

## Marine biodiversity through the Late Cenomanian–Early Turonian: palaeoceanographic controls and sequence stratigraphic biases

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**Abstract:** Changes in the marine macro- and microfauna, sedimentary geochemistry and surface-water palaeoproductivity through the last 500 000 years of the Cenomanian and first 300 000 years of the Turonian are documented. These are based on the succession at Eastbourne, the thickest and most complete section through the Late Cenomanian and Early Turonian in the Anglo-Paris Basin. Two levels of rapid faunal and geochemical change are identified, one coincident with a significant increase in siliciclastic input at the base of the Plenus Marls Member, and the other with a marked drop in surface water productivity near the top of the same unit. Faunal change is demonstrated to be largely a pattern of immigration–emigration rather than true extinction, and our sequence stratigraphical analysis shows that it was coincident with major sea-level changes. No evidence is found to support the hypothesis that reduced bottom water oxygenation developed and was responsible for extinctions amongst the benthos in mid-shelf environments. The onset of pure chalk facies is interpreted to mark the breakdown of shelf-break fronts and the spread of oligotrophic oceanic waters over much of the continental shelf, initiated by rising sea-level. The Cenomanian–Turonian event, far from recording a mass extinction of shelf fauna, is most probably an artifact caused by a significant switch in the nature of the surviving sedimentary record as a result of a major, but perfectly ordinary, oceanographic change.

**Keywords:** Cretaceous, anoxia, sequence stratigraphy, diversity, palaeoenvironment.

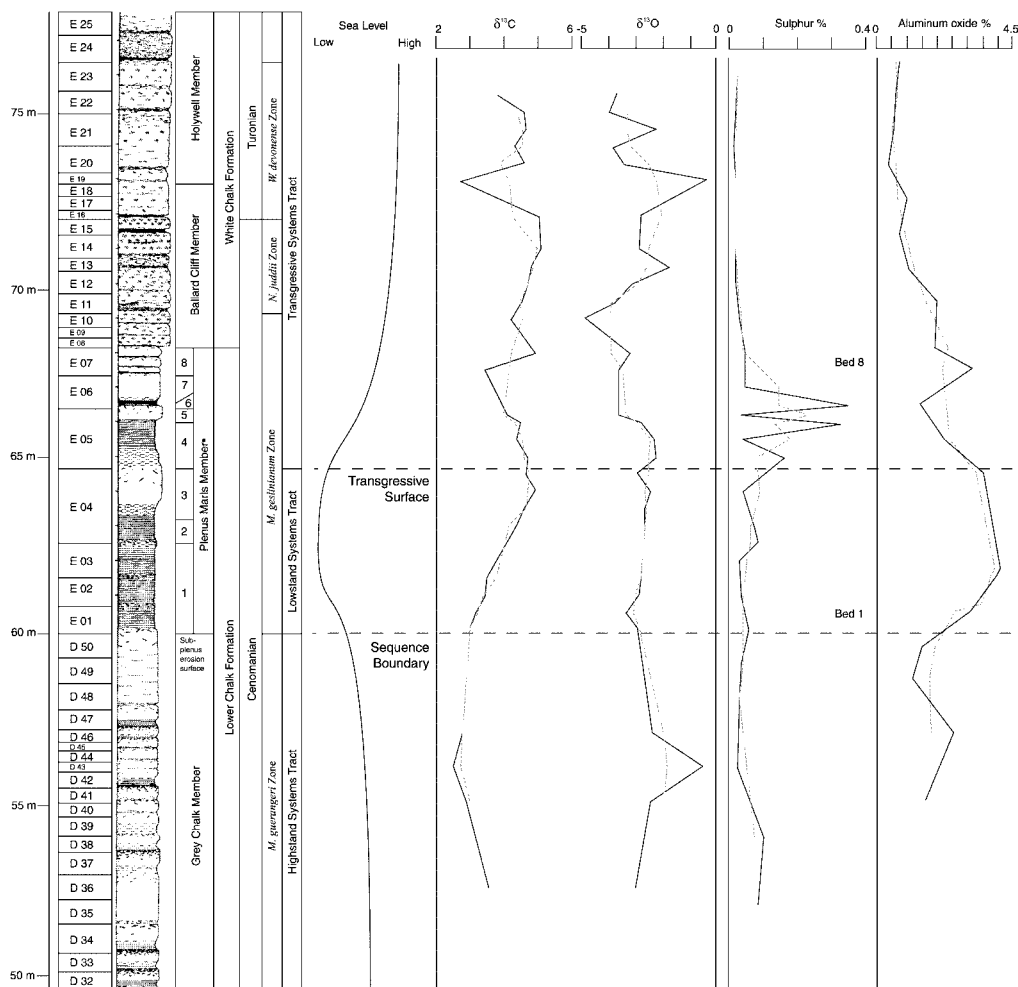
The time interval from the Late Cenomanian to Early Turonian has long been recognized as a period of major biotic and oceanographic change. Based on rates of faunal turnover, this period was identified as the third largest mass extinction in the post-Palaeozoic, only exceeded in size by the end-Cretaceous and Norian–Rhaetian events (Raup & Sepkoski 1982). In the marine realm, 7% of families, 26% of genera and 53% of species are estimated to have become extinct at the Cenomanian–Turonian boundary (Sepkoski 1989; Jablonski 1991; Harries 1993).

