

Journal Pre-proof

Evidence for changes in sea-surface circulation patterns and ~20° equatorward expansion of the boreal bioprovince during a cold snap of oceanic anoxic event 2 (late cretaceous)

Francesca Falzoni, Maria Rose Petrizzo



PII: S0921-8181(21)00263-0

DOI: <https://doi.org/10.1016/j.gloplacha.2021.103678>

Reference: GLOBAL 103678

To appear in: *Global and Planetary Change*

Received date: 14 June 2021

Revised date: 5 September 2021

Accepted date: 12 October 2021

Please cite this article as: F. Falzoni and M.R. Petrizzo, Evidence for changes in sea-surface circulation patterns and ~20° equatorward expansion of the boreal bioprovince during a cold snap of oceanic anoxic event 2 (late cretaceous), *Global and Planetary Change* (2021), <https://doi.org/10.1016/j.gloplacha.2021.103678>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2021 Published by Elsevier B.V.

EVIDENCE FOR CHANGES IN SEA-SURFACE CIRCULATION PATTERNS AND ~20° EQUATORWARD EXPANSION OF THE BOREAL BIOPROVINCE DURING A COLD SNAP OF OCEANIC ANOXIC EVENT 2 (LATE CRETACEOUS)

Francesca Falzoni^{a,*} francesca.falzoni1@gmail.com, Maria Rose Petrizzo^b
mrose.petrizzo@unimi.it

^aDipartimento di Scienze della Terra, dell'Ambiente e delle Risorse, Università degli Studi di Napoli Federico II, via Vicinale Cupa Cintia 21, 80126 Napoli, Italy

^bDipartimento di Scienze della Terra "A. Desio", Università degli Studi di Milano, via Mangiagalli 34, 20133, Milano, Italy

*Corresponding author.

Abstract

The Plenus Cold Event (PCE) temporarily interrupted the supergreenhouse conditions exacerbated during much of the Cenomanian–Turonian Oceanic Anoxic Event 2 (OAE 2). The PCE is crucial to the occurrence of Boreal benthic macroinvertebrates and of the nektonic belemnite *Praeactinocamax plenus* (after which the event is named) in Europe, and to the re-oxygenation of bottom waters in the Northern Hemisphere. However, its effects on the sea-surface circulation are unknown and evidence for changes in the biogeography of planktonic organisms are limited to the equatorward migration of the dinoflagellate cysts grouped in the *Cyclonephelium compactum–membraniphorum* morphological plexus.

This study presents new planktonic foraminiferal quantitative data from two complete OAE 2 records of the Anglo-Paris (Eastbourne, SE England) and Vocontian (Clot

Chevalier, SE France) basins that registered the equatorward pulse of Boreal macroinvertebrates during the PCE and have been extensively studied for bio- and chemostratigraphy.

At the onset of OAE 2 (before the PCE), planktonic foraminifera are mainly represented by oligo-mesotrophic Tethyan taxa (rotaliporids and whiteinellids) in both localities, but this assemblage is sharply replaced by cold and meso-to-eutrophic species (praeglobotruncanids, dicarinellids and muricohedbergellids) during the PCE. The cold-water assemblage shows strong affinities with the coeval fauna of the Norwegian Sea and yields the Boreal endemic species *Muricohedbergella krynina* and *Praeglobotruncana plenusiensis*. This observation combined with previously published data collected in other localities of the Northern Hemisphere and on other fossil groups suggest a ~20° equatorward expansion of the Boreal marine bioprovince during the PCE. Moreover, contrarily to the nektonic belemnitellids that were able to move independently of ocean circulation, planktonic organisms are passively transported by currents and changes in the planktonic foraminiferal assemblages documented in the Anglo-Paris and Vocontian basins have been interpreted to reflect the transition from a dominant influence of warm, saline, and thermally stratified waters carried by the proto-Gulf Stream before the PCE to cold and low-saline Boreal waters originated in the Norwegian Sea during the PCE. We suggest that such changes were forced by the equatorward shift of the proto-Arctic Front (i.e., the boundary between warm saline Tethyan-Atlantic and cold low-saline Boreal waters) from offshore Norway to Southern England. In this southerly position, the proto-Arctic Front represented an oceanographic barrier that limited the influence of the proto-Gulf Stream in the Anglo-Paris Basin, and favored the inflow of Boreal waters in the European epicontinental basins.

The sea-surface cooling and equatorward expansion of Boreal planktonic assemblages during the PCE are of the same order of magnitude of those reconstructed

between some glacial and interglacial intervals of the Plio-Pleistocene. Despite obvious differences between Cretaceous and Plio-Pleistocene paleogeography and climate dynamics, this study reviews the extent of environmental changes occurred during the PCE, provides evidence for a profound re-organization of the sea-surface circulation patterns and a more comprehensive overview of the equatorward migration of Boreal marine communities in the Northern Hemisphere.

Keywords

Plenus Cold Event, Oceanic Anoxic Event 2, Cenomanian–Turonian boundary interval; Cretaceous supergreenhouse; planktonic foraminifera; *Praeactinocamax plenus*

1. Introduction

The Cenomanian–Turonian boundary interval (Late Cretaceous) is characterized by Oceanic Anoxic Event 2 (OAE 2), a severe perturbation of the global carbon cycle that caused dysoxia/anoxia at the sea-floor. OAE 2 is testified lithologically by the occurrence of organic-rich lithologies in most deep-sea and hemipelagic records (i.e., Bonarelli Level and equivalents), and geochemically by a major positive (+2 to +4‰) $\delta^{13}\text{C}$ excursion ubiquitously found in well-preserved marine and terrestrial sequences (e.g., Schlanger and Jenkyns, 1976; Schlanger et al., 1987; Jenkyns et al., 2017). The late Cenomanian–Turonian also registered the highest sea-surface temperatures of the Late Cretaceous and likely of the past 120 myr (e.g., O'Brien et al., 2017; Huber et al., 2018), as a result of the activity of one or more Large Igneous Provinces (LIPs) that injected huge amounts of volcanogenically derived greenhouse gases in the ocean-atmosphere system (e.g., Turgeon and Creaser, 2008; du Vivier et al., 2014; Schröder-Adams et al., 2019).

However, this hot greenhouse phase was abruptly interrupted during the latest Cenomanian (~94 Ma) by a 40-200 kyr (Jarvis et al., 2011; Gangl et al., 2019; Boulila et al., 2020) cooling episode known as Plenus Cold Event (PCE: Jefferies, 1962, 1963; Gale and Christensen, 1996; Jarvis et al., 2011; Jenkyns et al., 2017). Different geochemical proxies obtained from the European epicontinental basins, the Western Interior Seaway (WIS) and the North and equatorial Atlantic Ocean suggest a 5 to 11°C drop in sea-surface temperatures, increased equator-to-pole temperature gradients, and a 400 to 600 ppmv decrease of the atmospheric $p\text{CO}_2$ levels, which has been generally related to the burial of organic matter during the initial phase of OAE 2 (e.g., Arthur et al., 1988; Kump and Arthur, 1999; Paul et al., 1999; Tsikos et al., 2004; Voigt et al., 2006; Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011; Jenkyns et al., 2017; Kuhnt et al., 2017; Gale et al., 2019). However, the timing and magnitude of cooling might have been modulated by local factors (O'Connor et al., 2020; Percival et al., 2020) and evidence for cooling are doubtful (Gangl et al., 2019; Petrizzo et al., 2021) or missing from the Southern Hemisphere and from the Pacific Ocean, where the OAE 2 interval is often incomplete (e.g., Ando et al., 2009; Jiménez Barrocoso et al., 2015; Falzoni et al., 2016a; Dickson et al., 2017; Robinson et al., 2019) or shows a noisy $\delta^{13}\text{C}$ record (Takashima et al., 2011) that complicates the chemostratigraphic correlations.

Coeval to the PCE, a repopulation event of benthic foraminifera in the WIS (Benthonic Zone: Eicher and Worstell, 1970; Eicher and Diner, 1985; Leckie, 1985) and a geochemical fingerprint for oxidation in several European epicontinental basins (Jenkyns et al., 2017; Clarkson et al., 2018; Danzelle et al., 2020) suggest a re-oxygenation phase of bottom waters temporarily interrupting dysoxia/anoxia at the sea floor, potentially associated to changes in the deep-water circulation patterns in the Anglo-Paris Basin (Zheng et al., 2013).

The typical OAE 2 hot greenhouse climate conditions re-established soon after the PCE likely as a response to a reduced rate of silicate weathering (Robinson et al., 2019; Percival et al., 2020) and/or to the LIP(s) reactivation after brief quiescence (Sullivan et al., 2020).

Despite its brief duration, abrupt cooling during the PCE had a deep impact on the evolutionary history and biogeography of organisms. In terrestrial ecosystems, the PCE likely favored the radiation of angiosperms and the proliferation of a cold and less humid savanna-type vegetation (Heimhofer et al., 2018). Certainly, the PCE affected the biogeographic distribution of marine macroinvertebrates in several European epicontinental basins. The occurrence of Boreal benthic bivalves (*Oxytoma seminudum* and *Chlamys arlesiensis*) and serpulids (*Hamulus* sp.), and of the Boreal nektonic belemnite *Praeactinocamax plenus* in several localities of Southern England (e.g., Dover, Eastbourne; Fig. 1A) was taken historically as the first evidence for cooling in the Anglo-Paris Basin (Jefferies, 1962, 1963). The same macrofossil assemblage, including several *P. plenus* specimens at different ontogenetic stages, was documented in a single correlative bed at Les Lattes (Vocontian Basin, SE France; Fig. 1B) indicating that Boreal taxa approached the northern margin of the tropical Tethyan Realm, where they found favorable environmental conditions to breed and complete their life cycle (Gale and Christensen, 1996; Christensen, 1997; Fig. 1B-C).

Nevertheless, the response of planktonic organisms to the PCE remains poorly investigated. Evidence for changes in the planktonic communities are currently limited to the equatorward migration of the Boreal dinoflagellate cysts grouped in the *Cyclonephelium compactum–membraniphorum* morphological plexus in sections of the Western Interior Seaway (WIS), in the western North Atlantic (New Jersey), in the Lower Saxony Basin (van Helmond et al., 2014, 2016; Eldrett et al., 2014), in Lincolnshire (eastern England: Hart et al., 1993) and in the Vocontian Basin (Vergons: Courtinat et al.,

1991). Moreover, Desmares et al. (2016) and Grosheny et al. (2017), documented an increased proportion of the left- to right-coiled planktonic foraminifera *Muricohedbergella delrioensis* in sections of the WIS and of the Vocontian Basin, a morphological feature that is controlled by the temperature of calcification in some living species (after Ericson, 1959).

In this study, we present a high-resolution quantitative analysis of planktonic foraminiferal assemblages in two European key localities showing an almost complete record of OAE 2, i.e. Eastbourne (Gun Gardens, SE England) in the Anglo-Paris Basin, and Clot Chevalier (SE France) in the Vocontian Basin (Fig. 1A-B-C). The Clot Chevalier section is correlated with the Les Lattes section, located about 20 km to the NW (Fig. 1B), where the Boreal macrofossil assemblage was discovered by Gale and Christensen (1996), which enables the comparison between the stratigraphic distributions and abundances of planktonic foraminifera and those of Boreal macrofossils within the same basin.

Innovation of this study compared to previous planktonic foraminiferal quantitative data presented for the Eastbourne section (Paul et al., 1999; Keller et al., 2001) is represented by the application of a successful methodology for the disaggregation of indurated carbonate-rich lithologies with acetic acid preserving the specimens wall-texture (after Lirer, 2000), and of a revised taxonomy (after Hasegawa, 1999; González-Donoso et al., 2007; Desmares et al., 2008, 2020; Falzoni et al., 2016b, Huber et al., 2017, submitted; Falzoni and Petrizzo, 2020), both improving species determinations.

Results of this study are combined with previously published geochemical and paleontological information with the aim of documenting the response of planktonic foraminifera to the PCE and of filling the gap in the reconstruction of environmental changes in surface waters during a cold snap of the Cretaceous supergreenhouse.

2. The OAE 2 and PCE record at Eastbourne (SE England)

The Cenomanian–Turonian transition at Eastbourne (SE England) contains one of the most expanded, complete, fossil-rich and well-studied OAE 2 records (e.g., Paul et al., 1999; Gale et al., 2005; Jenkyns et al., 2017, and references therein), which was deposited in the Anglo-Paris Basin at a paleolatitude of $\sim 35^\circ\text{N}$ (Fig. 1C). The section consists of 8 m-thick calcareous marls (Plenus Marl) pinched in between two dominant chalky successions assigned to the Grey Chalk Member and White Chalk Formation (see Gale et al., 2005 and references therein) (Fig. 2). A strongly burrowed omission surface (sub-Plenus erosion surface; Jefferies, 1962, 1963) separates the Grey Chalk from the overlying Plenus Marl and corresponds to a major sea-level fall and sequence boundary (Robaszynski et al., 1998; Wilmsen, 2003). An erosion surface is also present at the base of Bed 4 and it has been interpreted as a transgressive surface (Robaszynski et al., 1998; Gale et al., 2000). The typical $\delta^{13}\text{C}$ positive excursion registering the perturbation of the global carbon cycle during OAE 2 is comprised between the base of the Plenus Marl and the lower part of the Holywell Member (Fig. 2).

Jefferies (1963) distinguished eight lithological beds within the Plenus Marl according to their lithological features and paleontological content, including the stratigraphic range of the Boreal macrofauna, i.e., the belemnite *P. plenus*, the bivalves *Oxytoma seminudum* and *Chlamys arlesiensis*, and the serpulid worm *Hamulus* sp., that are documented at Eastbourne and in other sections of the English Chalk (e.g., Dover) (Fig. 2). Boreal macrofossils are abundant in Bed 4 and 5, but they are also found in the lower part of Bed 6 (Jefferies, 1962, 1963; Gale and Christensen, 1996; Paul et al., 1999). *Oxytoma seminudum* also occurs in Bed 2 and 8, and a single specimen of *P. plenus* was recognized in Bed 8 (Gale and Christensen, 1996) (Fig. 2). In addition, the Boreal dinoflagellate cysts *Cyclonephelium compactum–membraniphorum* first occur in Plenus

Marl Bed 2 at Lulworth (southern England: Fig. 1A; Dodsworth, 2000) and in Bed 7 at Eastbourne (Pearce et al., 2009) (Fig. 2).

The occurrence of Boreal macrofossils coincides with a series of positive $\delta^{18}\text{O}$ shifts obtained on bulk carbonates (Dover: Lamolda et al., 1994; Eastbourne: Paul et al., 1999; Tsikos et al., 2004) and on macrofossil shells that were carefully screened for diagenetic alteration (Voigt et al., 2004, 2006), and with a drop of the $\Delta^{13}\text{C}$ (i.e., $\delta^{13}\text{C}_{\text{carb}} - \delta^{13}\text{C}_{\text{org}}$) values, which reflects an atmospheric $p\text{CO}_2$ decrease (Jarvis et al., 2011), suggesting synchronicity between cooling and migration of Boreal species in the Anglo-Paris Basin (Gale and Christensen, 1996; Jenkyns et al., 2017) (Fig. 2).

3. The OAE 2 and PCE record at Clot Chevalier (Vocontian Basin, SE France)

The Clot Chevalier section (Vocontian Basin, SE France) consists of a 35 m-thick succession of limestones and marls deposited at a paleolatitude of $\sim 32^\circ\text{N}$ (Figs. 1B, C and 3). The section includes a 28 m-thick interval of organic-rich marls belonging to the Thomel Level, the local equivalent of the Donatelli Level and lithological expression of OAE 2 (e.g., Crumière, 1990), which has been subdivided into four lithological units: Th 1 to Th 4 (after Jarvis et al., 2011). Units Th 1 and Th 3 consist of grey marls with maximum TOC content of 1.5% (wt), while Th 2 and Th 4 consist of marly limestones with lower TOC content (Gale et al., 2019; Fig. 3). The base of Th1 is a sharply defined bioturbated surface indicating a minor hiatus and is correlative with the sub-Plenus erosion surface, suggesting erosion and/or non deposition and/or dissolution regionally developed in this stratigraphic interval (Gale et al., 2019). Unit Th 1 is thinner compared to other sections of the Vocontian Basin, and unit Th 2 is glauconitic-rich, thus the onset of the carbon-isotope positive excursion and of OAE 2 occur within a relatively condensed stratigraphic interval (Gale et al., 2019). By contrast, unit Th 3 is unusually expanded at Clot Chevalier (Gale et al., 2019). Given the shape of the $\delta^{13}\text{C}$ excursion and the different relative thickness of the

stratigraphic intervals between peak a and b compared to Eastbourne and other complete sections of the Vocontian Basin (e.g., Pont d'Issole: Grosheny et al., 2006; Jarvis et al., 2011), it is likely that the condensed stratigraphic interval at Clot Chevalier also includes the base of unit Th 3 (Figs. 2–3).

No Boreal macrofossils are found in this section but cooling during the PCE is suggested by a positive $\delta^{18}\text{O}$ excursion of bulk carbonates that was used to constrain the event in Gale et al. (2019), and by a drop in the $\Delta^{13}\text{C}$ values in unit Th 2 and in the lowermost part of unit Th 3 (Fig. 3).

4. The Plenus Carbon Isotope Excursion (Plenus CIE)

The stratigraphic extension of the PCE interval and the number of cooling episodes within the PCE in the English Chalk (Fig. 2) and elsewhere (O'Connor et al., 2020) have been differently interpreted by authors according to the range of the Boreal fauna, the $\delta^{18}\text{O}$ trends and/or the proxies to trace changes in atmospheric $p\text{CO}_2$ levels (Gale and Christensen, 1996; Jarvis et al., 2011; Jenkyns et al., 2017; O'Connor et al., 2020; Jeans et al., 2021). For this reason, and given the global nature of the carbon-isotope excursion, O'Connor et al. (2020) suggested to constrain the PCE to the stratigraphic interval comprised between the $\delta^{13}\text{C}$ peak a and b (Plenus CIE in Fig. 2), whether or not evidence for cooling is available.

