In such an “ammonium ocean,” both N fixation and ammonium assimilation resulted in the production of 15N-depleted biomass (Higgins et al., 2012; Kuypers et al., 2004), driving residual 15N enrichment of the remaining fixed N pool in the surface layer (Altabet & Francois, 1994; Hoch et al., 1994; Liu & Kaplan, 1989). It was assumed by Higgins et al. (2012) that the entire 15N-enriched fixed N pool was exhausted by denitrification and/or annamox, and was thus evacuated as N2 into the atmosphere in the open ocean. However, on continental margins of the proto-North Atlantic, where oxygen-deficient conditions were not as extreme during OAE2 (see van Helmond et al., 2014, 2015), δ15NOrg values are higher (<+3.5‰; Ruvalcaba Baroni et al., 2015), which could result from productivity dominated and driven by 15N-enriched nitrate (Naafs et al., 2019). Our data show that fully oxic conditions occurred at the same time in an epicontinental sea, where organic productivity collapsed and δ15NOrg rose to even higher values across the CTBE.

This rise of δ15NOrg, as opposed to the decline observed in deep oceanic environments, clearly shows that 15N-depleted OM produced by N fixation and ammonium assimilation was not deposited in the epicontinental basin. The main nutrient and cause of 15N depletion in the open ocean, ammonium, could not reach the shallow, distant epicontinental setting, as it was probably consumed and oxidized to nitrate in the intervening shallow oxygenated water masses. Moreover, there are no indications of upwelling in the study area. Yet, despite oligotrophic conditions, phytoplankton surely developed, as coccolithophores were the main calcium carbonate producers in this area; as such, there must have been enough fixed N to sustain algal productivity. We believe that productivity in this epicontinental setting was dominated by nitrate (and nitrite), which is in line with simulations of the global N cycle during OAE2 (Naafs et al., 2019).

Four possible sources of nitrate (and their respective δ15N values) are assumed for the epicontinental basin investigated. (a) In the modern, dissolved organic nitrogen (DON) is an important fixed N pool in the surface layer of oligotrophic oceans (Knapp et al., 2005). The δ15N of DON and δ15NOrg of shelf sediments in such settings—for example, in the South China Sea (Guye et al., 2009), North Atlantic, and North Pacific (Knapp et al., 2011)—are relatively high (3–6‰) and similar to those obtained in this study (5.5‰ on average). Although possible, this scenario does not take into account the non-actualistic, abnormal oceanographic conditions in the oceans across the CTBE. (b) In such paleoclimatic and paleogeographic settings, N fixation by diazotrophs must have occurred to some extent in the basin examined. Yet, due to a modest N isotope fractionation during N fixation, the newly fixed N exhibits δ15NOrg values < 3‰ lower than that of atmospheric N2 (e.g., Brandes & Devol, 2002; Karl et al., 1997), which cannot explain the drastic δ15NOrg
increase recorded in this work. Therefore, a heavier N source must have existed as well to compensate for the production of this relatively $^{15}$N-depleted newly fixed N. (c) Increased terrestrial and riverine input, which could theoretically explain the enriched $\delta^{15}N_{\text{org}}$ values to some extent (see Mayer et al., 2002; Voss et al., 2006), is unlikely, because there is extremely little siliciclastic material in the entire section examined, and no systematic change in its content is recorded across the CTBE. This is further confirmed by the $\delta^{13}C_{\text{org}}$ curve, which does not shift to lower values across the transition even though it is affected by more pronounced post-depositional oxidation in the aftermath of the CTBE. (d) We propose that the primary source of the high $\delta^{15}N_{\text{org}}$ was the strongly $^{15}$N-enriched nitrate delivered from the open ocean to the epicontinental setting during OAE2. The source of this nitrate was denitrification and anammox (anaerobic ammonium oxidation), which are associated with the residual $^{15}$N enrichment in nitrate (Brandes et al., 1998; Cline & Kaplan, 1975) and ammonium pools (Brunner et al., 2013; Dähnke & Thamdrup, 2016), respectively, with the latter undergoing nitrification en route in the oxic shallow water. The production of such strongly $^{15}$N-enriched nitrate surely required that the nitrate pool was depleted in oceanic settings during OAE2 by enhanced denitrification and anammox in deep oceans (as explained in Section 4.3). Because the level of bioavailable N in the epicontinental basin was low, even an insignificant supply of such strongly $^{15}$N-enriched nitrate was able to increase the bulk $\delta^{15}N$ of OM produced and preserved in the stratigraphic setting examined. In the modern, anomalously high $\delta^{15}N$ values of nitrate (ca. +9‰) recorded off southern California, where neither anammox nor denitrification takes place, are linked to the injection of isotopically heavy nitrate transported laterally by the California Undercurrent from an oxygen-deficient zone located more than 1,000 km away (Liu & Kaplan, 1989). This demonstrates that the ingestion of $^{15}$N-enriched nitrate is possible, even from a distant ocean region.