Major changes in the marine environment were taking place at this time. Sea level increased significantly through the Cenomanian to reach an all-time highstand for the Phanerozoic in the Early Turonian (Hancock & Kauffman 1979; Haq *et al.* 1987; Hallam 1992), possibly driven by a phase of rapid oceanic crust formation (Orth *et al.* 1993; Kerr 1998). During the Late Cenomanian there was a period of exceptionally high organic burial in outer shelf and ocean basinal environments, so much so that this interval has been characterized as Oceanic Anoxic Event (OAE) 2 (Schlanger & Jenkyns 1976; Jenkyns 1980). A positive  $\delta^{13}\text{C}$  excursion, coincidental with OAE 2, is now recognized on a global scale (Gale *et al.* 1993; Ulicny *et al.* 1997).

However, the chain of events linking environmental change and faunal extinction is far from agreed, and several contending theories have been put forward to explain the end-Cenomanian extinction event. Hut *et al.* (1987), using geochemical and faunal evidence from the Western Interior Basin, USA, proposed that there had been a series of stepped extinctions, possibly driven by sequential meteorite impacts. A

more widely supported view is that the Cenomanian–Turonian (C–T) extinction was initiated and driven by expansion of the oxygen minimum zone in the oceans, related to OAE 2 (Schlanger & Jenkyns 1976; Schlanger *et al.* 1987; Arthur *et al.* 1987; Jarvis *et al.* 1988; Kaiho & Hasegawa 1994; Busson & Corn e 1996; Hart 1996; Caus *et al.* 1997). Under this scenario the Late Cenomanian transgression resulted in eutrophication of surface waters which in turn led to dysoxic to anoxic conditions developing over much of the shelf. A third proposal is that the C–T extinction was a result of starvation. Paul & Mitchell (1994) and Paul *et al.* (1994) have pointed to the marked decline in productivity that occurred near the end of the Cenomanian and suggested that a simple decrease in food supply might explain much of the extinction. Finally, global cooling and glaciation has been proposed as the reason for at least some of the extinction at this time (Jeans *et al.* 1991).

At a yet more fundamental level, there remains some doubt as to whether there was any significant mass extinction across this interval of time at all. Banerjee & Boyajian (1996), working with high quality data on foraminifera, found much smaller levels of extinction (17% of genera). Fish and echinoderm family and genera data taken from Raup & Sepkoski's (1982) original analysis, but culled to include only monophyletic data and with ranges corrected, showed no evidence for significant extinction levels at the end Cenomanian (Patterson & Smith 1987, 1989). Furthermore, Hora & Marshall (1998) could find no evidence for a terminal Cenomanian extinction in marine faunas of the USA. Western Interior Basin after they had corrected for sampling biases.



**Fig. 1.** Stratigraphy of the uppermost Lower Chalk and basal White Chalk formations at Beachy Head, Eastbourne, Sussex, UK. The lithostratigraphical divisions follow Gale (1995, 1996). The sequence stratigraphy and sea-level curve are modified from Robaszynski *et al.* (1998). D32–E25 are numbered sedimentary couplets which are formed in response to 20 ka precession cycles (Gale 1995; Gale *et al.* 1999a). Also plotted are carbon- and oxygen-isotope values, and sulphur and aluminium oxide ( $\text{Al}_2\text{O}_3$ ) content (the latter being an indication of the percentage of clay in the sediment). To determine  $\text{Al}_2\text{O}_3$  content, powdered rock was dissolved using a lithium metaborate fusion prior to analysis by ICP-AES. Plenus Marl Member Bed 1 (couplets E1–E3) and Bed 8 (couplet E7) are highlighted for reference.