We follow the approach of chemostratigraphically constraining the PCE interval, but the Plenus CIE is herein extended from the onset of the second $\delta^{13}\text{C}$ build-up (i.e., below peak a) to peak b to account for the geochemical evidence for cooling and for the occurrence of Boreal species that are observed in the English Chalk from the top of Bed 1 and base of Bed 2, respectively (Fig. 2; see also the $\delta^{18}\text{O}$ record at Dover: Lamolda et al., 1994).

Therefore, the term Plenus CIE refers herein to the stratigraphic interval between the second $\delta^{13}\text{C}$ build-up (i.e., below peak a) and peak b at Eastbourne (Fig. 2) and Clot Chevalier (Fig. 3), while the term Plenus Cold Event (PCE) refers to the time interval(s) characterized by cooling identified based on the geochemical proxies and/or fossil record within the Plenus CIE.

5. Methodology

Rock samples from both sections were processed with acetic acid to obtain washed residues containing isolated planktonic foraminifera (see Lirer, 2000 and Falzoni et al., 2016b for detailed procedure), with the exception of samples from the Plenus Marl that were treated with peroxide water following the standard methodology.

The planktonic foraminiferal biostratigraphy applied in this study follows Falzoni and Petrizzo (2020) for Eastbourne, and Falzoni et al. (2016b) for Clot Chevalier. The stratigraphic range of relevant species is further discussed in section 6.

Quantitative analyses were performed at the species level on the $>125\ \mu\text{m}$ size fraction on a total number of 105 samples (68 for Eastbourne and 37 for Clot Chevalier) with a sampling resolution of 10 cm (Eastbourne) and of 20 to 120 cm (Clot Chevalier). Relative abundances, reported in Supplementary Table 1 (Eastbourne) and Supplementary Table 2 (Clot Chevalier), are based on the identification and counting of >300 planktonic foraminiferal specimens per sample to ensure statistical reproducibility (CLIMAP, 1976), unless samples contain less than 300 specimens. Three samples at Eastbourne (interval from 14.9 to 15.7 m) and several samples belonging to unit Th 3 at Clot Chevalier yield less than 20 specimens in the $>125\ \mu\text{m}$ size fraction. At Eastbourne, these three samples were selected from an interval characterized by abundant pelagic microcrinoids (see Gale, 2019), echinoids and fragments of other macroinvertebrates, suggesting changes in the depositional environment and/or in the ecologic features of

surface waters. Unit Th 3 at Clot Chevalier is characterized by abundant radiolaria and relatively high TOC content (Gale et al., 2019), thus the very rare occurrence of planktonic foraminifera in this interval is likely due to the establishment of eutrophic conditions.

The taxonomy applied in this study follows the online database for planktonic foraminifera available at <https://www.mikrotax.org> (Huber et al., 2016), which incorporates species original descriptions and illustrations and subsequent taxonomic studies, unless differently specified in Falzoni et al. (2016b) and Falzoni and Petrizzo (2020). Planispiral taxa include species that have been traditionally assigned to the polyphyletic genus *Globigerinelloides*, which is currently under revision (see taxonomic notes in Petrizzo et al., 2017). The taxonomy herein applied for this group follows Huber et al. (2021, under review), who assigned the species *bentonensis* to the new genus *Laeviella*. Biserial taxa include species of the genera *Protoheterohelix* and *Planoheterohelix* (following Haynes et al., 2015) that are herein grouped together as they are extremely rare in the >125 µm size fraction in the sections studied and are inferred to share similar paleoecological preferences (Petrizzo et al., 2020, 2021). The list of species included in each genus or morphogroup is reported in Supplementary Table 3 with the author(s) and year of description.

6. Biostratigraphic range of relevant planktonic foraminiferal species at Eastbourne and Clot Chevalier

The Plenus CIE as defined in this study is constrained by 4 relevant planktonic foraminiferal extinctions that are regarded as highly reliable for correlation at low-to-middle latitudes (Falzoni et al., 2018a), namely: 1) the HO (highest occurrence) of *Thalmaninella deeckeii* and of 2) *Thalmaninella greenhornensis* below the Plenus CIE, 3) the HO of *Rotalipora cushmani* that falls within the Plenus CIE, and 4) the HO of *Laeviella bentonensis* (= *Globigerinelloides bentonensis* of previous authors) at the top of the

Plenus CIE (Figs. 2–3). These events are documented approximately at the same stratigraphic level at Eastbourne and Clot Chevalier. However, the extinction of *R. cushmani* falls in a slightly earlier stratigraphic interval below peak a in the latter section, likely because of its rare occurrence at the top of its stratigraphic range, which coincides with a condensed and glauconitic-rich interval reflecting episodes of reduced or interrupted sedimentation (see Falzoni et al., 2016b for further explanation). The shape of the $\delta^{13}\text{C}$ profile in this interval and the position of peak a might have been also slightly modified by brief episodes of interruption of sedimentation. In fact, peak a falls in the middle of unit Th 2 at Pont d’Issole (Jarvis et al., 2011), whereas it falls at the top of unit Th 2 at Clot Chevalier (Fig. 3). Moreover, the highest $\delta^{18}\text{O}$ values within the Plenus CIE coincide with peak a at Clot Chevalier, while they fall above peak a in other stratigraphic sections of the Vocontian Basin (Jarvis et al., 2011; Danzile et al., 2020) as observed at Eastbourne. Therefore, the earlier extinction of *R. cushmani* at Clot Chevalier likely relies on the peculiar sedimentation patterns of this locality, while this bioevent in other deep-sea sections of the Vocontian Basin (e.g., Pont d’Issole: Grosheny et al., 2006, 2017) is clearly synchronous with Eastbourne.

Two planktonic foraminiferal species, *Praeglobotruncana plenusiensis* (Fig. 4.1) and *Muricohedbergella kyphoma* (Fig. 4.2), occur at Eastbourne in Bed 2 and 4, and in Bed 4 to 5, respectively, and their occurrences parallel the stratigraphic distribution of Boreal macrofossils, although single specimens of *M. kyphoma* also occur in two samples at the base of the section (Falzoni and Petrizzo, 2020; Fig. 2). *Praeglobotruncana plenusiensis* (at 4.8 m; Fig. 4.3) and *M. kyphoma* (at 4.8 and 5.7 m; Fig. 4.4) are also recognized in two glauconitic-rich samples at Clot Chevalier within the Plenus CIE (Fig. 3), although in a slightly earlier stratigraphic interval compared to Eastbourne, as observed for the extinction of *R. cushmani*, and likely depending on the condensed nature of this stratigraphic interval. In addition, the absence of *P. plenusiensis* and *M. kyphoma* at the

trough between peak a and b, where they are common at Eastbourne, might rely on the very rare occurrence of planktonic foraminifera in the organic-rich levels at the base of unit Th 3 at Clot Chevalier (4 specimens at 6.9 m and 16 specimens at 7.8 m).

Praeglobotruncana plenusiensis and *M. kyphoma* have been rarely documented in other localities: *Praeglobotruncana plenusiensis* was described from the uppermost *R. cushmani* to lowermost *W. archaeocretacea* Zone at Eastbourne (Falzoni and Petrizzo, 2020). A specimen illustrated by Leckie (1985; p. 147, pl. 2, figs. 2–3) from a correlative stratigraphic interval at Pueblo (WIS) and assigned to *Praeglobotruncana praehelvetica* might fall in its range of species variability (see taxonomic discussion in Falzoni and Petrizzo, 2020), but the absence of the illustration of the umbilical side prevents the full comparison with the type specimens of *praehelvetica* and *plenusiensis*, thus the occurrence of the latter species in the WIS needs to be verified with further studies. *Muricohedbergella kyphoma* was described from Hokkaido (Japan), where it shows a very discontinuous stratigraphic range and occurs in one sample below the first appearance of *R. cushmani* and in two samples above its extinction approximately falling in the middle *W. archaeocretacea* Zone in between $\delta^{13}\text{C}$ peak b and c (Hasegawa, 1999; Takashima et al., 2011).

7. Litho-, bio- and chemostratigraphic correlation of Clot Chevalier and Les Lattes (Vocontian Basin)

The litho-, bio- and chemostratigraphic record of Clot Chevalier is correlated with Les Lattes (Fig. 5) with the aim of stratigraphically constraining the occurrence of Boreal microfossils in the Vocontian Basin (Gale and Christensen, 1996) and of comparing the occurrence of Boreal microfossils with the planktonic foraminiferal data collected in this study.

The Cenomanian–Turonian transition at Les Lattes is extremely expanded (about 150 m). The section was deposited in a relatively shallow depositional environment, likely on the slope (Grosheny et al., 2017), as indicated by lithological characteristics, including the abundance of sandy layers, and paleontological evidences such as the occurrence of benthic taxa typical of shallow environments and of rare planktonic foraminifera (Gale and Christensen, 1996; Grosheny et al., 2017). Moreover, no black shales occur in this section and sediments are strongly bioturbated suggesting a well-oxygenated sea floor (Gale and Christensen, 1996; Grosheny et al., 2017). These observations indicate a shallower depositional environment compared to Clot Chevalier and to the other basinal sections of the Vocontian Basin (e.g., Pont d'Issole: Grosheny et al., 2006), where the Cenomanian–Turonian boundary interval is less than 35 m-thick and includes organic-rich layers (Gale, pers. comm., 2020).

Nevertheless, the Cenomanian–Turonian boundary interval at Clot Chevalier and Les Lattes is remarkably similar in several other litho-, bio- and chemostratigraphic features. First of all, the onset of the $\delta^{13}\text{C}$ positive excursion corresponds to the top of a bed bundle at Les Lattes (Grosheny et al., 2017) and to an erosional surface at Clot Chevalier (Gale et al., 2019), both marking a lithological change from carbonate-rich lithologies to marlstones (Lower Recessive Interval, LRI, at Les Lattes; Grosheny et al., 2017) or marls with higher TOC content (unit Th 1 at Clot Chevalier; Gale et al., 2019) (Fig. 5). The LRI of sections deposited at shallower depth is considered correlative to the Lower Black Shale (LBS) of deeper sections of the Vocontian Basin (Grosheny et al., 2017), and the latter coincides with unit Th 1 of Jarvis et al. (2011) and Gale et al. (2019) (Fig. 5).

The overlying stratigraphic interval is characterized by the occurrence of two glauconitic-rich levels: the lowermost level contains the highest occurrence of *R. cushmani* in both sections, while the uppermost glauconitic level lies just below the Boreal macrofossil assemblage at Les Lattes (Fig. 5). However, the lowermost glauconitic-rich

level is identified above an omission surface at the top of LRI at Les Lattes, while it is separated from the top of unit Th 1 by a ~1 m-thick stratigraphic interval corresponding to the lower part of unit Th 2 at Clot Chevalier (Fig. 5). This stratigraphic interval might be missing (not deposited/eroded) at Les Lattes, and this hypothesis would explain the absence of a clear second build-up in the $\delta^{13}\text{C}$ profile of this section, complicating the identification of the Plenus CIE.

Nevertheless, the glauconitic-rich interval at Les Lattes and the upper part of unit Th 2 at Clot Chevalier are likely correlative, and the bed violating the Boreal macrofossil assemblage in the former section is tentatively correlated with the bed lying just above the uppermost glauconitic-rich level at Clot Chevalier (*P. plenus* correlative bed in Fig. 5). This interpretation is supported by the following evidences: (a) the overlying stratigraphic interval is characterized by a sharp lithological change and likely contains peak b in both sections; and (b) the omission surface below the upper glauconitic-rich level at Les Lattes is likely correlative with that found below Bed 4 at Eastbourne (Gale and Christensen, 1996), thus it falls close to the trough between peak a and b.

8. Relative abundances of planktonic foraminifera at Eastbourne and Clot Chevalier

The relative abundances of planktonic foraminifera at Eastbourne and Clot Chevalier are plotted in Fig. 6A-B and presented below.

8.1 Eastbourne

Assemblages are generally dominated by the trochospiral unkeeled *Muricohedbergella* (up to 70%), *Whiteinella* (up to 63%) and *Pseudoclavihedbergella* (up to 67%) (Fig. 6A). Single- and double-keeled taxa usually represent a minor (<20%) component of the assemblage with few exceptions: *Rotalipora* reaches 46% of the

assemblage in one sample at 3.6 m and varies from 18 to 29% in Plenus Marl Bed 1. The abundance of *Praeglobotruncana* and *Dicarinella* is usually <10%, but it reaches 50% in Bed 2 and 3, and 40% in Bed 4, respectively. The relative abundance of *P. plenusiensis* is always lower than 1%. *Muricohedbergella kyphoma* and *M. planispira* together represent up to 34% of the assemblage in Bed 4 and 5 and are rare to absent in the other stratigraphic intervals. Planispiral taxa and *Marginotruncana* do not exceed 14% and 7% of the assemblage, respectively. The relative abundances of *Thalmaninella* and of biserial taxa is lower than 2% in the >125 μm size fraction. Biserial taxa are slightly more abundant in the >38 μm size fraction, but this small-sized assemblage is dominated by calcispheres.

8.2 Clot Chevalier

The planktonic foraminiferal assemblage at Clot Chevalier is dominated by *Praeglobotruncana* (up to 57%), *Whiteinella* (up to 40%), *Helvetoglobotruncana* (up to 34%), *Dicarinella* (up to 31%), and *Rotalipora* (up to 27%) (Fig. 6B). The relative abundance of *P. plenusiensis* is less than 1%. *Pseudoclavihedbergella* and *Muricohedbergella* represent minor components of the assemblage (usually <25%), with the exception of four samples (at 10.8, 11.7, 15.9 and 17.4 m), where planktonic foraminifera are very rare (less than 6 specimens occur in the >125 μm size fraction), and these taxa represent up to the 100% of the specimens. *Muricohedbergella planispira* and *M. kyphoma* together show their maximum abundance (8%) at 4.8 m and less than 1% of the assemblage in the overlying sample at 5.4 m. The relative abundance of biserial taxa is lower than 1% and are found only in few samples in the >125 μm size fraction. Sample at 12.6 m does not contain planktonic foraminifera larger than >125 μm , but small-sized planispiral and biserial taxa are documented in the >38 μm size fraction (Falzoni et al.,

2016b). The dominant component of the microfossil assemblage is represented by radiolaria in the lower and middle part of unit Th 3 (Fig. 6B).

8.3 Differences and similarities among microfossil assemblages at Eastbourne and Clot Chevalier.

The microfossil assemblages show some differences at Eastbourne and Clot Chevalier, including the occurrence of very abundant radiolaria and of *Helvetoglobotruncana praehelvetica* in the latter section. Moreover, there is an increase in the relative abundances of *Praeglobotruncana*, *Dicarinella* and *Marginotruncana* in the lower Turonian of Clot Chevalier that is not observed at Eastbourne, where assemblages are dominated by the trochospiral unkeeled taxa of the genera *Whiteinella* and *Muricohedbergella*.

Conversely, other features of the assemblages are similar in both sections: a) *Dicarinella*, *Praeglobotruncana* and *Muricohedbergella* increase in abundance within the Plenus CIE compared to the stratigraphic interval slightly above and below, although such increase is impressive at Eastbourne and less evident at Clot Chevalier; b) both assemblages yield *P. plenusensis* and *M. kyphoma* within the Plenus CIE, although with a significantly higher abundance of *M. kyphoma* at Eastbourne; c) *Thalmanninella*, *Rotalipora* and the planispiral taxa progressively disappear below, within and above the Plenus CIE, respectively; d) *Pseudoclavihedbergella* shows relatively low abundances within the Plenus CIE, whereas it shows an abundance peak (67% at Eastbourne and 80% at Clot Chevalier) slightly above the Plenus CIE, and subsequently disappears from the assemblage. The highest occurrences of *Thalmanninella* and *Rotalipora* represent true extinctions, whereas the disappearance of planispiral taxa and of *Pseudoclavihedbergella* is a temporary event (eclipse: Falzoni and Petrizzo, 2020), because the same species re-occur in younger assemblages.

The differences and similarities observed among planktonic foraminiferal assemblages are interpreted below according to the paleoecological preferences and paleobiogeographic distribution patterns of Cenomanian–Turonian planktonic foraminifera.

9. Paleoecology and paleobiogeographic distribution of Cenomanian–Turonian planktonic foraminifera

The paleoecological preferences of Cenomanian–Turonian planktonic foraminiferal taxa are mainly based on the intra-sample offsets in their stable-isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) composition, and on their biogeographic distribution patterns across latitudes. Additional information is provided by their abundance in near coastal, hemipelagic or pelagic settings which indicates tolerance to different salinity levels and capability to complete the life cycle in shallow or deeper environments (e.g., Leckie, 1987; Leckie et al., 1998; Hart, 1999; Premoli Silva and Sliter, 1999; Huber et al., 1999; Bornemann and Norris, 2007; Petrizzo et al., 2008; Ando et al., 2010; Petrizzo et al., 2020).

The paleoecology and paleobiogeographic distribution patterns of Cenomanian–Turonian planktonic foraminifera are discussed below and summarized in Fig. 7.