### 4.3. Nitrogen Nutrient Cycling

Sediments representing OAE2 on continental margins of the proto-North Atlantic are also $^{15}$N-enriched relative to those deposited in the deep ocean—although not to the same extent as those examined in this study—and were apparently deposited under intermediate conditions (recorded by intermediate $\delta^{15}N_{\text{org}}$) between an open ocean with anoxic, ammonium-rich bottom waters and a fully oxygenated epicontinental sea (represented by our data) during OAE2. Interestingly, the $^{15}$N enrichment is also observed in the Turonian above the OAE2 in the studied section, as is $^{15}$N depletion in many deep-water areas in the proto-North Atlantic (e.g., Junium & Arthur, 2007; Junium et al., 2018; Ruvalcaba Baroni et al., 2015), where anoxia persisted beyond the CTBE. This indicates that the compensating N isotope fractionation mechanism between epicontinental and oceanic settings continued for some time after the event, providing a continued supply of isotopically heavy nitrate. Enriched $\delta^{15}N_{\text{org}}$ during OAE2 (up to +7.5‰) have also been reported from the margins of the Tethys oceans (e.g., Frijia et al., 2019; Zhang et al., 2019), which suggests $^{15}$N enrichment occurred globally in shallow-marine epicontinental seas during OAE2. These high $\delta^{15}N_{\text{org}}$ Values have been mostly attributed to reduced oxygen depletion and increased N fixation, which we find insufficient to reconcile with such extremely high $\delta^{15}N_{\text{org}}$ Values. Our model provides an alternative explanation, consisting of lateral transport of shallow water carrying isotopically heavy nitrate from open oceans to epicontinental seas (Figure 3).

In $O_2$-deficient marine water, fixed nitrogen ($NH_4^+$, $NO_2^−$, and $NO_3^-$) is converted to gaseous nitrogen ($N_2$) through the processes of denitrification and anammox, which are responsible for most losses of biologically reactive nitrogen from the system and a marked decrease in $N : P$ ratios in the deep ocean (Arrigo, 2005). Both denitrifying and anammox bacteria are involved in nitrogen reduction in anoxic conditions; however, the factors which regulate the relative importance of these processes are still not fully understood (Lipfert et al., 2016). Nevertheless, it is now evident that anammox is a very important process in the global nitrogen cycle, contributing to as much as 50% of the removal of fixed nitrogen from the world’s oceans (Dalsgaard et al., 2005). Moreover, the process is significant in the marine N cycle, since it markedly reduces the abundance of fixed-N in upwelling waters, which ultimately is delivered to the ocean surface and shallow marine environments (Arrigo, 2005; Radice et al., 2019). This significant loss of biologically available N by denitrification and anammox was the most probable cause of the fixed N pool impoverishment in the surface layer during OAE2, which enabled the marked $^{15}$N enrichment of the residual fixed nitrogen. Thus, both the dinoflagellate and benthic foraminiferal crises during the CTBE seem to be linked to the collapse of
primary productivity in aquatic systems resulting from anomalies in the marine nutrient cycle: specifically, the loss of biologically reactive N in the widespread oceanic bottom-water oxygen minimum zones formed during OAE2. Because foraminiferal turnover across the CTBE, as observed here, is very similar to that described from other European shelf settings, such as the Anglo-Paris Basin (Hart, 1996; Jarvis et al., 1988; Leary & Peryt, 1991; Pearce et al., 2009), northern Spain (Peryt & Lamolda, 1996), the Central European Basin (Peryt & Wyrwicka, 1991, 1993), and even the Sergipe Basin, NE Brazil (Koutsoukos et al., 1990), in terms of taxonomic diversity and abundance, unfavorable environmental conditions related to a reduction in bioavailable N in surface waters may have occurred widely, at least within the entire European epicontinental sea. Geochemical investigations in these sections, of $\delta^{15}N_{org}$ in particular, would be useful to help verify the proposed hypothesis explaining the N cycling linkage between oceanic and epicontinental settings during the crisis.

5. Conclusions

Our study of dinoflagellate and benthic foraminiferal assemblages, as well as C and N isotope proxies, indicates highly oligotrophic conditions in the European shelf during the CTBE associated with a collapse of primary production. Because this event was associated with expanded oceanic bottom water anoxia during OAE2, we infer that benthos extinction in epicratonic seas resulted from anomalies in the oceanic nutrient cycle induced by denitrification combined with anammox activity. These processes resulted in a significant reduction in fixed N in aquatic systems due to the boosted production of N$_2$ within oxygen-depleted environments. Because fixed nitrogen is a critical nutrient for plant growth, these perturbations to the N cycle limited phytoplankton production in the euphotic zone. Thus, it is highly probable that under widespread
oxygen-deficient conditions on the ocean floor, denitrification and anammox were extremely intensive and the dominant drivers behind the reduction of the bioavailable N pool in epicontinental seas during Oceanic Anoxic Events. While primary productivity in the oceans was based on ammonium assimilation during the event, as recorded by depleted $\delta^{15}N_{\text{org}}$ values, our data indicates that in the epicontinental seas productivity was nitrate-based, as evidenced by enriched $\delta^{15}N_{\text{org}}$ values. We propose that lateral transport of shallow water from open oceans to the epicontinental seas was the source of the $^{15}$N-enriched nitrate.

**Conflict of Interest**

The authors declare no conflicts of interest relevant to this study.

**Data Availability Statement**

Readers can access raw data associated with this study in the public domain (https://zenodo.org/record/4446619#.YNW6mCBR02w).

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