Uncertainty therefore remains about both the cause and size of the C–T extinction. To address these problems we undertook a multidisciplinary investigation of an expanded succession spanning the Late Cenomanian and Early Turonian developed in relatively shallow-water (100–150 m deep) shelf chalks at Eastbourne, Sussex, on the south coast of England. The outcrops at Gun Gardens, Beachy Head, 3 km west of Eastbourne, Sussex [grid reference TG 585953 to 589954] and at Holywell, 1 km west of Eastbourne [TG 600965 to 600972] expose the thickest and most complete succession of Late Cenomanian and Early Turonian chalks in the Anglo-Paris basin (Jefferies 1962, 1963; Gale 1995, 1996; Gale & Hancock 1999). We have collected the macrofauna through this succession, sampling to a greater than 20 ka resolution using as reference the Milankovitch rhythmicity evident in the bedding. We have also measured a suite of physico-chemical parameters (total organic content, pyrite content, optical densitometry, clay content,  $\delta^{13}\text{C}$ , etc.) on a comparable timescale. Our aims were two-fold: first to establish the nature and timing of the faunal changes that took place amongst marine benthos, and second to establish how these events correlated with

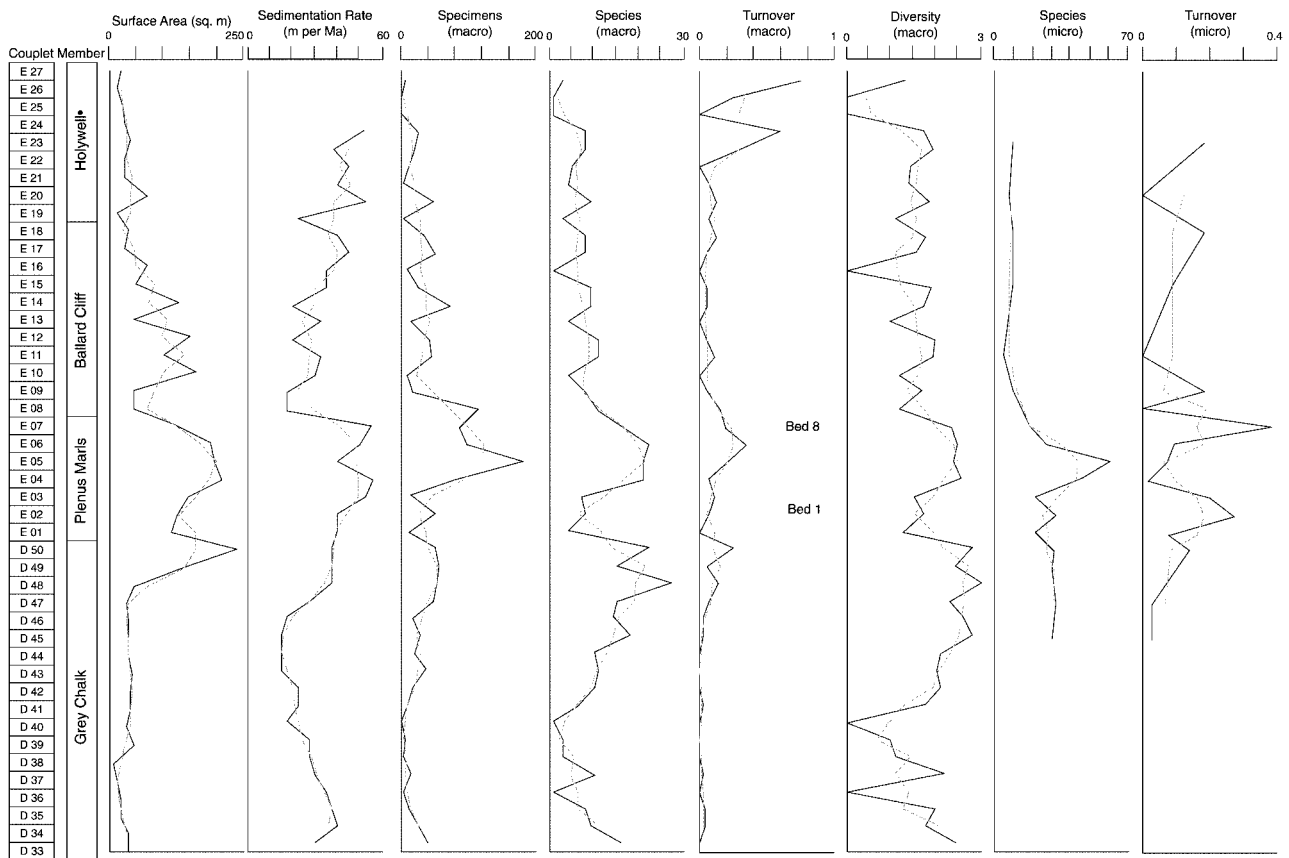
changes in sea-level, levels of bottom oxygenation, and surface productivity.