9.1 Stable-isotope paleoecology and life strategies of Cenomanian–Turonian planktonic foraminifera

Whiteinella species typically yield a stable-isotopic signature suggesting adaptation to the warmest/shallowest layers of the water column (Huber et al., 1999; Wendler et al., 2013; Falzoni et al., 2016a; Petrizzo et al., 2020, 2021) with the possible exception of *W. baltica* that may have lived slightly deeper (Huber et al., 1995; Bornemann and Norris, 2007; Petrizzo et al., 2020). Previous authors have noted the dominance of this group in lower Turonian assemblages (e.g., Zone à grosses globigerines: Sigal, 1955) and

suggested that *Whiteinella* was a meso- to eutrophic taxon characterized by a high reproductive potential and possible adaptation to upwelling regions (Hart, 1999; Premoli Silva and Sliter, 1999). However, upwelled waters are typically cold and yield small-sized species, therefore this interpretation is difficult to reconcile with the clear preference toward warm waters that is derived from their stable-isotope composition, and with an average test size of 300–700 μm for adult specimens (Falzoni et al., 2018b). By contrast, the increased abundance of *Whiteinella* in Tanzania was associated to a diminished siliciclastic input from land that likely led to a more oligotrophic upper water column (Petruzzo et al., 2017).

A similar preference toward warm/surface and relatively oligotrophic layers of the water column is inferred from the limited stable-isotope data available for their descendant *Helvetoglobotruncana* species (Wendler et al., 2013; Huber and Petruzzo, 2014; Falzoni et al., 2016a).

The paleoecological preferences of planispiral taxa are still poorly constrained owing to their generally small-size, which complicates the acquisition of species-specific stable-isotope data, and the unclear taxonomy of this polyphyletic group (Huber et al., 2021, under review). However, planispirals inhabited the thick winter mixed layer in the Albian–Cenomanian of the western Atlantic Ocean (Blake Nose: Leckie et al., 2002; Petruzzo et al., 2008) and in the latest Cenomanian–earliest Turonian (within OAE 2) at southern latitudes in the southeast Indian Ocean (Mentelle Basin: Petruzzo et al., 2021), and were absent during episodes of reduced stratification in the Cenomanian–Turonian of the WIS (Elderbak and Leckie, 2016), suggesting adaptation to cool waters within a relatively stratified oligo-mesotrophic upper water column.

Rotalipora and *Thalmaninella* (rotaliporids) stable isotopes suggest that this group inhabited cold/deep layers of the water column close to the thermocline, although with some differences observed among species and through time (Huber et al., 1999; Petruzzo

et al., 2008; Ando et al., 2010). Accordingly, rotaliporids are typically found in pelagic settings of the Tethyan Realm and have been traditionally interpreted as strictly oligotrophic, with *Thalmanninella* usually regarded as the most stenotopic taxon (Leckie, 1987; Leckie et al., 1998; Hart, 1999; Premoli Silva and Sliter, 1999). Dwarf specimens of *R. cushmani* were observed in sediments deposited in corridors of about 80 m of estimated depth, separating a series of carbonate platforms in Central Sahara (Grosheny et al., 2017). However, the occurrence of fully developed large-sized (400-800 μm) morphotypes in deeper water settings (Falzoni et al., 2012b) and in the pelagic Tethyan Realm (Coccioni et al., 2016) indicates that this species required a relatively thick and stratified upper water column to complete its life cycle.

Pseudoclavihedbergella yields stable isotope data supporting a deep water habitat at or below the thermocline within a well-stratified water column (Norris and Wilson, 1998; Coxall et al., 2007) with possible adaptation to the nutrient-rich and oxygen-poor layers of the nutricline (Coccioni et al., 2006; Coxall et al., 2007). Episodic increases in abundance of *Pseudoclavihedbergella* are found in several basins within the Tethyan Ocean below and above the Bonarelli Level and equivalents, indicating tolerance to high nutrient concentrations before and after black shale deposition (Coccioni et al., 2006).

Limited stable-isotope data are available for Cenomanian–Turonian biserial species, but they usually yield stable-isotope values suggesting adaptation from shallow to intermediate layers of the upper water column (Huber et al., 1999; Wilson et al., 2002; Wendler et al., 2013). Biserial taxa likely represented the most eutrophic planktonic foraminiferal group in this stratigraphic interval (e.g., Leckie et al., 1998; Premoli Silva and Sliter, 1999; Elderbak and Leckie, 2016) and their acme (i.e., *Heterohelix* shift) documented within $\delta^{13}\text{C}$ peak b and c in the WIS and in several Tethyan and Central Atlantic sections is indicative of high nutrient concentrations and of a poorly stratified upper water column (e.g., Leckie et al., 1998; Nederbragt and Fiorentino, 1999; Caron et

al., 2006; Keller et al., 2008; Falzoni et al., 2018a). However, increases in biserials were also observed in normal environmental settings in the Turonian (Huber et al., 1999; 2017; Haynes et al., 2015) suggesting that they were adapted to a wide range of water mass conditions and/or benefitted from seasonally favorable ecological contexts.

The stable-isotope signature of *Muricohedbergella* species indicates adaptation to relatively cold/deep layers of the water column in open ocean settings at low latitudes (Norris and Wilson, 1998; Wilson et al., 2002; Ando et al., 2010; Petrizzo et al., 2008), but they likely inhabited shallower layers at the higher latitudes of the Southern Hemisphere, probably because sea-surface waters were cooler (Falzoni et al., 2016a; Petrizzo et al., 2020, 2021). Nevertheless, *Muricohedbergella* shows great tolerance to different ecological conditions and lived from low salinity coastal environments to normal salinity open ocean settings, clearly pointing to an opportunistic meso-eutrophic life strategy (e.g., Leckie, 1987; Leckie et al., 1998; Hart, 1999; Premoli Silva and Sliter, 1999).

Praeglobotruncana species yield intermediate oxygen isotope values between surface and thermocline taxa and have been interpreted as intermediate or winter mixed layer dwellers (Petrizzo et al., 2008, 2020; Falzoni et al., 2016a), although they might have lived deeper near the thermocline (Huber et al., 1999; Ando et al., 2010). Interestingly, *Praeglobotruncana* shifted from the thermocline to the mixed layer across the Albian–Cenomanian transition at Blake Nose in the NW Atlantic Ocean, when surface waters became cooler and poorly stratified (Ando et al., 2010).

Dicarinella possesses a stable-isotope signature suggesting adaptation to cold waters and lived close to the permanent thermocline in different localities at low to mid-latitudes (Huber et al., 1999; Wendler et al., 2013; Falzoni et al., 2016a; Petrizzo et al., 2020). A shift toward a shallower habitat at higher latitudes (as observed for *Muricohedbergella*) is consistent with the stable-isotope data obtained for several *Dicarinella* species in the Southern Hemisphere (Petrizzo et al., 2020, 2021).

A shallower habitat of *Muricohedbergella* and *Dicarinella* at higher latitudes and the migration of *Praeglobotruncana* toward shallower layers of the water column as a response to climate cooling at the Albian/Cenomanian boundary suggest that the main ecological factor controlling their distribution and abundance was the sea-surface temperature rather than the depth, and that these taxa do not require a well-stratified water column to thrive and complete their life cycle. This interpretation is consistent with a preference toward meso-eutrophic (*Muricohedbergella*) or mesotrophic (*Praeglobotruncana* and *Dicarinella*) conditions that were suggested in previous studies (Hart, 1999; Premoli Silva and Sliter, 1999).

Marginotruncana species likely adopted different life strategies. During their interval of maximum diversification in the late Turonian–Santonian, different species inhabited all available ecological niches from the mixed layer to the thermocline (Falzoni et al., 2016a; Petrizzo et al., 2020, 2021). Currently, there are no stable-isotope data available for the species occurring at Eastbourne and Clot Chevalier (mostly represented by *M. caronae*), but their relative abundances show similar trends compared to *Dicarinella* and *Praeglobotruncana* suggesting similar preferences toward cold waters, although *Marginotruncana* is usually regarded as a more oligotrophic taxon (Premoli Silva and Sliter, 1999).

9.2 Paleobiogeographic distribution of Cenomanian–Turonian planktonic foraminifera in Northern Europe

Whiteinella, *Rotalipora*, *Thalmaninella*, *Pseudoclavhedbergella*, the planispiral and biserial taxa represent the dominant group of a typical Tethyan assemblage with a paleobiogeographic distribution mainly confined to the tropical-subtropical latitudinal belts.

These taxa progressively decrease in abundance toward the high latitudes, with *Whiteinella* approaching the paleolatitude of 55° or 60° in the Northern and Southern

Hemisphere, respectively (e.g., Leckie, 1987; Leckie et al., 1998; Hart, 1999; Premoli Silva and Sliter, 1999; Gradstein et al., 1999; Petrizzo et al., 2020). The absence/rarity/delayed occurrence of *Helvetoglobotruncana* outside the oligotrophic Tethyan Realm in the lower Turonian (Huber and Petrizzo, 2014 and reference therein) suggest a more stenotopic ecology compared to their whiteinellid ancestors that might be explained by a limited tolerance toward a less stratified water column and/or higher nutrient concentrations. Accordingly, the northern European record of *Helvetoglobotruncana* coincides with Lincolnshire (eastern England; paleolatitude of about 45°N) (Hart et al., 1993). Similarly, no planispiral taxa are documented north of this locality in the same stratigraphic interval (Hart et al., 1993; Gradstein et al., 1999). Pseudoclavihedbergellids and rotaliporids progressively disappear moving northward along the eastern coast of UK and are very rare in the northern North Sea (Moray Firth region) that broadly coincides with the northern limit of their paleobiogeographic distribution (Hart et al., 1989; King et al., 1989). Rare specimens assigned to *Pessagnoina simplex* (morphologically similar and likely phylogenetically related to *Pseudoclavihedbergella simplicissima*, see Georgescu, 2009) and a single specimen of *Thalmarinaia cf. greenhornensis* are also documented in the southernmost hole drilled along the eastern margin of the Norwegian Sea at a paleolatitude of about 50°N, but both taxa do not occur further north in the late Cenomanian (Gradstein et al., 1999). Biserial taxa occur throughout the Cenomanian–Turonian transition at Eastbourne (Keller et al., 2001; Falzoni and Petrizzo, 2020), and are generally regarded as having a wide paleobiogeographic distribution (Premoli Silva and Sliter, 1999). However, they are not documented along the eastern coast of UK above the extinction of *R. cushmani* throughout the uppermost Cenomanian (Hart et al., 1993), although this gap in their stratigraphic record might have been amplified by the small size and poor preservation of specimens. Moreover, biserial taxa might have been sometimes overlooked (e.g., in King et al., 1989) owing to their poor biostratigraphic value in this

interval. However, very rare specimens are reported from the upper Cenomanian–lower Turonian of the Norwegian Sea (Gradstein et al., 1999), testifying their rare occurrence north of 50°N.

By contrast, the paleobiogeographic distribution of *Muricohedbergella*, *Praeglobotruncana*, *Dicarinella*, and *Marginotruncana* is broad and supports their preference toward cooler waters: *Muricohedbergella* has a cosmopolitan distribution, but its relative abundance progressively increases toward the high latitudes, where the tropical taxa become rare to absent (e.g., Hart, 1999; Premoli Silva and Sliter, 1999; Gradstein et al., 1999). *Praeglobotruncana* and *Dicarinella* were also widely distributed across latitudes (Premoli Silva and Sliter, 1999), with the exception of the WIS, where, however, keeled taxa are very rare and assemblages are dominated by unkeeled trochospiral and biserial taxa throughout the latest Cenomanian–Turonian (Leckie et al., 1998; Elderbak and Leckie, 2016). Overall, *Praeglobotruncana* and *Dicarinella* generally show higher relative abundances in Northern Europe (King et al., 1989; Gradstein et al., 1999) compared to low latitude Tethyan or Atlantic localities (e.g., Tunisia: Nederbragt and Fiorentino, 1999; Morocco: Keller et al., 2008). Accordingly, the stratigraphic interval correlative with the Plenus Marl is characterized by abundant *Praeglobotruncana* in the chalk facies of the central and southern North Sea at a paleolatitude of 40–50°N (*Praeglobotruncana* Zone of King et al., 1989) and by floods of *Dicarinella* and hedbergellids at higher latitudes offshore Norway and in the northern North Sea at a paleolatitude of 50°–55°N (Gradstein et al., 1999), which coincides with the northernmost record of planktonic foraminifera in Europe.

Marginotruncana is at the beginning of its stratigraphic range and is globally very rare in this stratigraphic interval, but it occurs in the northern North Sea and in the Norwegian Sea at a paleolatitude of 55°N, where this genus shows relatively higher species diversity compared to lower latitude sites in the lower Turonian (King et al., 1989; Gradstein et al., 1999).

10. Planktonic foraminiferal abundances, oxygen isotope and $\Delta^{13}\text{C}$ trends at Eastbourne and Clot Chevalier

The cumulative abundances of planktonic foraminifera at Eastbourne and Clot Chevalier separated in two groups are plotted in Fig. 8. The first group (Group 1 in Figs. 7 and 8) includes the genera *Whiteinella*, *Rotalipora*, *Thalmanninella*, *Pseudoclavhedbergella*, the planispiral and biserial taxa, which share a paleobiogeographic distribution and/or higher relative abundances in the tropical-subtropical latitudinal belt. The second group (Group 2) includes the genera *Muricohedbergella*, *Praeglobotruncana*, *Dicarinella*, and *Marginotruncana* that show a broader or cosmopolitan distribution and/or higher relative abundances at mid-high latitudes (Figs. 7 and 8).

The cumulative abundances of these two assemblages are plotted against the available proxies for paleotemperature trends ($\delta^{18}\text{O}$ values of bulk carbonates and, for Eastbourne, of macrofossils shells) and atmospheric $p\text{CO}_2$ levels ($\Delta^{13}\text{C}$) (Fig. 8), with the aim of identifying possible causal links between variations of these environmental parameters and abundances of planktonic foraminiferal taxa.

10.1. Eastbourne

In the absence of a significant diagenetic overprint, the $\delta^{18}\text{O}$ values of bulk samples provide a mixed signal registered by pelagic and benthic organisms, but the dominant component is usually represented by the coccolith-rich fine fraction that calcifies in the photic zone. Oxygen-isotope data of macrofossils at Eastbourne were determined on well-preserved belemnites (*P. plenus*), brachiopods (mainly *Orbirhynchia multicostata* and *Orbirhynchia wiesti*) and bivalves (oysters, *Inoceramus pictus* and *Spondylus* sp.) (Voigt et al., 2006), the former actively swimming in the relatively shallow waters of the European

epicontinental basins (Christensen, 1997; Wilmsen et al., 2010), and the latter two tracing temperature variations of bottom waters (Voigt et al., 2006) at about 300 m depth in the Anglo-Paris Basin (Hay, 2008).

Generally, the $\delta^{18}\text{O}$ values exhibited by macrofossils parallel the $\Delta^{13}\text{C}$ trends and suggest that changes in the temperature of the relatively shallow water column at Eastbourne were ultimately linked to changes in the atmospheric $p\text{CO}_2$ levels (Fig. 8). Little mismatches between these two proxies and the $\delta^{18}\text{O}_{\text{bulk}}$ trends (e.g., between 14 and 16 m) might be related to a different sampling resolution, and/or diagenetic alteration affecting one or more proxies. The influence of salinity on the $^{18}\text{O}/^{16}\text{O}$ composition of samples cannot be isolated from that of paleotemperatures but it is generally considered very low at Eastbourne because of the limited siliciclastic input observed in the section and significant distance from the land (Pearce et al., 2009).

The relative abundances of planktonic foraminiferal Group 1 vs. Group 2 broadly parallel the trend shown by $\delta^{18}\text{O}$ (particularly those exhibited by macrofossils) and $\Delta^{13}\text{C}$ values throughout the section. Group 1 generally shows higher relative abundances when geochemical proxies indicate higher atmospheric CO_2 concentrations and water temperature (e.g., between 6 and 8.2 m and between 14 and 15 m), while the opposite is observed for Group 2 (e.g., between 8.5 and 12.5 m).

Geochemical data indicate that warm conditions prevailed at the onset of OAE 2 (Plenus Marl Bed 1), likely resulting from the injection of volcanogenically-derived greenhouse gases in the ocean-atmosphere system (e.g., Leckie et al., 2002; Erba, 2004; Turgeon and Creaser, 2008; du Vivier et al., 2014). No Boreal macrofossils are documented in this interval in the Anglo-Paris Basin and sea-surface waters were dominated by planktonic foraminiferal taxa of Group 1 (up to the 80% of the assemblage) (Fig. 8).

A first evidence for cooling within the Plenius CIE is testified by a shift in the $\delta^{18}\text{O}$ and $\Delta^{13}\text{C}$ values from the uppermost part of Bed 1 to the middle part of Bed 3, suggesting that the first cooling episode lasted slightly longer than indicated by Jenkyns et al. (2017) and Jeans et al. (2021) (i.e., to the top of Bed 2; see Fig. 2). In this interval, we observe the occurrence of the bivalve *O. seminudum* at Dover (Gale and Christensen, 1996), the LO of the planktonic foraminiferal *P. plenusiensis*, and the sharp increase in the abundance of *Praeglobotruncana* (the dominant group) and of *Dicarinella* at Eastbourne (Fig. 8).

The overlying stratigraphic interval (upper part of Bed 3) shows a minor $\delta^{18}\text{O}$ negative excursion and slightly higher $\Delta^{13}\text{C}$ values, likely recording a transient and moderate warming episode that is supported by a gap in the stratigraphic distribution of Boreal macrofossils and is coeval to a slight increase in the abundance of Group 1 among planktonic foraminifera.