## Materials and methods

### Stratigraphy

The lithostratigraphy of the Eastbourne section has been described in detail most recently by Gale (1995, 1996) and Paul *et al.* (1999), and the bio- and sequence stratigraphy updated by Robaszynski *et al.* (1998, fig. 4). The lithostratigraphical terminology follows Gale & Hancock (1999). Summaries are provided in Fig. 1.

Conspicuous decimetre-scale alternations of more and less marly chalk are evident throughout these beds and can be correlated regionally (Gale 1989, 1995, 1996). Gale *et al.* (1999a) used spectral analysis of grey-scale densitometry, a proxy for measuring carbonate content, to identify cycle frequencies. This work demonstrated the presence of 20, 40, 100 and 400 ka orbital frequencies and confirmed that the dominant bed-scale cyclicality at Eastbourne coincides with the 20 ka precession cycle. The stratigraphical interval that forms the focus of this study thus encompasses 40 couplets, implying a time span



**Fig. 2.** Plots of surface area available for macrofossil collection, sedimentation rate and faunal diversity against numbered sedimentary couplets (D33 to E27) representing 20 ka intervals (see Fig. 1). Numbers of specimens and species of calcitic macrofossils and species turnover are based on >1800 individuals collected from air-weathered surfaces. Numbers of specimens and species of calcitic macrofossils and species turnover are derived from data in Paul & Donovan (1998). Plenus Marls Member Bed 1 (couplets E1–E3) and Bed 8 (couplet E7) are highlighted for reference.

of approximately 800,000 years. The 20 ka couplets are indicated in Fig. 1.

### Palaeontological sampling

The succession at Eastbourne is richly fossiliferous, and its macrofauna has been systematically collected from available air-weathered surfaces over two field seasons. All complete specimens and fragments identifiable to at least generic level cropping out on weathered faces were collected for preparation and identification in the laboratory. More than 1800 specimens were collected from the time interval that is the focus of this paper, and are now housed in the Natural History Museum, London. Specimens were recorded to the nearest 5 cm against a sedimentary log and subsequently referred to numbered Milankovitch couplets. We estimated the surface area from which collections were made by measuring the area of exposure of each bedding couplet (Fig. 2).

The fauna is dominated by calcitic-shelled forms (96%), namely echinoderms (49.8%), calcite molluscs (27.9%), brachiopods (9.1%), and other invertebrate groups—mostly scleractinian corals and serpulids (9.3%). Species diversity was calculated for each rhythmic couplet (corresponding to a 20 ka interval). We applied various metrics to estimate species diversity, all of which gave broadly similar patterns. Results are presented for just one, the Shannon–Weaver index (Shannon & Weaver 1948), a widely employed measure of alpha diversity (Fig. 2). In the case of echinoderms, 69% of the material collected was of isolated ossicles, many tens or hundreds of which are to be found in a single individual (e.g. asteroid marginal ossicles or isolated cidaroid plates or spines). We omitted all such modular

skeletal material from our count of total numbers of individuals so as to avoid overestimating biomass. The Shannon–Weaver index works best with large sample sizes. Throughout much of the succession we have 50 or more specimens per cycle, but couplets D35–D41, and E25 and above, yielded fewer than 25 individuals and consequently no emphasis is placed on results from these intervals. To smooth out for errors associated with small sample sizes, we also plotted results using a three-point moving average of these data. Faunal turnover is calculated as the number of taxa that last appear in each interval divided by the total number of taxa present.

The distribution of species of benthic foraminifera from immediately beneath the Plenus Marls Member to the Holywell Member is taken from Paul & Donovan (1998, fig. 5.4) and Paul *et al.* (1999). Their data is not appropriate for calculating diversity indices, since absolute numbers are not available (C.R.C. Paul pers. comm. 1998), but their data does allow us to plot species numbers and turnover (Fig. 2).

### Geochemical and micropalaeontological sampling

Unweathered sediment samples were taken every 50 cm and splits from these used to determine various geochemical and micropalaeontological parameters.

**Whole rock  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ .** Samples were cleaned with 10%  $\text{H}_2\text{O}_2$  and acetone and then dried at 60°C. They were then reacted with purified orthophosphoric acid at 90°C and analysed on-line using the VG Isocarb device and prism mass spectrometer at Oxford University. Normal corrections were applied and the results presented in ‰

deviation from the PDB belemnite standard. The raw data and a smoothed curve, based on a three-point moving average, are presented (Fig. 1).

**Pyrite content.** We followed the procedures of Raiswell *et al.* (1988) to obtain values for sulphur and Fe-soluble iron in our samples, and used these to calculate their degree of pyritization (DOP). Their method is only applicable to samples with >0.15% total organic content. Consequently it was applicable to just two horizons, Beds 4 and 6 of the Plenus Marls Member.