The interval between the base of Bed 4 and the top of Bed 5 is characterized by the highest $\delta^{18}\text{O}$ values (macrofossil shell: Voigt et al., 2004, 2006) and the maximum abundance and diversity of the Boreal macrofossil assemblage (Gale and Christensen, 1996; Paul et al., 1999), and likely records the second and coldest episode within the Plenius CIE. Planktonic foraminiferal assemblages yield the short-lived species *P. plenusiensis* and show an acme of *M. kyphoma* and of *Dicarinella* that together represent the 85% of the assemblage in the $>125\ \mu\text{m}$ size fraction. The composition of this assemblage yielding abundant *Dicarinella* and *M. kyphoma*, and rare *P. plenusiensis* is exclusive of this stratigraphic interval.

The interval from Bed 6 to Bed 7 records an abrupt decrease of the macrofossil $\delta^{18}\text{O}$ and a parallel increase of the $\Delta^{13}\text{C}$ values, both suggesting a return to warmer conditions, with temperature comparable or higher than those recorded in Bed 1. A single $\delta^{18}\text{O}$ data point of bulk carbonates at the base of Bed 7 (at 13 m) apparently indicates an opposite

trend, but the $^{18}\text{O}/^{16}\text{O}$ composition of this sample might be biased by diagenetic alteration. A second gap in the stratigraphic distribution of Boreal macrofossils and the recovery of Group 1 among planktonic foraminifera are observed in this interval (Fig. 8).

Macroinvertebrates from Bed 8 yield higher $\delta^{18}\text{O}$ values compared to those of Bed 7, although significantly lower than specimens of Bed 4 to 5, suggesting relative cooling compared to the underlying stratigraphic interval (Bed 7), but warmer temperatures compared to those registered in Bed 4 and 5. The same trend is reflected by changes in the $\Delta^{13}\text{C}$ values and is also supported by the occurrence of a single specimen of *P. plenus* in Bed 8 instead of the multiple specimens found in Bed 4–5 (Gale and Christensen, 1996). In Bed 8, the planktonic foraminiferal assemblages show an increase in the abundance of *Muricohedbergella* (mainly *M. delrioensis*) that replaces *Dicarinella* and *M. kyphoma* within Group 2. This assemblage is very similar to that observed in other intervals of the Grey and White Chalk that are characterized by slight positive $\delta^{18}\text{O}$ shifts but are not accompanied by the occurrence of Boreal macrofossils.

Geochemical proxies indicate that the deposition of the Ballard Cliff Member occurred when bottom water temperatures reached the maximum values within OAE 2 and coincided with the disappearance of Boreal macrofossils in the Anglo-Paris Basin. Planktonic foraminiferal taxa belonging to Group 1 represent up to the 80% of the assemblage in this stratigraphic interval.

In summary, by combining oxygen-isotope and $\Delta^{13}\text{C}$ trends, the stratigraphic range of Boreal macrofossils and the planktonic foraminiferal biostratigraphic and quantitative data presented in this study, we suggest that the PCE was represented by two distinct cooling episodes of shallow waters in the Anglo-Paris Basin, each one characterized by a distinctive planktonic foraminiferal assemblage: 1) a first moderate episode of cooling (uppermost part of Bed 1 to the middle of Bed 3), when assemblages are dominated by *Praeglobotruncana* and yield the short-lived *P. plenusiensis*, and 2) a second more severe

episode of cooling (base of Bed 4 to top of Bed 5), when assemblages are dominated by *Dicarinella* and *M. kyphoma*, and also yield *P. plenusiensis*. The third brief cooling event that is suggested by a weak positive shift of the benthic macrofossil $\delta^{18}\text{O}$ values and by the occurrence *O. seminudum* and of a single specimen of *P. plenus* (Bed 8) is not reflected by significant changes in planktonic foraminiferal assemblages that are equally dominated by whiteinellids (Group 1) and *M. delrioensis* (Group 2), in the absence of *P. plenusiensis* and *M. kyphoma* (Fig. 8).

10.2. Clot Chevalier

The $\delta^{18}\text{O}_{\text{bulk}}$ and $\Delta^{13}\text{C}$ trends are slightly decoupled at Clot Chevalier (e.g., within the Plenus CIE). The $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{org}}$ records in this section ideally reproduce the peaks and troughs of the positive excursion typically associated to OAE 2 (see Gale et al., 2019), and thus it is unlikely that their trends have been deeply affected by diagenetic alteration. Moreover, the excellent correlation ($R^2=0.91$) between the $\delta^{13}\text{C}$ of S-bound phytane and TOC suggests that the $\delta^{13}\text{C}_{\text{TOC}}$ records primary water-column processes of organic carbon-isotope fractionation (Gale et al., 2019). By contrast, the $\delta^{18}\text{O}_{\text{bulk}}$ is generally more susceptible to diagenetic alteration (e.g., Schrag et al., 1995) and changes in salinity are poorly constrained in the Cretaceous Basin.

At Clot Chevalier, the relative abundances of Group 1 vs. Group 2 closely mirror the $\delta^{18}\text{O}$ trends in the lower part of the section (0 to 7 m), and within most of the Plenus CIE (Fig. 8). There is no clear relationship between planktonic foraminiferal abundances and the $\delta^{18}\text{O}$ trends above 7 m, however, the abundances of both groups closely parallel the $\Delta^{13}\text{C}$ trend between 7 and 20 m, suggesting a close relationship between atmospheric $p\text{CO}_2$ levels and the composition of planktonic foraminiferal assemblages in the latest Cenomanian. Only two $\Delta^{13}\text{C}$ data points are available above 20 m, but the increased

abundance of taxa belonging to Group 2 in the upper part of unit Th 3 and Th 4 above peak c is correlative with a drop in the $\Delta^{13}\text{C}$ values and $p\text{CO}_2$ drawdown observed at Lambruisse (~5 km to the NE of Clot Chevalier, Fig. 1B; Danzelle et al., 2020).

At Clot Chevalier sea-surface warming at the onset of OAE 2 is testified by a decrease in the $\delta^{18}\text{O}$ values of bulk carbonates that parallels an increase in the abundance of planktonic foraminiferal taxa belonging to Group 1 (unit Th 1).

The overlying stratigraphic interval, broadly corresponding to unit Th 2 and to the lower part of unit Th 3, falls within the Plenus CIE. Among planktonic foraminifera, we highlight the occurrence of *M. kyphoma* and *P. plenusiensis* and an increase in the abundance of *Muricohedbergella planispira*, *Praeglobobulimina* and *Dicarinella* compared to the underlying stratigraphic interval. The maximum abundance of *M. kyphoma*, as well as the extinction of *R. cushmani*, fall in a slightly earlier stratigraphic interval (below peak a) compared to Eastbourne, but this diachronism might result from episodes of non deposition at Clot Chevalier, as discussed above (section 6). Moreover, it is unclear whether samples collected at 6.9 and 7.8 m still register cooling as suggested by the $\Delta^{13}\text{C}$ values or warmer conditions as suggested by the $\delta^{18}\text{O}$ trends. Assemblages show the dominance of Group 2 in these two samples, but estimation of the relative abundances is biased by the very rare occurrence of planktonic foraminifera in the >125 μm size fraction (4 and 16 specimens, respectively).

In summary, the very rare occurrence of planktonic foraminifera in the lowermost part of unit Th 3, the condensed nature of this stratigraphic interval, and/or the sampling resolution did not allow recognition of possible distinct cold episodes within the Plenus CIE at Clot Chevalier. Nevertheless, the highest $\Delta^{13}\text{C}$ values obtained for this section above peak b suggest higher atmospheric $p\text{CO}_2$ levels that likely forced a return to warmer sea-surface temperatures as confirmed by the dominance of Group 1 (50 to 80%) in this stratigraphic interval.

11. Significance of changes in the dominant planktonic foraminiferal groups

The dominance of planktonic foraminiferal Group 1 when geochemical proxies indicate warmer climate conditions and/or higher atmospheric $p\text{CO}_2$ concentrations, and of Group 2 when geochemical proxies indicate cooler waters and/or lower $p\text{CO}_2$ levels, suggests that the variations in sea-surface temperatures, which were primarily controlled by changes of the atmospheric CO_2 concentration (Laugié et al., 2020), exerted a primary control on the composition of the assemblages during the Cenomanian–Turonian transition in the Anglo-Paris and Vocontian basins. This is not surprising because sea-surface temperatures represent the principal ecological factor controlling planktonic foraminiferal vertical and latitudinal distributions in modern oceans (e.g., Bé and Tolderlund, 1971).

However, planktonic foraminifera are pelagic organisms passively transported by sea-surface currents, which regulate the heat transport from the equator to the poles and are ultimately controlled by the direction and strength of prevailing winds (e.g., trade winds, westerlies). Accordingly, the variations observed in the planktonic foraminiferal assemblages through stratigraphy do not simply reflect changes in sea-surface temperatures, but broadly mirror the dominance of different surface water masses characterized by different physico-chemical properties (i.e., temperature and salinity), each yielding a distinctive assemblage, as observed in Pleistocene and modern oceans (e.g., Peeters et al., 2004; Kucera et al., 2005).

The paleoecological preferences of planktonic foraminifera that dominated the assemblages at Eastbourne and Clot Chevalier during the warmer intervals (i.e., Group 1) suggest that most of them (i.e., *Rotalipora*, *Thalmanninella*, *Pseudoclavhedbergella* and the planispirals) are not expected to benefit directly from increasing sea-surface

temperatures, unless this condition would have favored the development of a thermally stratified and relatively oligotrophic upper water column with a strong temperature gradient between the warm surface layers and the thermocline. Given the properties of this water mass and the paleogeographic location of Eastbourne, we suggest that the abundance of Group 1 reflects the influence of the proto-Gulf Stream, which conveyed warm saline and thermally stratified surface waters originated in the Tethyan-Central Atlantic Ocean to the European mid-high latitudes. The proto-Gulf Stream was already established in the Valanginian (Early Cretaceous) according to the paleobiogeographic distribution of belemnites (Alsen and Mutterlose, 2009), and is predicted by modelling of the sea-surface circulation patterns and Nd isotope data of the mid-Cretaceous (Poulsen et al., 1998; Puc at et al., 2005).

By contrast, the paleoecological preferences and paleobiogeographic distribution patterns of *Muricohedbergella*, *Præglotruncana*, *Dicarinella*, and *Marginotruncana* (Group 2) indicate that these taxa were adapted to a cooler and relatively poorly stratified water mass. The strong affinities between this assemblage and the coeval fauna documented offshore Norway (Graustein et al., 1999) and in the northern North Sea (King et al., 1989) suggest that these taxa were carried at lower latitudes by Boreal waters and were capable of surviving at lower latitudes by shifting to a deeper and cooler layer of the water column, or alternatively, by becoming highly seasonal with peak abundances concentrated in the coldest season. This Boreal, poorly stratified, surface water mass was also relatively low-saline compared to the Tethyan-Central Atlantic surface waters, because of the reduced net evaporation at high latitudes and the fresh water discharge from surrounding continents (Hay and Floegel, 2012; Ladant et al., 2020). Additional evidence for a Boreal origin of this assemblage is provided by the acme of *Dicarinella* paralleling the stratigraphic range of *P. plenus* at Eastbourne indicating similar affinity to cold waters, and by the co-occurrence of *M. kyphoma* and *P. plenusiensis* with the Boreal

macrofossils and their absence or discontinuous stratigraphic distribution at lower latitudes (e.g., Japan: Hasegawa, 1999), suggesting that both species might be endemic of the Boreal Realm. The acme of *M. kyphoma* at Eastbourne, coinciding with the coolest episode of the PCE, suggests that this species might have had a biogeographic distribution comparable to that of the modern polar (*Neogloboquadrina pachyderma*) or subpolar species (e.g., *Neogloboquadrina incompta* or *Turborotalita quinqueloba*) that thrive in the Boreal Realm northern of 60°N, but are progressively less common to absent at lower latitudes (e.g., Bé, 1977; Kucera et al., 2005; Kucera, 2007; Kretschmer et al., 2016). Accordingly, the highest abundances of *Neogloboquadrina pachyderma* at low latitudes are found in the upwelling regions, which are typically characterized by cool temperatures and low salinities (Darling et al., 2017).

12. Evidence for changes in sea-surface circulation patterns and equatorward shift of the proto-Arctic Front during the PCE

As discussed above, the alternating dominance of Group 1 vs. Group 2 is best explained by changes in the dominant surface water mass (Tethyan-Central Atlantic vs. Boreal waters) entering the Anglo-Paris and Vocontian basins.

The boundary between the warm saline Atlantic surface waters carried at the northern mid-high latitudes by the Gulf Stream and the Boreal cold surface waters flowing southward through the Norwegian Sea is a well recognizable oceanographic feature of the modern North Atlantic Ocean generally referred to as Arctic Front (e.g., Piechura and Walczowski, 1995; Raj et al., 2019). The Arctic Front is normally subject to seasonal and longer-term poleward or equatorward migrations, the latter being directly related to climate change such as the interglacial and glacial cycles of the Plio-Pleistocene. During these intervals, the position of the Arctic Front determined the poleward contraction or equatorward expansion of the planktonic foraminiferal Boreal bioprovince and ultimately

controlled the biogeographic distribution of the polar and subpolar species in the Atlantic Ocean (e.g., Fronval et al., 1998; Wright and Flower, 2002; Eynaud et al., 2009; Alonso-Garcia et al., 2011; Naafs et al., 2010; Kretschmer et al., 2016).

Reasonably, planktonic foraminiferal bioprovinces reacted to climate change with similar poleward contractions or equatorward expansions following the position of the proto-Arctic Front during the Cretaceous, although the Norwegian Sea was much narrower at that time.

12.1 Onset of OAE 2 (before the PCE)

At the onset of OAE 2, planktonic foraminiferal assemblages are dominated by Tethyan taxa (Group 1) indicating that the dominant surface water mass was supplied by the proto-Gulf Stream, which conveyed warm saline and thermally stratified Tethyan-Central Atlantic waters to the Anglo-Paris and Vocontian basins through the corridor between the Welsh and the Armorican Massif (Figs. 1C and 9A). Branches of the proto-Gulf Stream flowing southward through the Vocontian Basin and the Bay of Biscay are consistent with the reconstructed atmospheric circulation patterns of that time (Fluteau et al., 2007; Pearce et al., 2009; Hay and Floegel, 2012; Fig. 9A). However, the occurrence of radiolaria at Clot Chevalier suggests an additional direct influence of Tethyan waters in the Vocontian Basin (Fig. 9A), as radiolaria are commonly found in the Tethys (e.g., Umbria-Marche Basin: Coccioni and Luciani, 2004; Tunisia: Caron et al., 2006), but not in the North Atlantic (Blake Nose: Huber et al., 1999) and in the Anglo-Paris Basin (e.g., Paul et al., 1999; Keller et al., 2001; this study). Secondary branches of the proto-Gulf Stream likely moved northward in the proto-North Atlantic and in the North Sea, the latter being testified by the common occurrence of whiteinellids, pseudoclavibergellids and rotaliporids (Group 1) in late Cenomanian sections of Lincolnshire and in the Moray Firth region of the North Sea (King et al., 1989; Hart et al., 1993; Fig. 9A). By contrast,

assemblages of the northern North Sea and southern Norwegian Sea yield mixed species belonging to Group 2 (muricohedbergellids and praeglobotruncanids) and Group 1 (whiteinellids) in the absence of taxa that require a well-stratified water column, suggesting mixing of the Tethyan and Boreal components in this region. The identification of the Boreal dinoflagellate cysts *Cyclonephelium compactum–membraniphorum* in the northern Norwegian Sea throughout the middle-late Cenomanian (Radmacher et al., 2015; van Helmond et al., 2016) points to a dominant and stable influence of Boreal waters further north (Fig. 9A). This latitudinal distribution of taxa suggests that the proto-Arctic Front was positioned consistently north of the Moray Firth and south of the northern Norwegian Sea in this stratigraphic interval, and likely fluctuated seasonally between these regions (Fig. 9A).

During the Cenomanian–Turonian boundary interval, a branch of the North Atlantic subtropical gyre entered the WIS via the Gulf of Mexico and moved northward along the eastern side of the seaway, while cold Boreal waters flowed southward along the western side; as a result, the front between these two surface water masses developed mostly in a NNE-SSW direction and exhibited minor latitudinal variations during OAE 2 (Elderbak and Leckie, 2016; Lowery et al., 2018 and references therein) (Fig. 9A). At the onset of OAE 2, Boreal waters likely reached at least the paleolatitude of 35°N on the western side of the WIS (Lowery et al., 2018), but the Boreal dinoflagellate cysts *Cyclonephelium compactum–membraniphorum* are only documented at about 55°N (Alberta, Canada: van Helmond et al., 2016).

Undetermined belemnitellids co-occur with *Inoceramus pictus* in two non-adjacent beds of the upper Cenomanian of Siberia (~60°N; Fig. 9A) (Košťák and Wiese, 2008). Both levels cannot be more precisely dated in the absence of additional stratigraphic information, but the occurrence of belemnitellids in the upper Cenomanian of Siberia is significant because together with the identification of *Praeactinocamax* aff. *plenus* in the

lower Turonian (Košťák and Wiese, 2008), suggests that this group has a wider stratigraphic distribution at higher latitudes compared to the southern Russia Platform and European epicontinental basins, confirming its affinity for Boreal waters.

12.2 During the PCE

The sharp variation in planktonic foraminiferal assemblages that led to the dominance (up to 85%) of Boreal taxa during the PCE at Eastbourne (Fig. 8) is unlikely to have been caused by the weakening of the proto-Gulf Stream, because the increased latitudinal temperature gradient established in this interval (Forster et al., 2007; Sinninghe Damsté et al., 2010) should have caused a more efficient poleward heat transport, as opposite to a warmer equable climate in which the strength of winds and surface currents was likely reduced (Kidder and Worsley, 2010; May and Floegel, 2012). Therefore, the sharp increase in the abundance of *Fraeglobotruncana* (top Bed 1–middle Bed 3), and later of *Dicarinella* and *M. kyphoma* (Beds 4–5) at Eastbourne (Fig. 8) is best explained by a reinforced N to S inflow of Boreal waters through the Norwegian Sea, which led to the equatorward shift of the proto-Arctic Front and to the parallel step-wise expansion of the planktonic foraminiferal biozones during moderate (first episode) and intense (second episode) cooling (Fig. 9B). In addition, the rare (15%) but continuous occurrence of Tethyan taxa at Eastbourne during the coolest phase of the PCE (Beds 4–5) suggests that the proto-Arctic Front fluctuated around southern England, and it allowed a limited supply of Tethyan waters entering the Anglo-Paris Basin during the warmer season (Fig. 9B). In this southerly position, the proto-Arctic Front might have represented an oceanographic barrier that forced the proto-Gulf Stream to a dominant SW to NE direction at subtropical latitudes, favoring the incursion of Boreal waters (and of Boreal endemic taxa) in the European epicontinental seas and in the Vocontian Basin (Fig. 9B). This reconstruction is supported by the equatorward expansion of the Boreal dinoflagellate cysts

Cyclonephelium compactum–membraniphorum that are identified in Lincolnshire (Hart et al., 1993), in the Anglo-Paris and Lower Saxony basins and in the subtropical Vocontian Basin (Vergons: Courtinat et al., 1991). Moreover, the occurrence of *P. plenus* in Bavaria (southern Germany: Wilmsen et al., 2010) and the increased diversity of *Dicarinella* species at the extinction level of *R. cushmani* in Switzerland (Chrummflueschlucht: Westermann et al., 2010) and northern Spain (Ganuza: Lamolda et al., 1997), as observed in Lincolnshire (Hart et al., 1993), suggest that Boreal waters might have entered the Estella Basin through the Bay of Biscay and might have expanded to the east of the Vocontian Basin in the northern Tethyan Realm.

In addition, the dominant SW to NE direction of the proto-Gulf Stream allowed Boreal surface waters flowing southward on the western side of the Atlantic Ocean, as suggested by the bloom of the Boreal dinoflagellate cysts *Cyclonephelium compactum–membraniphorum* at Bass River (New Jersey) slightly northern of 30°N (van Helmond et al., 2014). New Jersey represents the southernmost locality with documented Boreal endemic species in the Atlantic Ocean; moreover, Boreal dinoflagellate cysts are found exclusively in this stratigraphic interval (van Helmond et al., 2014, 2016), suggesting the establishment of exceptional environmental conditions that did not reoccur throughout the Cenomanian–Turonian boundary interval. The planktonic foraminifera *Muricohedbergella kyphoma* and *P. plenusiensis* have never been documented in the western Atlantic, but the increased abundance of *Praeglobotruncana*, *Dicarinella* and *Muricohedbergella* coinciding with sea-surface cooling after the onset of OAE 2 at the 28°N Blake Nose Plateau (Huber et al., 1999) might indicate that the influence of Boreal waters reached the western subtropical North Atlantic (Fig. 9B).

In the same stratigraphic interval, the Boreal dinoflagellate cysts *Cyclonephelium compactum–membraniphorum* were recognized in several stratigraphic records of Texas (Shell Iona-1 Core: Eldrett et al., 2014; Lozier Canyon: Dodsworth, 2016), suggesting a

significant influx of Boreal surface waters in the southern-central region of the WIS at the paleolatitude of 30-35°N that is in agreement with the regional water mass circulation reconstructed by Eldrett et al. (2017) (Fig. 9B). However, the paleontological record of the PCE is less diverse in the WIS compared to Europe, as there is no evidence for the occurrence of belemnitellids before the middle Turonian (Christensen, 1997) and of the other Boreal macroinvertebrates of the Plenus fauna. Moreover, *Praeglobotruncana* and *Dicarinella* are extremely rare and planktonic foraminiferal trochospiral taxa are exclusively represented by the unkeeled *Muricohedbergella* and *Whiteinella* at Pueblo, Colorado (Leckie et al., 1998; Elderbak and Leckie, 2016). The occurrence of *Whiteinella* supports the existence of warm Tethyan surface currents flowing northward on the eastern side of the WIS, which likely persisted in this stratigraphic interval (Elderbak and Leckie, 2016; Lowery et al., 2018 and reference therein).

During the PCE, belemnitellids expanded their biogeographic distribution from Siberia (Košťák and Wiese, 2008) to the European epicontinental basins (Gale and Christensen, 1996; Wilmsen et al., 2010) via the North Pole and the Norwegian Sea (Košťák and Wiese, 2008), an immigration route already exploited by Boreal belemnites in the Early Cretaceous (Alsen and Mutterlose, 2009) and/or through the Turgai Channel (Fig. 9B) (Baraboshkin et al., 2003), as suggested by the occurrence of *P. plenus* in Kazakhstan (Gale et al., 1999) (Fig. 9B). The occurrence of belemnitellids at ~35°N on the Russian Platform indicates a parallel equatorward expansion of the Boreal bioprovince of the same order of magnitude (about 20°) of that observed in the European basins and in the North Atlantic. The acme of *Praeglobotruncana*, hedbergellids, and of large-sized dicarinellids identified above the extinction of *R. cushmani* in Caucasus (Tur, 1996) would support the influence of Boreal waters in this region deviating to the west for the Coriolis Effect (Fig. 9B). However, the occurrence of the planktonic foraminiferal assemblage is not

constrained by chemostratigraphy and further studies are required to verify whether it falls within the Plenus CIE or in a slightly younger stratigraphic interval.

12.3 Middle phase of OAE 2 (after the PCE)

After the PCE, Tethyan planktonic foraminifera dominated the assemblages at Eastbourne and Clot Chevalier (Fig. 8) indicating a poleward migration of the proto-Arctic Front that allowed the proto-Gulf Stream to become again the dominant sea-surface water mass entering the Anglo-Paris and Vocontian basins. However, the position of the proto-Arctic Front in this stratigraphic interval (i.e., between $\delta^{13}\text{C}$ peak b and c) is more difficult to constrain. The uppermost Cenomanian to lower Turonian assemblages of the northern North Sea and offshore Norway are overall very similar to that dominating during the PCE (King et al., 1989; Gradstein et al., 1999) and there is no additional stratigraphic information to discriminate within different intervals of the *W. archaeocretacea* Zone (or equivalent zones) of the Boreal Realm. Moreover, the influence of Tethyan surface waters in Northern Europe can be traced only based on the abundance of *Whiteinella* and the occurrence of *Pseudoclavidhedbergella*, because the Tethyan assemblage is depauperated of rotaliporids and planispirals. *Pseudoclavidhedbergella* is not documented north of southern England above the Plenus CIE, but it becomes very rare and temporarily disappears from the lowermost Turonian assemblages also at lower latitudes (Falzoni and Petrizzo, 2020), therefore, its absence does not provide reliable information to trace the influence of Tethyan waters in Northern Europe. Several *Whiteinella* species are instead reported in Lincolnshire, while in the northern North Sea and offshore Norway they show low diversity and discontinuous stratigraphic distributions (Hart et al., 1993; King et al., 1989; Gradstein et al., 1999), suggesting that Tethyan waters reached at least the central North Sea.

A coeval poleward contraction of the biogeographic distribution of belemnitellids including *P. plenus* after the PCE is consistent with the identification of specimens assigned to *P. aff plenus* in the lowermost Turonian of Siberia (Košťák and Wiese, 2008), and their absence at lower latitudes. Nevertheless, the occurrence of *Cyclonephelium compactum–membraniphorum* in several European epicontinental basins and in the WIS (Pearce et al., 2009; Eldrett et al., 2014; van Helmond et al., 2016) suggests a persisting supply of Boreal surface waters after the PCE in these regions, or alternatively that these Boreal dinoflagellates cysts became seasonal and adapted to lower latitude environments.

13. Broader implications

13.1 Ocean circulation

This study suggests significant changes in the sea-surface circulation patterns of the Northern Hemisphere with a reinforced N to S inflow of Boreal surface waters during the PCE. However, circulation changes also involved deeper waters as suggested by a positive shift in the Neodymium isotope record of the English Chalk (Eastbourne: Zheng et al., 2013; Dover: O'Connor et al., 2020) and geochemical evidence for re-oxygenation of the sea-floor in several European epicontinental basins (Jenkyns et al., 2017; Clarkson et al., 2018; Danzelle et al., 2020), and by the coeval “Benthonic Zone” (Eicher and Worstell, 1970; Eicher and Diner, 1985; Leckie, 1985) that was likely favored by the supply of bottom cool and oxygen-rich waters interrupting dysoxia/anoxia at the sea-floor in the WIS (e.g., Elderbak and Leckie, 2016; Eldrett et al., 2017). Accordingly, environmental changes during the PCE were not limited to global cooling but included a major re-organization of the ocean circulation patterns that involved surface and deeper layers of the water column.

13.2 Plio-Pleistocene vs. Cretaceous

The paleobiogeographic distribution and abundance of polar and subpolar planktonic foraminiferal species including *Neogloboquadrina pachyderma* in different North Atlantic sites suggest that the Arctic Front migrated from 70°-60°N north of Iceland and Scandinavia during the warm interglacials to 50°-45°N near Brittany (Alonso-Garcia et al., 2011) or along the Iberian margin (Eynaud et al., 2009; Naafs et al., 2010; Kretschmer et al., 2016) during the peak and terminal phase of the Plio-Pleistocene cold intervals, implying a 10° to 25° latitudinal shift of the Arctic Front between warmer and colder states. Such latitudinal shifts were controlled by mean sea-surface temperature variations of 6°–15°C in the NE Atlantic Ocean (Martrat et al., 2007; Neais et al., 2013; Rasmussen et al., 2016; Rodrigues et al., 2017).

The ~20° equatorward shift of the proto-Arctic front during the coolest phase of the PCE from the Norwegian Sea (~55°N) to southern England (~35°N) and the comparable equatorward migration of Boreal assemblages in the European epicontinental basins (Fig. 9B) are therefore of the same order of magnitude of that reconstructed for some glacial-interglacial cycles of the Plio-Pleistocene. The 5°–11°C sea-surface temperature drop estimated through TEX₈₆ paleothermometry in the North-Central Atlantic (Newfoundland Basin: Sinninghe Damsté et al., 2010) and the 12°C temperature decrease reconstructed through the oxygen isotope values of nektonic and benthic macrofossils at Eastbourne (~300 m depth) during the PCE (Voigt et al., 2006) are comparable to the range of sea-surface temperature changes that are typically found between the glacial and interglacial states of the Plio-Pleistocene.

Further comparison between the PCE and the Plio-Pleistocene glacial intervals are hampered by the different paleogeography of the Atlantic Ocean, by the most probable absence of permanent polar ice sheets, and by a generally stable warm equable climate in the early Late Cretaceous with mean sea-surface temperatures significantly higher than during more recent intervals of Earth history (e.g., Hay, 2016; Huber et al., 2018; Hay et

al., 2019). Nevertheless, these observations provide new insights into the extent of cooling and environmental changes occurred during the PCE compared to the background hot greenhouse climate conditions that prevailed during most of OAE 2.

10. Conclusions

This study presents a review of environmental changes occurred during the latest Cenomanian Plenus Cold Event and their effects on the biogeographic distribution of Boreal marine organisms reconstructed through new planktonic foraminiferal quantitative data collected from two continuous records of OAE 2 at Eastbourne (~35°N in the Anglo-Paris Basin) and Clot Chevalier (~32°N in the Vercortan Basin) combined with previously published geochemical and paleontological information.

Our major conclusions include:

- Chemo- and biostratigraphy: we suggest a revised definition of the Plenus Carbon Isotope Excursion (Plenus CIE) previously introduced by O'Connor et al. (2020) to chemostratigraphically constrain the PCE, that is herein extended from the second $\delta^{13}\text{C}$ build-up below peak a to peak b to account for the stratigraphically lowest (i.e., below peak a) evidences for cooling, $p\text{CO}_2$ drawdown, occurrence of Boreal macro- and microfossils, and changes in the sea-surface circulation patterns observed in the Anglo-Paris Basin. The revised Plenus CIE is biostratigraphically constrained by the step-wise extinction of the planktonic foraminiferal *T. deeckeri* and *T. greenhornensis* (below the Plenus CIE), and of *R. cushmani* and of *L. bentonensis* (within the Plenus CIE).

- Planktonic foraminiferal response to the PCE: this group of calcareous pelagic microfossils shows changes in the taxonomic composition of assemblages (i.e., occurrence of the Boreal endemic species *Muricohedbergella kyphoma* and *Praeglobotruncana plenusiensis*) and an increased abundance of cold meso-to-eutrophic taxa closely paralleling the geochemical evidence for sea-surface cooling and the range of Boreal macrofossils in the Anglo-Paris Basin. Specifically, at Eastbourne assemblages are dominated by *Praeglobotruncana* during the first event of moderate cooling (Plenus Marl top Bed 1–middle Bed 3), and by *Dicarinella* and *M. kyphoma* during the second event of intense cooling (Plenus Marl Bed 4–5). However, contrarily to the underlying stratigraphic interval within the Plenus CIE, slight cooling and the rare occurrence of Boreal macrofossils in Plenus Marl Bed 8 are not accompanied by significant changes in planktonic foraminiferal assemblages. In the subtropical Vocontian Basin, we observe the occurrence of *M. kyphoma* and *P. plenusiensis* and the increased (although to a lower extent compared to Eastbourne) abundance of *Praeglobotruncana*, *Dicarinella* and *Muricohedbergella* within the Plenus CIE. However, the identification of different cooling episodes is hampered by the condensed nature of this stratigraphic interval and rare occurrence of planktonic foraminifera in the upper part of the Plenus CIE.
- Significance of changes in the planktonic foraminiferal assemblages: planktonic foraminifera are passively transported by sea-surface currents, and thus register changes in the dominant circulation patterns. The cold-water meso-eutrophic planktonic foraminiferal assemblage dominating during the PCE shows strong affinities with the coeval fauna documented offshore Norway (~50°–55°N), reflecting the inflow of a cold Boreal low-saline and poorly stratified water mass

originated in the Norwegian Sea that reached the subtropical Vocontian Basin through the North Sea and Anglo-Paris seaway. By contrast, the abundance of tropical-subtropical Tethyan planktonic foraminifera at the onset of OAE 2 and after the PCE testifies the dominance of warm, saline and thermally stratified surface waters likely carried to the European mid-high latitudes by the proto-Gulf Stream.

- Location of the proto-Arctic Front and biogeographic distribution of Boreal taxa: we suggest that the dominant influence of Tethyan vs. Boreal waters was ultimately controlled by the position of the proto-Arctic Front, which shifted of $\sim 20^\circ$ from the Norwegian Sea at the onset of OAE 2 to southern England-Bay of Biscay (E Atlantic) and New Jersey (W Atlantic) during the coolest phase of the PCE. In this southerly position, the proto-Arctic Front represented an oceanographic barrier that limited the inflow of the proto-Gulf Stream in the corridor between the Welsh and Armorican Massif, favoring the inflow of Boreal surface waters into the European epicontinental basins and the $\sim 20^\circ$ equatorward migration of Boreal communities. The Vocontian Basin represents the European southernmost locality reached by Boreal species among planktonic foraminifera (*M. kyphoma* and *P. plenusiensis*), and dinoflagellate cysts (*C. compactum-membraniphorum*), but the nektonic belemnite shells (*P. plenus*) and the benthic bivalves (*C. arlesiensis* and *O. seminudum*) and serpulids (*Hamulus* sp.) of the Plenus fauna show the same biogeographic distribution. In the WIS, the NNE-SSW front between Boreal and Tethyan waters probably slightly rotated anticlockwise during the PCE and allowed Boreal surface waters and dinoflagellate cysts to reach the southern-central region of the WIS. A $\sim 20^\circ$ latitudinal shift of Boreal assemblages from $55\text{-}60^\circ\text{N}$ might have also occurred in the Russian Platform, implying that the PCE had a supra-

regional impact on the biogeographic distribution of a large component of the marine biota and led to a major re-organization of the sea-surface and intermediate circulation patterns of the Northern Hemisphere.

- Extent of cooling and environmental changes during the PCE: the sea-surface temperature variations and the equatorward expansion of the Boreal planktonic bioprovince reconstructed for the PCE in the Atlantic and European epicontinental basins are comparable to that occurred during some glacial-interglacial cycles of the Plio-Pleistocene. Despite the background conditions (climate, paleogeography) of the Cretaceous supergreenhouse and of the Plio-Pleistocene icehouse are not comparable, this observation underlines the magnitude of environmental changes occurred during the PCE and its effects on the sea-surface currents and biogeography of Boreal marine communities in the Northern Hemisphere.

Acknowledgments

We warmly thank the editor Maoyan Zhu for handling the manuscript, Mark Leckie and an anonymous reviewer for their careful revisions and thoughtful comments and suggestions that greatly improved the quality of this manuscript. Agostino Rizzi (CNR, Italy) is thanked for his assistance at the Scanning Electron Microscope (SEM). We acknowledge funds through PRIN 2017RX9XXY to E. Erba and the support of the Italian Ministry of University and Research (MUR), project “Dipartimenti di Eccellenza 2018–2022, Le Geoscienze per la Società: Risorse e loro evoluzione”.