**Palaeoproductivity indices.** We use three proxies for surface palaeoproductivity: the total organic content of sediments, quantitative analysis of key nannofossil taxa thought to indicate high productivity, and point-counts of calcisphere and foraminiferal abundance.

The total organic carbon (TOC) of a sediment is dependent upon primary productivity in the overlying waters and on sediment accumulation rate (Muller & Suess 1979; Berger & Heruga 1992; Middelburg *et al.* 1993). Higher productivity in the overlying water column results in a greater flux of organic matter to the sea bed where its preservation is heavily dependent upon sediment accumulation rates. Faster accumulation rates result in more TOC being preserved in the sediment. Consequently, TOC can stand as a reliable proxy for primary productivity only if variation in sediment accumulation rates can be factored out. The 20 ka Milankovitch rhythmicity evident in the section allows us to estimate absolute sediment accumulation rates and thus improves the reliability of TOC as a productivity indicator. TOC values were determined by the Fossil Fuels Research Group, Newcastle University. 100 mg of chalk sample was reacted with 18% HCl in a porous Leco crucible and rinsed three times with distilled water to decarbonate the sample. Measurements were made using a Leco CS 244 carbon-sulphur analyser.

The biogeographic distribution of living and fossil nannoplankton is controlled primarily by surface water temperature and productivity (e.g. Brand 1994; Burnett *et al.* in press). Consequently certain species are now widely established as productivity indicators in the Cretaceous (e.g. Roth & Krumbach 1986; Roth 1989; Watkins 1989; Erba *et al.* 1992; Windley 1995; Street 1999). Specifically, the genera *Zeugrhabdotus* and *Biscutum* are recognized as high productivity indicators, characteristic of eutrophic environments. In all these studies, increases in *Zeugrhabdotus* and *Biscutum* were found to correspond to decreases in the relative abundances of *Watznaueria*. Since *Watznaueria* is typically the dominant genus in Cretaceous assemblages this may in part be a closed sum effect, rather than recording a decrease in absolute abundances of *Watznaueria*. Nonetheless, it appears clear that *Zeugrhabdotus* and *Biscutum* were better able to exploit eutrophic conditions than *Watznaueria* and so an index based on the relative abundance of these taxa should record productivity change. The prime limitation on this method is that *Watznaueria* is also the most robust of these genera and so its abundance will increase with deteriorating preservation.

For each sample, the percentage represented by each indicator taxon was found from counts of coccolith assemblages, which were continued until 100 specimens of *Watznaueria* had been counted. This resulted in coccolithophorid assemblage counts of between 150 and 220 individuals. The productivity index *P* was then calculated as:

$$P = \frac{\% \text{ Zeugrhabdotus spp.} + \% \text{ Biscutum spp.}}{\% \text{ Watznaueria spp.}}$$

The relative abundance of calcispheres, predominantly pithonellids, and foraminiferans present in sediment samples was determined by point-counts from thin-sections, using 400 points per slide.

### Sequence analysis and sea-level change

Previous authors have proposed different interpretations for the depositional environment of the Plenus Marls Member. Jefferies (1962, 1963) concluded that its formation was initiated by a fall in sea level,

which caused cut-down in base level and generated an increased clay input into the basin. Jarvis *et al.* (1988) assumed an overall rise in sea level from the base of the Plenus Marls Member into the overlying White Chalk Formation, based on evidence from foraminiferal assemblages and features of the sediment. However, both Hancock (1990) and Jeans *et al.* (1991) thought the Plenus Marls Member and overlying White Chalk Formation to be regressive, because they interpreted the coarser bioclastic sediments and the nodularity of these beds to be a product of lower sea levels.

Robaszynski *et al.* (1998) applied sequence stratigraphical analysis to Cenomanian successions across the Anglo-Paris Basin and identified six basin-wide sequence packages developed across a variety of facies. They placed a sequence boundary (base of Cenomanian sequence 6) at the base of the Plenus Marls Member and interpreted Beds 1–3 as a lowstand systems tract. The Bed 3–4 boundary was interpreted as a transgressive surface, and the higher part of the Plenus Marls Member (Beds 4–8) and the overlying Ballard Cliff Member they placed within a transgressive systems tract.

We follow the scheme of Robaszynski *et al.* (1998) and here add supportive evidence for their interpretation. The sub-plenus erosion surface is known locally to channel deeply into the underlying chalks towards the basin margins (Jefferies 1963), and passes laterally into hardground surfaces over much of the platform. We endorse its identity as a sequence boundary, and note that a correlative surface can be traced into eastern Europe and central Asia (Gale *et al.* 1999b).