References

- Alonso-Garcia, M., Sierro, F.J., Flores, J.A., 2011. Arctic front shifts in the subpolar North Atlantic during the Mid-Pleistocene (800–400 ka) and their implications for ocean circulation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 311, 268–280.
- Alsen, P., Mutterlose, J., 2009. The early Cretaceous of North-East Greenland: a crossroads of belemnite migration. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280, 168–182.
- Ando, A., Nakano, T., Kaiho, K., Kobayashi, T., Kokado, E., Khim, B.K., 2009. Onset of seawater $^{87}\text{Sr}/^{86}\text{Sr}$ excursion prior to Cenomanian–Turonian Oceanic Anoxic Event 2? New Late Cretaceous strontium isotope curve from the central Pacific Ocean. *The Journal of Foraminiferal Research* 39, 322–334.
- Ando, A., Huber, B.T., MacLeod, K.G., 2010. Depth habitat reorganization of planktonic foraminifera across the Albian/Cenomanian boundary. *Paleobiology* 36, 357–373. doi:10.1666/09027.1.
- Arthur, M.A., Dean, W.E., Pratt, L.M., 1988. Geochemical and climatic effects of increased marine organic carbon burial at the Cenomanian/Turonian boundary. *Nature* 335, 714–717.
- Baraboshkin, E.Y., Alekseev, A.S., Kopaevich, L.F., 2003. Cretaceous palaeogeography of the north-eastern Peri-Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* 196, 177–208.
- Bé, A.W.H., 1977. An ecological, zoogeographic and taxonomic review of Recent planktonic foraminifera. In: Ramsey, A.T.S., (Eds), *Oceanic micropaleontology*, London Academic Press, Vol. 1, 1–100.
- Bé, A.W.H., Tolderlund, D.S., 1971. Distribution and ecology of planktonic foraminifera. In: Funnell, B.M., Riedel, W.R., (Eds), *The micropaleontology of oceans*. London Cambridge University Press, 105–150.

- Bornemann, A., Norris, R.D., 2007. Size-related stable isotope changes in Late Cretaceous planktic foraminifera: implications for paleoecology and photosymbiosis. *Marine Micropaleontology* 65, 32–42.
- Boullila, S., Charbonnier, G., Spangenberg, J.E., Gardin, S., Galbrun, B., Briard, J., Le Callonnec, L., 2020. Unraveling short-and long-term carbon cycle variations during the Oceanic Anoxic Event 2 from the Paris Basin Chalk. *Global and Planetary Change* 186, 103126.
- Caron, M., Dall'Agnolo, S., Accarie, H., Barrera, E., Kauffman, E.G., Amédro, F., Robaszynski, F., 2006. High-resolution stratigraphy of the Cenomanian–Turonian boundary interval at Pueblo (USA) and Wadi Bahlool (Tunisia): stable isotope and bio-events correlation. *Geobios* 39, 171–200.
- Christensen, W.K., 1997. Paleobiogeography and migration in the Late Cretaceous belemnite family Belemnitellidae. *Acta palaeontologica polonica* 42, 457–495.
- Clarkson, M.O., Stirling, C.H., Jenkyns, H.C., Dickson, A.J., Porcelli, D., Moy, C.M., Pogge von Strandmanne, P.A.E., Cooke, J.R., Lenton, T.M., 2018. Uranium isotope evidence for two episodes of deoxygenation during Oceanic Anoxic Event 2. *Proceedings of the National Academy of Sciences* 115(12), 2918–2923.
- CLIMAP Project Members (1976). The surface of the ice-age Earth. *Science* 191, 1131–1137.
- Coccioni, R., Luciani, V., 2004. Planktonic foraminifera and environmental changes across the Bonarelli Event (OAE2, latest Cenomanian) in its type area: a high-resolution study from the Tethyan reference Bottaccione section (Gubbio, Central Italy). *The Journal of Foraminiferal Research* 34, 109–129.
- Coccioni, R., Luciani, V., Marsili, A., 2006. Cretaceous oceanic anoxic events and radially elongated chambered planktonic foraminifera: Paleoecological and paleoceanographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 235, 66–92.

- Coccioni, R., Sideri, M., Frontalini, F., Montanari, A., 2016. The *Rotalipora cushmani* extinction at Gubbio (Italy): Planktonic foraminiferal testimonial of the onset of the Caribbean large igneous province emplacement. The stratigraphic record of Gubbio: Integrated stratigraphy of the late cretaceous-paleogene Umbria-Marche Pelagic Basin, Geological Society of America Special Paper 524, 79–96.
- Courtinat, B., Crumière, J.P., Méon, H., Schaaf, A., 1991. Les associations de kystes de dinoflagellés du Cénomanién-Turonien de Vergons (Bassin Vocontien France). *Geobios* 24, 649–666.
- Coxall, H.K., Wilson, P.A., Pearson, P.N., Sexton, P.F., 2007. Iterative evolution of digitate planktonic foraminifera. *Paleobiology* 33, 495–516.
- Crumière, J.P., 1990. Crise anoxique à la limite Cénomanién-Turonien dans le bassin subalpin oriental (Sud-Est de la France). Relation avec l'eustatisme. *Geobios Mémoire Spécial* 11, 189–203.
- Danzelle, J., Riquier, L., Baudin, F., Thomazo, C., Pucéat, E., 2020. Nitrogen and carbon cycle perturbations through the Cenomanian-Turonian oceanic anoxic event 2 (~ 94 Ma) in the Vocontian Basin (SE France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 538, 109442.
- Darling, K.F., Wade, C.M., Siccha, M., Trommer, G., Schulz, H., Abdolalipour, S., Kurasawa, A., 2017. Genetic diversity and ecology of the planktonic foraminifers *Globigerina bulloides*, *Turborotalita quinqueloba* and *Neogloboquadrina pachyderma* off the Oman margin during the late SW Monsoon. *Marine Micropaleontology* 137, 64–77.
- Desmares, D., Grosheny, D., Beaudoin, B., 2008. Ontogeny and phylogeny of Upper Cenomanian rotaliporids (Foraminifera). *Marine Micropaleontology* 69, 91–105.
- Desmares, D., Crognier, N., Bardin, J., Testé, M., Beaudoin, B., Grosheny, D., 2016. A new proxy for Cretaceous paleoceanographic and paleoclimatic reconstructions:

Coiling direction changes in the planktonic foraminifera *Muricohedbergella delrioensis*.

Palaeogeography, Palaeoclimatology, Palaeoecology 445, 8–17.

Desmares, D., Testé, M., Broche, B., Tremblin, M., Gardin, S., Villier, L., Masure, E., Grosheny, D., Morel, N., Raboeuf, P., 2020. High-resolution biostratigraphy and chemostratigraphy of the Cenomanian stratotype area (Le Mans, France). Cretaceous Research 106, 104198, 1–15.

Dickson, A.J., Saker-Clark, M., Jenkyns, H.C., Bottini, C., Erba, E., Russo, F., Gorbanenko, O., Naafs, B.D.A., Pancost, R.D., Robinson, S.A., van den Boorn, S.H.J.M., Idiz, E., 2017. A Southern Hemisphere record of global trace-metal drawdown and orbital modulation of organic-matter burial across the Cenomanian–Turonian boundary (Ocean Drilling Program Site 1138, Kerguelen Plateau). Sedimentology 64, 186–203.

Dodsworth, P., 2000. Trans-Atlantic dinoflagellate cyst stratigraphy across the Cenomanian–Turonian (Cretaceous) Stage boundary. Journal of Micropalaeontology 19, 69–84.

Dodsworth, P., 2016. Palynostratigraphy and palaeoenvironments of the Eagle Ford Group (Upper Cretaceous) at the Lozier Canyon outcrop reference section, west Texas, USA. Palynology 40, 357–378.

Du Vivier, A.D., Selby, D., Sageman, B.B., Jarvis, I., Gröcke, D.R., Voigt, S., 2014. Marine $^{187}\text{Os}/^{188}\text{Os}$ isotope stratigraphy reveals the interaction of volcanism and ocean circulation during Oceanic Anoxic Event 2. Earth and Planetary Science Letters 389, 23–33.

Eicher, D.L., Worstell, P., 1970. Cenomanian and Turonian foraminifera from the Great Plains, United States. Micropaleontology 16, 269–324.

Eicher, D.L., Diner, R., 1985. Foraminifera as indicators of water mass in the Cretaceous Greenhorn Sea, Western Interior. In: Pratt, L.M., Kauffman, E.G., Zelt, F.B., (Eds.),

Fine-grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes, Field Trip Guidebook, Society of Economic Paleontologists and Mineralogists 4, 60–71.

Elderbak, K., Leckie, R.M., 2016. Paleocirculation and foraminiferal assemblages of the Cenomanian–Turonian Bridge Creek Limestone bedding couplets: Productivity vs. dilution during OAE2. *Cretaceous Research* 60, 52–77.

Eldrett, J.S., Minisini, D., Bergman, S.C., 2014. Decoupling of the carbon cycle during Ocean Anoxic Event 2. *Geology* 42, 567–570.

Eldrett, J.S., Dodsworth, P., Bergman, S.C., Wright, M., Minisini, D., 2017. Water-mass evolution in the Cretaceous Western Interior Seaway of North America and equatorial Atlantic. *Climate of the Past* 13, 855–878

Erba, E., 2004. Calcareous nannofossils and Mesozoic oceanic anoxic events. *Marine Micropaleontology* 52, 85–106.

Ericson, D.B., 1959. Coiling direction of *Globigerina pachyderma* as a climatic index. *Science* 130, 219–220.

Eynaud, F., De Abreu, L., Voelker, A., Schönfeld, J., Salgueiro, E., Turon, J. L., Penaud, A., Toucanne, S., Nauquitch, F., Sánchez Goñi, M.F., Malaizé, B., Cacho, I., 2009. Position of the Polar Front along the western Iberian margin during key cold episodes of the last 45 ka. *Geochemistry, Geophysics, Geosystems* 10, Q07U05, doi:10.1029/2009GC002398.

Falzone, F., Petrizzo, M.R., Clarke, L.J., MacLeod, K.G., Jenkyns, H.C., 2016a. Long-term Late Cretaceous oxygen- and carbon-isotope trends and planktonic foraminiferal turnover: A new record from the southern midlatitudes. *GSA Bulletin* 128, 1725–1735.

Falzone, F., Petrizzo, M.R., Jenkyns, H.C., Gale, A.S., Tsikos, H., 2016b. Planktonic foraminiferal biostratigraphy and assemblage composition across the Cenomanian–

- Turonian boundary interval at Clot Chevalier (Vocontian Basin, SE France). *Cretaceous Research* 59, 69–97.
- Falzone, F., Petrizzo, M.R., Caron, M., Leckie, R.M., Elderbak, K., 2018a. Age and synchronicity of planktonic foraminiferal bioevents across the Cenomanian–Turonian boundary interval (Late Cretaceous). *Newsletters on Stratigraphy* 51, 343–380.
- Falzone, F., Petrizzo, M.R., Valagussa, M., 2018b. A morphometric methodology to assess planktonic foraminiferal response to environmental perturbations: the case study of Oceanic Anoxic Event 2, Late Cretaceous. *Bollettino della Società Paleontologica Italiana* 57, 103–124.
- Falzone, F., Petrizzo, M.R., 2020. Patterns of planktonic foraminiferal extinctions and eclipses during Oceanic Anoxic Event 2 at Eastbourne (SE England) and other mid-low latitude locations. *Cretaceous Research* 116, 104593.
- Fluteau, F., Ramstein, G., Besse, J., Guiraud, R., Masse, J.P., 2007. Impacts of palaeogeography and sea level changes on mid-Cretaceous climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 247, 357–381.
- Forster, A., Schouten, S., Moriya, K., Wilson, P.A., Sinninghe Damsté, J.S., 2007. Tropical warming and intermittent cooling during the Cenomanian/Turonian oceanic anoxic event 2: Sea surface temperature records from the equatorial Atlantic. *Paleoceanography*, 22, PA1219, doi:10.1029/2006PA001349.
- Fronval, T., Jansen, E., Hafliðason, H., Sejrup, H.P., 1998. Variability in surface and deep water conditions in the Nordic seas during the last interglacial period. *Quaternary Science Reviews* 17, 963–985.
- Gale, A.S., Christensen, W.K., 1996. Occurrence of the belemnite *Actinocamax plenus* in the Cenomanian of SE France and its significance. *Bulletin of the Geological Society of Denmark* 43, 68–77.

- Gale, A.S., Hancock, J.M., Kennedy, W.J., 1999. Biostratigraphical and sequence correlation of the Cenomanian successions in Mangyschlak (W. Kazakhstan) and Crimea (Ukraine) with those in southern England. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 69, 67–86.
- Gale, A.S., Smith, A.B., Monks, N.E.A., Young, J.A., Howard, A., Wray, D.S., Huggett, J.M., 2000. Marine biodiversity through the Late Cenomanian–Early Turonian: palaeoceanographic controls and sequence stratigraphic biases. *Journal of the Geological Society* 157, 745–757.
- Gale, A.S., Kennedy, W.J., Voigt, S., Walaszczyk, I., 2005. Stratigraphy of the Upper Cenomanian–Lower Turonian Chalk succession at Eastbourne, Sussex, UK: Ammonites, inoceramid bivalves and stable carbon isotopes. *Cretaceous Research* 26, 460–487.
- Gale, A.S., Jenkyns, H.C., Tsikos, H., van Breugel, Y., Sinninghe Damsté, J.S., Bottini, C., Erba, E., Russo, F., Falzoni, F., Petrizzo, M.R., Dickson, A.J., Wray, D.S., 2019. High-resolution bio- and chemostratigraphy of an expanded record of Oceanic Anoxic Event 2 (Late Cenomanian–Early Turonian) at Clot Chevalier, near Barrême, SE France (Vocontian Basin, SE France). *Newsletters on Stratigraphy* 52, 97–129. Doi: 10.1127/nos/2018/0145.
- Gale, A.S., 2019. Microcrinoids (Echinodermata, Articulata, Roveacrinida) from the Cenomanian–Santonian chalk of the Anglo-Paris Basin: taxonomy and biostratigraphy. *Revue de Paléobiologie* 38, 397–533.
- Gangl, S.K., Moy, C.M., Stirling, C.H., Jenkyns, H.C., Crampton, J.S., Clarkson, M.O., Ohneiser, C., Porcelli, D., 2019. High-resolution records of Oceanic Anoxic Event 2: insights into the timing, duration and extent of environmental perturbations from the palaeo-South Pacific Ocean. *Earth and Planetary Science Letters* 518, 172–182.

- Georgescu, M.D., 2009. Upper Albian-lower Turonian non-schackoinid planktic foraminifera with elongate chambers: morphology reevaluation, taxonomy and evolutionary classification. *Revista Española de Micropaleontología*, 41, 255–293.
- González-Donoso, J.M., Linares, D., Robaszynski, F., 2007. The rotaliporids, a polyphyletic group of Albian-Cenomanian planktonic foraminifera: emendation of genera. *Journal of Foraminiferal Research* 37, 175–186.
- Gradstein, F.M., Kaminski, M.A., Agterberg, F.P., 1999. Biostratigraphy and paleoceanography of the Cretaceous seaway between Norway and Greenland. *Earth-Science Reviews* 46, 27–98.
- Grosheny, D., Beaudoin, B., Morel, L., Desmares, D., 2006. High-resolution biostratigraphy and chemostratigraphy of the Cenomanian–Turonian Boundary Event in the Vocontian Basin, S-E France. *Cretaceous Research* 27, 629–640.
- Grosheny, D., Ferry, S., Lecuyer, C., Thomas, A., Desmares, D., 2017. The Cenomanian–Turonian Boundary Event (CTBE) on the southern slope of the Subalpine Basin (SE France) and its bearing on a probable tectonic pulse on a larger scale. *Cretaceous Research* 72, 39–65.
- Hart, M.B., Bailey, H.W., Ciftenden, S., Fletcher, B.N., Price, R.J., Swiecicki, A. 1989. Cretaceous. In: Jenkins, D.G., Murray, J.W., (Eds.) *Stratigraphical Atlas of Fossil Foraminifera*, Second Edition, Ellis Horwood Limited, Chichester, England, 273–371.
- Hart, M.B., Dodsworth, P., Duane, A.M., 1993. The late Cenomanian event in eastern England. *Cretaceous Research* 14, 495–508.
- Hart, M.B., 1999. The evolution and biodiversity of Cretaceous planktonic Foraminifera. *Geobios* 32, 247–255.
- Hasegawa, T., 1999. Planktonic foraminifera and biochronology of the Cenomanian–Turonian (Cretaceous) sequence in the Oyubari area, Hokkaido, Japan. *Paleontological Research* 3, 173–192.

- Hay, W.W., 2008. Evolving ideas about the Cretaceous climate and ocean circulation. *Cretaceous Research* 29, 725–753.
- Hay, W.W., Floegel, S., 2012. New thoughts about the Cretaceous climate and oceans. *Earth-Science Reviews*, 115, 262–272.
- Hay, W.W., 2016. Toward understanding Cretaceous climate—An updated review. *Science China Earth Sciences* 60, 5–19.
- Hay, W.W., DeConto, R.M., de Boer, P., Flögel, S., Song, Y., Stepashko, A., 2019. Possible solutions to several enigmas of Cretaceous climate. *International Journal of Earth Sciences* 108, 587–620.
- Haynes, S.J., Huber, B.T., Macleod, K.G., 2015. Evolution and phylogeny of mid-Cretaceous (Albian–Coniacian) biserial planktic foraminifera. *Journal of Foraminiferal Research* 45, 42–81.
- Heimhofer, U., Wucherpfennig, N., Acattoli, T., Schouten, S., Schneebeli-Hermann, E., Gardin, S., Keller, G., Kentsch, S., Kujau, A., 2018. Vegetation response to exceptional global warmth during Oceanic Anoxic Event 2. *Nature Communications* 9, 1–8, DOI: 10.1038/s41467-018-06319-6.
- Huber, B.T., Hodell, D.A., Hamilton, C.P., 1995. Middle–Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients. *Geological Society of America Bulletin* 107, 1164–1191.
- Huber, B.T., Leckie, R.M., Norris, R.D., Bralower, T.J., CoBabe, E., 1999. Foraminiferal assemblage and stable isotopic change across the Cenomanian-Turonian boundary in the subtropical North Atlantic. *Journal of Foraminiferal Research* 29, 392–417.
- Huber, B.T., Petrizzo, M.R., 2014. Evolution and taxonomic study of the Cretaceous planktic foraminiferal genus *Helvetoglobotruncana* Reiss, 1957. *Journal of Foraminiferal Research* 44, 40–57.

- Huber, B.T., Petrizzo, M.R., Young, J.R., Falzoni, F., Gilardoni, S.E., Bown, P.R., Wade, B.S., 2016. Pforams@ microtax. *Micropaleontology* 62, 429–438.
- Huber, B.T., Petrizzo, M.R., Watkins, D.K., Haynes, S.J., MacLeod, K.G., 2017. Correlation of Turonian continental margin and deep-sea sequences in the subtropical Indian Ocean sediments by integrated planktonic foraminiferal and calcareous nannofossil biostratigraphy. *Newsletters on Stratigraphy* 50, 141–185.
- Huber, B.T., MacLeod, K.G., Watkins, D.K., Coffin, M.F., 2018. The rise and fall of the Cretaceous Hot Greenhouse climate. *Global and Planetary Change* 167, 1–23.
- Huber, B.T., Petrizzo, M.R., Falzoni, F., 2021. Taxonomy and phylogeny of Albian–Maastrichtian planispiral planktonic foraminifera traditionally assigned to *Globigerinelloides*. *Micropaleontology*, under review.
- Jarvis, I., Lignum, J.S., Gröcke, D.R., Jenkyns, H.C., Pearce, M.A., 2011. Black shale deposition, atmospheric CO₂ drawdown, and cooling during the Cenomanian–Turonian Oceanic Anoxic Event. *Paleoceanography* 26, PA3201, doi:10.1029/2010PA002081.
- Jeans, C.V., Wray, D.S., Williams, C.T., Bland, D.J., Wood, C.J., 2021. Redox conditions, glacio-eustasy, and the status of the Cenomanian–Turonian Anoxic Event: new evidence from the Upper Cretaceous Chalk of England. *Acta Geologica Polonica* 71, 1–50, doi: 10.24425/agp.2020.134556.
- Jefferies, R.P.S., 1962. The palaeoecology of the *Actinocamax plenus* subzone (lowest Turonian) in the Anglo-Paris Basin. *Palaeontology* 4, 609–647.
- Jefferies, R.P.S., 1963. The stratigraphy of the *Actinocamax plenus* subzone (Turonian) in the Anglo-Paris Basin. *Proceedings of the Geologists' Association* 74, 1-33.
- Jenkyns, H.C., Dickson, A.J., Ruhl, M., Boorn, S.H., 2017. Basalt-seawater interaction, the Plenus Cold Event, enhanced weathering and geochemical change: Deconstructing

Oceanic Anoxic Event 2 (Cenomanian–Turonian, Late Cretaceous). *Sedimentology* 64, 16–43.

Jiménez Berrocoso, Á., Huber, B.T., MacLeod, K.G., Petrizzo, M.R., Lees, J.A., Wendler, I., Coxall, H., Mweneinda, A.K., Falzoni, F., Birch, H., Haynes, S. J., Bown, P.R., Robinson, S.A., Singano, J.M., 2015. The Lindi Formation (upper Albian–Coniacian) and Tanzania Drilling Project Sites 36–40 (Lower Cretaceous to Paleogene): Lithostratigraphy, biostratigraphy and chemostratigraphy. *Journal of African Earth Sciences* 101, 282–308.

Keller, G., Han, Q., Adatte, T., Burns, S., 2001. Paleoenvironment of the Cenomanian–Turonian transition at Eastbourne, England. *Cretaceous Research* 22, 391–422.

Keller, G., Adatte, T., Berner, Z., Chellai, E.H., Stueben, D., 2008. Oceanic events and biotic effects of the Cenomanian-Turonian anoxic event, Tarfaya Basin, Morocco. *Cretaceous Research* 29, 976–994.

Kidder, D.L., Worsley, T.R., 2010. Phanerozoic large igneous provinces (LIPs), HEATT (haline euxinic acidic thermal transgression) episodes, and mass extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295, 162–191.

King, C., Bailey, H.W., Burch, C., King, A.D., 1989. Cretaceous of the North Sea. In: Jenkins, D.G., Murray, J.W., (Eds.) *Stratigraphical Atlas of Fossil Foraminifera*, Second Edition, Ellis Horwood Limited, Chichester, England, 372–417.

Košťák, M., Wiese, F., 2008. Lower Turonian record of belemnite *Praeactinocamax* from NW Siberia and its palaeogeographic significance. *Acta Palaeontologica Polonica* 53, 669–678.

Kretschmer, K., Kucera, M., Schulz, M., 2016. Modeling the distribution and seasonality of *Neoglobobulimina pachyderma* in the North Atlantic Ocean during Heinrich Stadial 1. *Paleoceanography* 31, 986–1010.

- Kucera, M., Weinelt, M., Kiefer, T., Pflaumann, U., Hayes, A., Weinelt, M., Chen, M.-T., Mix, A.C., Barrows, T.T., Cortijo, E., Duprat, J., Juggins, S., Waelbroeck, C., 2005. Reconstruction of sea-surface temperatures from assemblages of planktonic foraminifera: multi-technique approach based on geographically constrained calibration data sets and its application to glacial Atlantic and Pacific Oceans. *Quaternary Science Reviews* 24, 951–998.
- Kucera, M., 2007. Chapter Six: Planktonic foraminifera as tracers of past oceanic environments. In: Hillaire-Marcel C., De Vernal, A., (Eds.), *Proxies in Late Cenozoic Paleooceanography*, Elsevier, Amsterdam, 213–262.
- Kuhnt, W., Holbourn, A.E., Beil, S., Aquit, M., Krawczyk, T., Flögel, S., Chellai, E.H., Jabour, H., 2017. Unraveling the onset of Cretaceous Oceanic Anoxic Event 2 in an extended sediment archive from the Tarfaya-Laayoune Basin, Morocco. *Paleoceanography* 32, 923–946.
- Kump, L.R., Arthur, M.A., 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. *Chemical Geology* 161, 181–198.
- Ladant, J.B., Poulsen, C.J., Fluteau, F., Tabor, C.R., MacLeod, K.G., Martin, E.E., Haynes, S.J., Rostami, M.A., 2020. Paleogeographic controls on the evolution of Late Cretaceous ocean circulation. *Climate of the Past* 16, 973–1006.
- Lamolda, M.A., Gorostidi, A., Paul, C.R.C., 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 Research* 15, 143–164.
- Lamolda, M.A., Gorostidi, A., Martínez, R., López, G., Peryt, D., 1997. Fossil occurrences in the Upper Cenomanian–Lower Turonian at Ganuza, northern Spain: An approach to Cenomanian/Turonian boundary chronostratigraphy. *Cretaceous Research* 18, 331–353.

- Laugié, M., Donnadieu, Y., Ladant, J.B., Green, J. A., Bopp, L., Raison, F., 2020. Stripping back the modern to reveal the Cenomanian–Turonian climate and temperature gradient underneath. *Climate of the Past* 16, 953–971.
- Leckie, R.M., 1985. Foraminifera of the Cenomanian–Turonian boundary interval, Greenhorn Formation, Rock Canyon Anticline, Pueblo, Colorado. In: Pratt, L.M., Kauffman, E.G., Zelt, F.B. (Eds.), *Fine-grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes*, Field Trip Guidebook, Society of Economic Paleontologists and Mineralogists 4, 139–149.
- Leckie, R.M., 1987. Paleoecology of mid-Cretaceous planktonic foraminifera: A comparison of open oceans and epicontinental sea assemblages. *Micropaleontology* 33, 164–176.
- Leckie, R.M., Yuretrich, R.F., West, G.L.O., Finkelstein, D., Schmidt, M., 1998. Paleooceanography of the southwestern Western Interior Sea during the time of the Cenomanian–Turonian boundary (Late Cretaceous). In: Dean, W., Arthur, M.A. (Eds.), *Stratigraphy and Paleoenvironments of the Cretaceous Western Interior Seaway*. *SEPM Concepts in Sedimentology and Paleontology* 6, 101–126.
- Leckie, R.M., Bralower, T.J., Cashman, R., 2002. Oceanic anoxic events and plankton evolution: Biotic response to tectonic forcing during the mid-Cretaceous. *Paleoceanography* 17, doi: 10.1029/2001PA000623.
- Lirer, F., 2000. A new technique for retrieving calcareous microfossils from lithified lime deposits. *Micropaleontology* 46, 365–369.
- Lowery, C.M., Leckie, R.M., Bryant, R., Elderbak, K., Parker, A., Polyak, D.E., Schmidt, M., Snoeyenbos-West, O., Sterzinar, E., 2018. The Late Cretaceous Western Interior Seaway as a model for oxygenation change in epicontinental restricted basins. *Earth-Science Reviews* 177, 545–564.

- Martrat, B., Grimalt, J.O., Shackleton, N.J., de Abreu, L., Hutterli, M.A., Stocker, T.F., 2007. Four climate cycles of recurring deep and surface water destabilizations on the Iberian margin. *Science* 317, 502–507.
- Mitchell, S.F., 2019. The Chalk Group (Upper Cretaceous) of the Northern Province, eastern England—a review. *Proceedings of the Yorkshire Geological Society* 62, 153–177.
- Naafs, B.D.A., Stein, R., Hefter, J., Khélifi, N., De Schepper, S., Haug, G.H., 2010. Late Pliocene changes in the North Atlantic current. *Earth and Planetary Science Letters* 298, 434–442.
- Naafs, B.D.A., Hefter, J., Gruetzner, J., Stein, R., 2013. Warming of surface waters in the mid-latitude North Atlantic during Heinrich events. *Paleoceanography* 28, 153–163.
- Nederbragt, A.J., Fiorentino, A., 1999. Stratigraphy and palaeoceanography of the Cenomanian–Turonian Boundary Event in Oued Mellegue, north-western Tunisia. *Cretaceous Research* 20, 47–62.
- Norris, R.D., Wilson, P.A., 1998. Low-latitude sea-surface temperatures for the mid-Cretaceous and the evolution of planktic foraminifera. *Geology* 26, 823–826.
- O'Brien, C.L., Robinson, S.A., Fancost, R.D., Sinninghe Damsté, J.S., Schouten, S., Lunt, D.J., Alsenz, H., Bonemann, A., Bottini, C., Brassell, S.C., Farnsworth, A., Forster, A., Huber, B.T., Inglis, G.N., Jenkyns, H.C., Linnert, C., Littler, K., Markwick, P., McAnena, A., Mutterlose, J., Naafs, B.D.A., Püttmann, W., Sluijs, A., van Helmond, A.G.M.N., Vellekoop J., Wagner, T., Wrobel, N.E., 2017. Cretaceous sea-surface temperature evolution: Constraints from TEX₈₆ and planktonic foraminiferal oxygen isotopes. *Earth Science Reviews* 172, 224–247.
- O'Connor, L.K., Jenkyns, H.C., Robinson, S.A., Remmelzwaal, S.R., Batenburg, S.J., Parkinson, I.J., Gale, A.S., 2020. A re-evaluation of the Plenus Cold Event, and the links between CO₂, temperature, and seawater chemistry during OAE 2.

Paleoceanography and Paleoclimatology 35, e2019PA003631, doi: 10.1029/2019PA003631.

Paul, C.R.C., Lamolda, M.A., Mitchell, S.F., Vaziri, M.R., Gorostidi, A., Marshall, J.D., 1999. The Cenomanian–Turonian boundary at Eastbourne (Sussex, UK): a proposed European reference section. *Palaeogeography, Palaeoclimatology, Palaeoecology* 150, 83–121.

Pearce, M.A., Jarvis, I., Tocher, B.A., 2009. The Cenomanian–Turonian boundary event, OAE2 and palaeoenvironmental change in epicontinental seas: new insights from the dinocyst and geochemical records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280, 207–234.

Peeters, F.J., Acheson, R., Brummer, G.J.A., De Ruijter, W.P., Schneider, R.R., Ganssen, G.M., Ufkes, E., Kroon, D., 2004. Vigorous exchange between the Indian and Atlantic oceans at the end of the past five glacial periods. *Nature* 430, 661–665.

Percival, L.M.E., van Helmond, N.A.G.M., Selby, D., Goderis, S., Claeys, P., 2020. Complex Interactions Between Large Igneous Province Emplacement and Global-Temperature Changes During the Cenomanian-Turonian Oceanic Anoxic Event (OAE 2). *Paleoceanography and Paleoclimatology* 35, e2020PA004016.

Petrizzo, M.R., Huber, B.T., Wilson, P.A., MacLeod, K.G., 2008. Late Albian paleoceanography of the western subtropical North Atlantic. *Paleoceanography* 23, PA1213. doi:10.1029/2007PA001517.

Petrizzo, M.R., Jiménez Berrocoso, Á., Falzoni, F., Huber, B.T., MacLeod, K.G., 2017. The Coniacian–Santonian sedimentary record in southern Tanzania (Ruvuma Basin, East Africa): Planktonic foraminiferal evolutionary, geochemical and palaeoceanographic patterns. *Sedimentology* 64, 252–285.

Petrizzo, M.R., Huber, B.T., Falzoni, F., MacLeod, K.G., 2020. Changes in biogeographic distribution patterns of southern mid-to high latitude planktonic foraminifera during the

- Late Cretaceous hot to cool greenhouse climate transition. *Cretaceous Research*, 115, 104547.
- Petrizzo, M.R., Watkins, D.K., MacLeod, K.G., Hasegawa, T., Huber, B.T., Batenburg, S.J., Kato, T., 2021. Exploring the paleoceanographic changes registered by planktonic foraminifera across the Cenomanian-Turonian boundary interval and Oceanic Anoxic Event 2 at southern high latitudes in the Mentelle Basin (SE Indian Ocean). *Global and Planetary Change* 103595, doi.org/10.1016/j.gloplacha.2021.103595.
- Piechura, J., Walczowski, W., 1995. The Arctic front: structure and dynamics. *Oceanologia* 37, 47–73.
- Poulsen, C.J., Seidov, D., Barron, E.J., Peterson, W.H., 1998. The impact of paleogeographic evolution on the surface oceanic circulation and the marine environment within the mid-Cretaceous Tethys. *Paleoceanography* 13, 546–559.
- Premoli Silva, I., Sliter, W.V., 1993. Cretaceous paleoceanography: Evidence from planktonic foraminiferal evolution. In: Barrera, E., Johnson, C.C., (Eds.), *The Evolution of the Cretaceous Ocean-Climate System*. Special Papers of the Geological Society of America 332, 301–328. doi:10.1130/0-8137-2332-9.301.
- Pucéat, E., Lécuyer, C., Reisberg, L., 2005. Neodymium isotope evolution of NW Tethyan upper ocean waters throughout the Cretaceous. *Earth and Planetary Science Letters* 236, 705–720.
- Radmacher, W., Mangerud, G., Tyszka, J., 2015. Dinoflagellate cyst biostratigraphy of Upper Cretaceous strata from two wells in the Norwegian Sea. *Review of Palaeobotany and Palynology* 216, 18–32.
- Raj, R. P., Chatterjee, S., Bertino, L., Turiel, A., Portabella, M., 2019. The Arctic Front and its variability in the Norwegian Sea. *Ocean Science* 15, 1729–1744.

- Rasmussen, T.L., Thomsen, E., Moros, M., 2016. North Atlantic warming during Dansgaard-Oeschger events synchronous with Antarctic warming and out-of-phase with Greenland climate. *Scientific Reports* 6, 20535, 1–12.
- Robaszynski, F., Gale, A.S., Juignet, P., Amédéo, F., Hardenbol, J., 1998. Sequence stratigraphy in the Upper Cretaceous series of the Anglo-Paris Basin: exemplified by the Cenomanian stage. *SEPM (Society for Sedimentary Geology) Special Publication* 60, 363–386.
- Robinson, S.A., Dickson, A.J., Pain, A., Jenkyns, H.C., O'Brien, C.L., Farnsworth, A., Lunt, D.J., 2019. Southern Hemisphere sea-surface temperatures during the Cenomanian–Turonian: implications for the termination of Oceanic Anoxic Event 2. *Geology* 47, 131–134.
- Rodrigues, T., Alonso-García, M., Hodell, D.A., Rufino, M., Naughton, F., Grimalt, J.O., Voelker, A.H.L., Abrantes, F., 2011. A 1-Ma record of sea surface temperature and extreme cooling events in the North Atlantic: A perspective from the Iberian Margin. *Quaternary Science Reviews* 172, 118–130.
- Schlanger, S.O., Jenkyns, H.C., 1976. Cretaceous oceanic anoxic events: Causes and consequences. *Geologie en Mijnbouw* 55, 179–184.
- Schlanger, S.O., Arthur, M.A., Jenkyns, H.C., Scholle, P.A., 1987. The Cenomanian–Turonian Oceanic Anoxic Event, I. Stratigraphy and distribution of organic carbon-rich beds and the marine $\delta^{13}\text{C}$ excursion. Geological Society, London, *Special Publications* 26, 371–399.
- Schrag D.P., DePaolo, D.J., Richter, F.M., 1995. Reconstructing past sea surface temperatures: correcting for diagenesis of bulk marine carbonate. *Geochimica et Cosmochimica Acta* 59, 2265–2278.
- Schröder-Adams, C.J., Herrle, J.O., Selby, D., Quesnel, A., Froude, G., 2019. Influence of the high Arctic igneous province on the Cenomanian/Turonian boundary interval,

Sverdrup Basin, High Canadian Arctic. *Earth and Planetary Science Letters* 511, 76–88.