In mid- to deep shelf environments, such as at Eastbourne, Beds 1–3 are well-developed, but towards the basin margins, the erosion surface at the base of Bed 4 onlaps Beds 1–3 and a remanié Bed 4 assemblage is found in sediment immediately overlying the sub-plenus erosion surface. Beds 4–8 and the lower part of the Ballard Cliff Member show progressive onlap onto the platforms around the Anglo-Paris Basin. For example, over the East Midlands Shelf, in north Norfolk, UK, Bed 7 rests directly on the sub-plenus erosion surface. In Normandy in the southwestern part of the Anglo-Paris Basin, the increasing onlap onto the basin margins in the higher part of the Plenus Marls and Ballard Cliff members provides unequivocal evidence of sea-level rise through this interval, as does the facies succession. For example, in Sarthe, NW France, nannofossil chalks of *M. geslinianum* and *N. juddii* Zone age rest directly upon Late Cenomanian shallow marine sands (Juignet 1974).

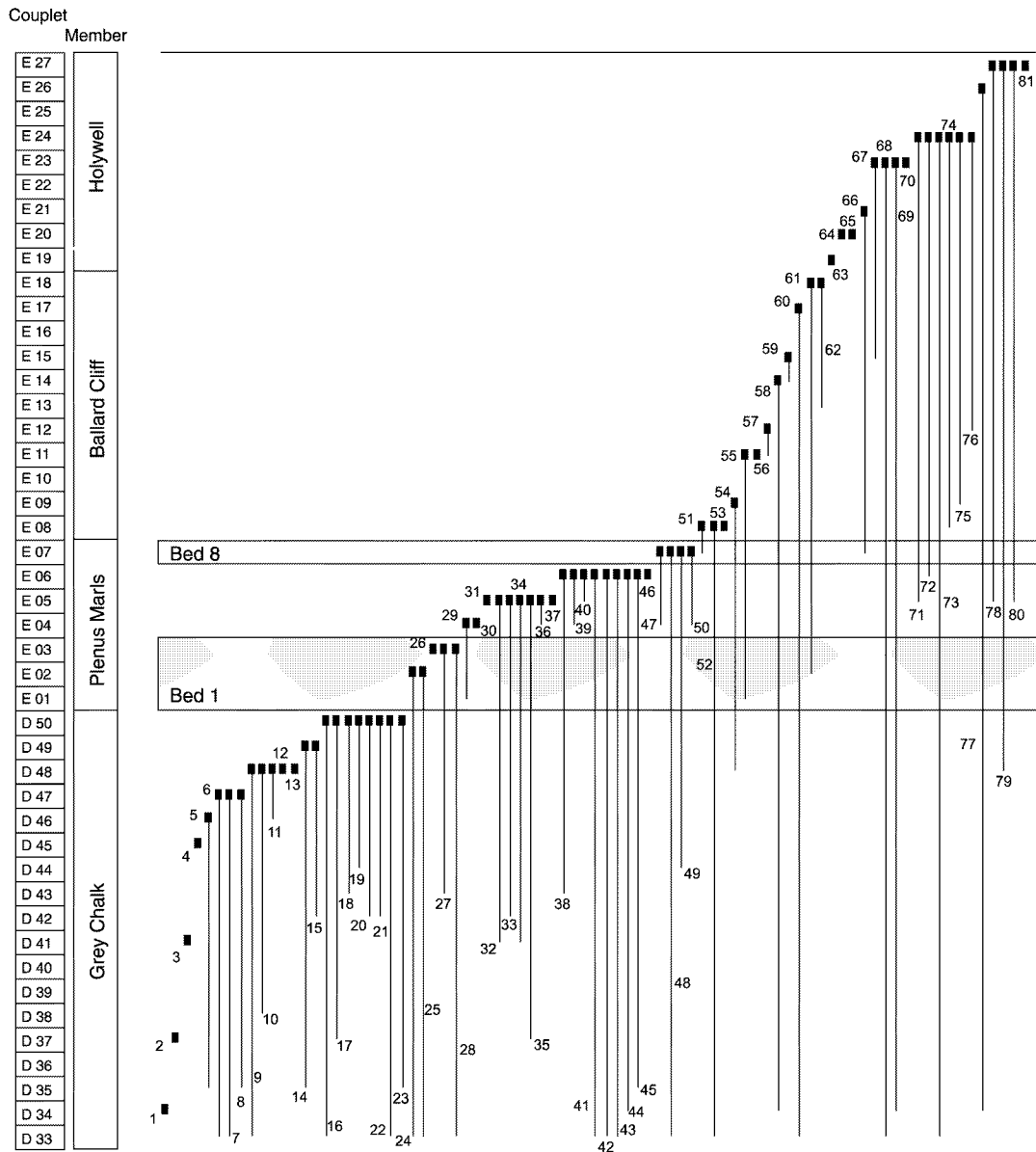
## Results

### Changes in benthic biodiversity

**Macrofauna.** At Eastbourne, species numbers increase to a maximum in the Grey Chalk Member a little below the sub-plenus erosion surface and then drop significantly in bed 1 (couplets E1–E3) of the Plenus Marls Member (Fig. 2). However, species numbers rebound to pre-Plenus Marls Member levels in bed 2 (couplet E4) and remain high to bed 6. In beds 7 and 8 (couplet E7) species numbers begin to decline steeply and remain low throughout the Ballard Cliff and lower Holywell members. There is no consistent match between species numbers and either surface area or specimen numbers collected (Fig. 2).

Diversity, as measured by the Shannon–Weaver index (Fig. 2), rises towards the top of the Grey Chalk Member (D42–D50), and then drops sharply in Bed 1 (E1–E3) of the Plenus Marls Member. Higher in the Plenus Marls Member diversity rapidly recovers to levels equalling that in the upper part of the Grey Chalk Member, although the fauna is distinct. A second decline in diversity occurs from couplet E7, after which it remains relatively stable and low.

An indication of the rate at which the biota was changing is provided by plotting where taxa appear and disappear through the section (Fig. 3). Clustering of first and last occurrences highlights positions in the section where there is unusually fast



**Fig. 3.** Range distribution of 81 calcitic-shelled macrofossils found in the latest Cenomanian–earliest Turonian of Eastbourne, arranged in order of last appearance. Vertical scale (D33–E27) represents numbered sedimentary couplets representing 20 ka intervals, as in Fig. 1. Taxa 1–81 as follows: 1, *Hirudocidaris* sp.; 2, *Valettaster ocellatus* (Forbes); 3, *Concinnithyrus subundata* (J. Sowerby); 4, *Tylocidaris* (*Oedematocidaris*) *asperula* (Roemer); 5, *Glyphocyphus radiatus* (Agassiz); 6, *Camerogalerus cylindricus* (Lamarck); 7, cidarid spine type C; 8, cidarid spine type G; 9, *Orbirhynchia multicostata* Pettitt; 10, cidarid spine type K; 11, *Ditrupa* sp.; 12, *Tiaromma michelini* (Agassiz); 13, *Tylocidaris* cf. *clavigera* (Mantell); 14, *Limaria elongata* (J. de C. Sowerby); 15, *Plicatula inflata* (J. de C. Sowerby); 16, *Amphidonte obliquata* (Pulteney); 17, *Glomerula gordialis* (von Schlotheim); 18, *Micrabacia coronula* (Goldfuss); 19, *Neitheia quinquecostata* (J. Sowerby); 20, *Ophiotitanos tenuis* Spencer; 21, *Plagiostoma globosum* J. de C. Sowerby; 22, *Praerotularia saxonica* (Geinitz); 23, *Salenia petalifera* Desmarest; 24, '*Nymphaster*' *radiatus* Sladen; 25, *Chlamys beaveri* (J. Sowerby); 26, *Isocrinus* sp.; 27, *Monticlarella rectifrons* (Pictet); 28, *Oxytoma pectinata* (J. de C. Sowerby); 29, *Crania* sp.; 30, *Orbirhynchia multicostata* Pettitt; 31, *Echinocyphus intermedius* Smith & Wright; 32, *Hepteria septemsulcata* (Lamarck); 33, *Holaster gregoryi* Lambert; 34, *Onchotrochus serpentinum* Duncan; 35, *Tennocidaris* (*Stereocidaris*) sp. nov.; 36, *Terebratulina nodulosa* Etheridge; 37, *Terebratulina protostriatula* Owen; 38, *Calliderma smithae* (Forbes); 39, cidarid spine H; 40, *Entolium membranaceum* (Nilsson); 41, *Holaster* sp.; 42, *Sternotaxis trecensis* (Leymerie); 43, *Oxytoma seminudum* (Dames); 44, *Plicatula barroisi* Peron; 45, *Stauranderaster coronatus* (Forbes); 46, *Tennocidaris* (*Stereocidaris*) sp.; 47, *Actinocamax plenus* (Blainville); 48, cidarid spine type D; 49, *Cottaldia bennettiae* (Koenig); 50, *Pycinaster humilis* Spencer; 51, *Discoides subuculus* (Leske); 52, *Neomicrorbis crenatostrata* (Münster); 53, *Nymphaster coombii* (Forbes); 54, *Tetragramma variolare* (Brongniart); 55, *Conulus castanea* (Brongniart) var. *rhotomagensis* (Agassiz); 56, *Prionocidaris* sp.; 57, *Prionocidaris* sp.; 58, *Atreta nilsoni* (Hagenow); 59, *Grasirhynchia martini* (Mantell); 60, *Proliserpula ampullacea* (J. Sowerby); 61, *Grasirhynchia grasiana* (d'Orbigny); 62, *Monticlarella jefferiesi* Owen; 63, *Nymphaster obtusus* (Forbes); 64, *Terebratulina lata* (Etheridge); 65, *Terebratulina* sp.; 66, *Hirudocidaris hirudo* (Sorignet); 67, *Cardiaster truncatus* Goldfuss; 68, *Pycnodonte vesicularis* (J. Sowerby); 69, *Spondylus latus* (J. Sowerby); 70, *Terebratulina striatula* (Mantell); 71, cidarid spine, type A; 72, *Crateraster quinqueloba* (Goldfuss); 73, *Camerogalerus minimus* (Desor); 74, *Mytiloides* sp.; 75, *Orbirhynchia wiesti* (Quenstedt); 76, *Roveacrinus* sp.; 77, *Inoceramus* sp.; 78, *Anomia papyracea* d'Orbigny; 79, *Hemiaster nasutus* (Sorignet) 80, cidarid spine, type B; 81, cidarid spine, type E.