Scotese, C.R., 2016. PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project. <http://www.earthbyte.org/paleomap-paleoatlas-for-gplates/>.

Sigal, J., 1955. Notes micropaléontologiques nord-africaines. 1 Du Cénomanién au Santonien: zones et limites en faciès pélagique: *Compte Rendus Sommaires des séances de la Société Géologique de France* 8, 157–160.

Sinninghe Damsté, J.S., van Bentum, E.C., Reichert, G.J., Pross, J., Schouten, S., 2010. A CO₂ decrease-driven cooling and increased latitudinal temperature gradient during the mid-Cretaceous Oceanic Anoxic Event 2. *Earth and Planetary Science Letters* 293, 97–103.

Sullivan, D.L., Brandon, A.D., Eldrett, J., Bergman, S.C., Wright, S., Minisini, D., 2020. High resolution osmium data record three distinct pulses of magmatic activity during cretaceous Oceanic Anoxic Event 2 (OAE-2). *Geochimica et Cosmochimica Acta* 285, 257–273.

Takashima, R., Nishi, H., Yamataka, T., Tomosugi, T., Fernando, A.G., Tanabe, K., Moriya, K., Kawabe, F., Miyashi, K., 2011. Prevailing oxic environments in the Pacific Ocean during the mid-Cretaceous Oceanic Anoxic Event 2. *Nature communications* 2, 234, 1–5.

Tsikos, H., Jenkyns, H.C., Walsworth-Bell, B., Petrizzo, M.R., Forster, A., Kolonic, S., Erba, E., Premoli Silva, I., Baas, M., Wagner, T., Sinninghe Damsté, J.S., 2004. Carbon-isotope stratigraphy recorded by the Cenomanian–Turonian Oceanic Anoxic Event: Correlation and implications based on three localities. *Journal of the Geological Society of London* 161, 711–719.

- Tur, N.A., 1996. Planktonic foraminifera recovery from the Cenomanian-Turonian mass extinction event, northeastern Caucasus. Geological Society, London, Special Publications 102, 259–264.
- Turgeon, S.C., Creaser, R.A., 2008. Cretaceous Oceanic Anoxic Event 2 triggered by a massive magmatic episode. *Nature*, 454, 323–326, doi:10.1038/nature07076
- van Helmond, N.A.G.M., Sluijs, A., Reichert, G.J., Sinninghe Damsté, J.S., Slomp, C.P., Brinkhuis, H., 2014. A perturbed hydrological cycle during Oceanic Anoxic Event 2. *Geology* 42, 123–126.
- van Helmond, N.A.G.M., Sluijs, A., Papadomanolaki, M., Plint, A.G., Gröcke, D., Pearce, M.A., Eldrett, J.S., Trabucho-Alexandre, J., Walaszczyk, I., van de Schootbrugge, B., Brinkhuis, H., 2016. Equatorward phytoplankton migration during a cold spell within the Late Cretaceous super-greenhouse. *Bioessences* 13, 2859–2872.
- Voigt, S., Gale, A.S., Flögel, S., 2004. Mid-latitude shelf seas in the Cenomanian–Turonian greenhouse world: Temperature evolution and North Atlantic circulation. *Paleoceanography*, 19, PA4020, doi:10.1029/2004PA001015.
- Voigt S., Gale A.S., Voigt T., 2006. Sea-level change, carbon cycling and palaeoclimate during the Late Cenomanian of northwest Europe; an integrated palaeoenvironmental analysis. *Cretaceous Research* 27, 836–858.
- Voigt, S., Erbacher, J., Mutterlose, J., Weiss, W., Westerhold, T., Wiese, F., Wilmsen, M., Wonik, T., 2008. The Cenomanian – Turonian of the Wunstorf section – (North Germany): Global stratigraphic reference section and new orbital time scale for Oceanic Anoxic Event 2. *Newsletters on Stratigraphy* 43, 65–89.
- Wendler, I., Huber, B.T., MacLeod, K.G., Wendler, J.E., 2013. Stable oxygen and carbon isotope systematics of exquisitely preserved Turonian foraminifera from Tanzania—Understanding isotopic signatures in fossils. *Marine Micropaleontology* 102, 1–33.

- Westermann, S., Caron, M., Fiet, N., Fleitmann, D., Matera, V., Adatte, T., Föllmi, K.B., 2010. Evidence for oxic conditions during oceanic anoxic event 2 in the northern Tethyan pelagic realm. *Cretaceous Research* 31, 500–514.
- Wiese, F., Košťák, M., Wood, C.J., 2009. The Upper Cretaceous belemnite *Praeactinocamax plenus* (Blainville, 1827) from Lower Saxony (Upper Cenomanian, northwest Germany) and its distribution pattern in Europe. *Paläontologische Zeitschrift* 83, 309–321.
- Wilmsen, M., 2003. Sequence stratigraphy and palaeoceanography of the Cenomanian Stage in northern Germany. *Cretaceous Research* 24, 525–568.
- Wilmsen, M., Niebuhr, B., Chellouche, P., 2010. Occurrence and significance of Cenomanian belemnites in the lower Danubian Cretaceous Group (Bavaria, southern Germany). *Acta Geologica Polonica* 60, 237–241.
- Wilson, P.A., Norris, R.D., Cooper, M.J., 2002. Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal calcite from the core of the Turonian tropics on Demerara Rise. *Geology* 30, 607–610.
- Wright, A.K., Flower, B.P., 2002. Surface and deep ocean circulation in the subpolar North Atlantic during the mid-Pleistocene revolution. *Paleoceanography* 17, 20–1.
- Zachos, J.C., Stott, L.D., Lohmann, K.C., 1994. Evolution of early Cenozoic marine temperatures. *Paleoceanography* 9, 353–387.
- Zheng, X.Y., Jenkyns, H.C., Gale, A.S., Ward, D.J., Henderson, G.M., 2013. Changing ocean circulation and hydrothermal inputs during Ocean Anoxic Event 2 (Cenomanian–Turonian): Evidence from Nd-isotopes in the European shelf sea. *Earth and Planetary Science Letters* 375, 338–348.

Figure captions

Fig. 1. 1A) Location of Cenomanian–Turonian sections in Southern England (Anglo-Paris Basin) discussed in the text (modified after Mitchell, 2019). 1B) Location of Cenomanian–Turonian sections in South East France (Vocontian Basin) discussed in the text (modified after Gale et al., 2019). Fig. 1C) Late Cenomanian paleogeographic map of the Anglo-Paris and Vocontian Basin (modified after Gale et al., 2019) with location of sections in (1) Southern England and (2) South East France.

Fig. 2. Litho-, bio- and chemostratigraphy, oxygen isotope of bulk carbonates and macrofossil shells, and $\Delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{carb}} - \delta^{13}\text{C}_{\text{org}}$) of the Eastbourne section (after Gale et al., 2005, Tsikos et al., 2004; Voigt et al., 2006, and Jarvis et al., 2011). Identification of the $\delta^{13}\text{C}$ positive peaks a, b, and c follows Jarvis et al. (2006) and Voigt et al. (2008), see discussion in Falzoni et al. (2018a). Definition of the OAE 2 interval after Jenkyns et al. (2017). Plenus Carbon Isotope Excursion (Plenus CIE) according to O'Connor et al. (2020) and this study (light grey band). The stratigraphic range of Boreal macrofossils follows Paul et al. (1999) and Gale and Christensen (1996); the latter is based on the Jefferies' collection of Dover deposited in the Sedgwick museum (Cambridge). The stratigraphic range of the dinoflagellate cysts *Cyclonephelium compactum-membraniphorum* is after Pearce et al. (2009) for Eastbourne, and Dodsworth (2000) for Lulworth. Planktonic foraminiferal data of the Eastbourne section are after Falzoni and Petrizzo (2020). Stratigraphic intervals characterized by cooling during the PCE according to different studies (dark grey).

Fig. 3. Litho-, bio- and chemostratigraphy, oxygen-isotope of bulk carbonates, and $\Delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{carb}} - \delta^{13}\text{C}_{\text{org}}$) of the Clot Chevalier section (after Falzoni et al., 2016b and Gale et al., 2019). Please note that there is a ~50 cm upward shift of the bioevents and of the

$\delta^{13}\text{C}_{\text{carb}}$ curve compared to the stratigraphic log of Falzoni et al. (2016b) due to the erroneous position of meter 0 that was placed at the base of the section instead of ~50 cm above. This mistake was corrected in Gale et al. (2019) and the log is herein modified accordingly. As a result, the planktonic foraminiferal bioevents fall in the same position relative to the $\delta^{13}\text{C}_{\text{carb}}$ curve but are shifted ~50 cm upward relative to lithostratigraphy compared to the original illustration of Falzoni et al. (2016b). OAE 2 interval after Jenkyns et al. (2017). PCE interval (cooling) after Gale et al. (2019) and based on the $\delta^{18}\text{O}$ record. Plenus CIE and stratigraphic distribution of the planktonic foraminiferal species *P. plenusiensis* and *M. kyphoma* according to this study.

Fig. 4. Scanning Electron Microscope images of the planktonic foraminiferal species *Praeglobotruncana plenusiensis* and *Muricohedbergella kyphoma* identified at Eastbourne and Clot Chevalier: 1A–C, *P. plenusiensis* (holotype, Eastbourne, 11.2 m); 2A–C, *M. kyphoma* (Eastbourne, 11.8 m); 3A–C, *P. plenusiensis* (Clot Chevalier, 4.8 m); 4A–C, *M. kyphoma* (Clot Chevalier, 4.8 m).

Fig. 5. Litho-, bio- and chemostratigraphic correlation of Les Lattes and Clot Chevalier (Vocontian Basin). Litho-, bio- and chemostratigraphy of Les Lattes after Gale and Christensen (1996) and Grosheny et al. (2017). Litho-, bio- and chemostratigraphy of Clot Chevalier after Falzoni et al. (2016b) and Gale et al. (2019) (see caption of Fig. 3 for further explanation). The $\delta^{13}\text{C}$ positive peaks at Les Lattes are tentatively identified in this study based on the similarities between the $\delta^{13}\text{C}$ peaks and troughs of the carbon-isotope profile obtained at Clot Chevalier and the available litho- and biostratigraphic data (see text for further explanation). The suggested position of the *Praeactinocamax plenus* correlative bed at Clot Chevalier lies rightly above the

second glauconitic-rich interval in agreement with observations at Les Lattes (see text for further explanation). Abbreviations: T= turbidites; LRI =Lower Recessive Interval (after Grosheny et al., 2017).

Fig. 6. Relative abundances of planktonic foraminiferal genera at A) Eastbourne and B) Clot Chevalier. The relative abundances of *Muricohedbergella planispira*, *M. kyphoma* and *Praeglobotruncana plenusiensis* are plotted at species level, because they are discussed separately in the text. The relative abundances of radiolaria are plotted for Clot Chevalier, as this group dominated the pelagic assemblage in several samples. The planktonic foraminiferal assemblage is divided in two groups according to the paleoecological preferences and paleobiogeographic distribution patterns of taxa (see text for further explanation)

Fig. 7. Summary of the paleoecological preferences, life strategies, and paleobiogeographic distribution patterns in Northern Europe of Cenomanian–Turonian planktonic foraminiferal genera and morphogroups. See text and caption of Fig. 8 for description of Group 1 and 2. Scale bar = 100 μm .

Fig. 8. Relative abundances of planktonic foraminiferal genera plotted against the stratigraphic distribution of the Boreal macrofossils (Jefferies, 1963; Gale and Christensen, 1996; Paul et al., 1999) and of *M. kyphoma* and *P. plenusiensis* (Falzoni and Petrizzo, 2020), and the available proxies for paleotemperature and $p\text{CO}_2$ levels at Eastbourne and Clot Chevalier (after Tsikos et al., 2004; Voigt et al., 2006; Jarvis et al., 2011; Gale et al., 2019). Oxygen-isotope values obtained on macrofossil shells at Eastbourne were measured on brachiopods (*Orbirhynchia multicosata* and *O. wiesti*), bivalves (oysters, *Inoceramus pictus* and *Spondylus* sp.),

and on the belemnite *Praeactinocamax plenus* (Voigt et al., 2006). Paleotemperatures were calculated on the $\delta^{18}\text{O}$ values of macrofossils considering seawater $\delta^{18}\text{O}$ values of -0.6‰ and are adjusted to account for salinity according to Zachos et al. (1994) (after Voigt et al., 2006). Planktonic foraminiferal genera are divided in two groups as follows: Group 1 includes the genera *Whiteinella*, *Pseudoclavhedbergella*, *Rotalipora*, *Thalmanninella*, *Whiteinella*, the planispiral and biserial taxa; Group 2 includes the genera *Muricohedbergella*, *Praeglobotruncana*, *Dicarinella* and *Marginotruncana*. The Plenus CIE is according to the definition given in this study. Intervals characterized by cooler sea-surface temperatures within the Plenus CIE are identified by combining geochemical trends and paleontological data. Eastbourne: (1 = light blue band) First episode (moderate cooling); (2 = dark blue band) Second episode (severe cooling). A possible third episode of slight cooling (3? = light blue band) does not correspond to significant changes in the planktonic foraminiferal assemblages. Clot Chevalier: a single cooling episode is identified within the Plenus CIE (dark blue band), which is overlaid by an interval with very rare planktonic foraminifera that might register the end of cooling (? = light blue band) (see text for further explanation). Abbreviations: *Rot.*= *Rotalipora*; *Thalm.*= *Thalmanninella*; *Praeglobot.*= *Praeglobotruncana*; *Pseudoclavhedb.*= *Pseudoclavhedbergella*; *Muricohedb.* = *Muricohedbergella*; *Helv.*= *Helvetoglobotruncana*; *Marginotr.*= *Marginotruncana*.

Fig. 9. Paleogeographic reconstruction for the latest Cenomanian (94 Ma) (Scotese, 2016) and dominant sea-surface currents according to this study and previous works (Poulsen et al., 1998; Baraboshkin et al., 2003; Pucéat et al., 2005; Košťák and Wiese, 2008; Hay, 2008; Pearce et al., 2009; Hay and Floegel, 2012; Elderbak and Leckie, 2016; Eldrett et al., 2017; Lowery et al., 2018). 9A) Onset of OAE 2 (before

the PCE). 9B) During the coldest interval of the PCE, corresponding to the interval of Plenius Marl Beds 4–5 at Eastbourne. Source of data: *P. plenius* and Boreal benthic macroinvertebrates (Mangyshlak: Gale et al., 1999; Eastbourne: Jefferies, 1962, 1963; Lower Saxony Basin: Wiese et al., 2009; Vocontian Basin: Gale and Christensen, 1996; Bavaria: Wilmsen et al., 2010); *P. aff. plenius* and other belemnitellids are recognized in Siberia from three non-adjacent beds across the Cenomanian–Turonian boundary interval, but their occurrence is not constrained by chemostratigraphy (Košťák and Wiese, 2008); Boreal dinoflagellate cysts of the *Cyclonephelium compactum–membraniphorum* plexus (northern Norwegian Sea: Radmacher et al., 2015; Lincolnshire: Hart et al., 1993; Alberta: van Helmond et al., 2016; New Jersey: van Helmond et al., 2014; Texas: Eldrett et al., 2014; Dodsworth, 2016; Vocontian Basin: Courtinat et al., 1991); planktonic foraminifera (Norway: Gradstein et al., 1999; North Sea: King et al., 1989; Lincolnshire: Hart et al., 1993; Eastbourne and Clot Chevalier: this study; Switzerland: Westermann et al., 2010; Blake Nose: Huber et al., 1990; Ganuza, Spain: Lamolda et al., 1997; Pueblo, Colorado: Leckie, 1985; Caucasus: Tur, 1996. Abbreviations: pAF= proto-Arctic Front (white dashed line in the Norwegian Sea [Fig. 9A] and North Atlantic [Fig. 9B]), WISF= front between warm Tethyan and cold Boreal surface waters in the WIS (white dashed line in the WIS); A= Alberta (Canada), T= Texas, NJ= New Jersey; BN= Blake Nose; nS: northern Norwegian Sea; sN= southern Norwegian Sea; nNS= northern North Sea; MF: Moray Firth; Li= Lincolnshire; E= Eastbourne; LS= Lower Saxony Basin; G= Ganuza; V= Vocontian Basin; Sw: Switzerland; B: Bavaria; C= Caucasus; M= Mangyshlak; S= Siberia.

Supplementary Table 1. Relative abundances (%) of planktonic foraminiferal genera and species identified at Eastbourne. Abbreviations: GC= Grey Chalk; PM= Plenus Marl; WC= White Chalk.

Supplementary Table 2. Relative abundances (%) of planktonic foraminiferal genera and species identified at Clot Chevalier.

Supplementary Table 3. List of the species included in each genus or morphogroup occurring at Eastbourne and Clot Chevalier.

Journal Pre-proof

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof

Highlights

- Planktonic foraminiferal quantitative abundances across OAE 2 are provided for Eastbourne (Anglo-Paris Basin) and Clot Chevalier (Vocontian Basin).
- Assemblages are dominated by *Rotalipora* and *Whiteinella* at the onset of OAE 2 and by *Praeglobotruncana*, *Dicarinella* and *Muricohedbergella* during the PCE.
- The planktonic foraminifera *M. kyphoma* and *P. plenusiensis* are Boreal endemic species and their range at Eastbourne parallel that of Boreal macrofossils.
- The biogeography of Boreal marine organisms expanded ~20° equatorward during the PCE in the Atlantic and European epicontinental basins and likely on the Russian Platform.
- The proto-Arctic Front shifted ~20° equatorward in the Atlantic Ocean during the PCE and favored the southern migration of Boreal taxa in the European epicontinental basins.