faunal turnover taking place. For benthic macrofauna turnover continued at moderate levels through the latest part of the Grey Chalk Member and the Plenus Marls Member. However, two peaks stand out indicating periods where turnover rates doubled, one at the base of the Plenus Marl Member (couplet D50–E1), the other in Plenus Marls Beds 5–8 (couplets E6–E7) (Figs 2, 3).

*Benthic foraminifera.* The uppermost part of the Grey Chalk Member is characterized by high species richness (35–40 species per sample), coincidental with highest macrofaunal diversity (Fig. 2). Thereafter diversity drops more or less continuously through the Plenus Marls Member to approximately 14–18 species per sample by Bed 8. At the start of the Ballard Cliff Member species diversity declines still further, to 6–12 species, and remains at this low level through the lower Holywell Member.

The turnover in benthic foraminifera remains below 15% throughout most of the section, except for two brief intervals when rates more or less double (Fig. 2). The first of these periods of enhanced turnover is in Bed 1 of the Plenus Marls Member, where some 27% of the species have their last occurrence. This coincides with a marked rise in the clay content of the sediment. The second, and much larger, turnover peak occurs in Bed 8 of the Plenus Marls Member, where 38% of standing diversity have their last occurrence.

*Trace fossils.* The chalk and marl sediments at Eastbourne are pervasively and densely burrowed throughout the Cenomanian and Turonian succession. Burrows are particularly conspicuous at omission surfaces (Bromley 1975), where contrasts in sediment colour highlight the presence of large *Thalassinoides* and *Planolites*. *Chondrites* is common as both reworking within *Thalassinoides* and free within the sediment. White filled *Chondrites* are abundant at the base of Plenus Marls Member Bed 3, and define a marker event that can be traced to NW Germany (Ernst *et al.* 1983; Gale 1996). Other ichnogenera represented in the Plenus Marls Member include the meniscate genus *Taenidium*, common in Beds 4, 5, 7 and 8, and the vertical to sub-vertical shafts of *Bathichmus*, which occur frequently in Bed 1 and pass down through the sub-plenus erosion surface. As many as six to eight cross-cutting tiers of burrows can be recognized within single horizons. The diversity and cross-cutting relationships of the traces present demonstrate that multitiered bioturbation, similar to that figured from the Maastrichtian chalks of Denmark (Bromley 1996), is present throughout the Plenus Marls Member and overlying White Chalk.

#### *Changes in palaeoproductivity*

All three palaeoproductivity indicators suggest a marked drop in palaeoproductivity within Bed 7 of the Plenus Marls Member.

The values of TOC throughout the Eastbourne section are low (<0.25%) but show a consistent pattern (Fig. 4). In the Grey Chalk and Plenus Marls members, up to Bed 5 (couplet E5), values fluctuate from 0.05 to 0.15, with a mean of about 0.1. In Bed 6 of the Plenus Marls Member, TOC values reach their highest value, at 0.21%, but in Bed 7 (couplet E6) fall to 0.05 and remain consistently low through the remainder of the Plenus Marls, Ballard Cliff and lower Holywell members.

Correcting for differences in sedimentation accumulation rates does not alter the general pattern described above. Specifically, the sharp drop in TOC at Bed 7 is an order of magnitude too large to be explained simply by the slight decrease in sedimentation rate observed towards the top of the Plenus Marls Member and through the Ballard Cliff Member.

Our nannoplankton productivity index (*P*) shows an almost identical pattern (Fig. 4). Values are highest in the uppermost part of the Grey Chalk Member, a few metres beneath the sub-plenus erosion surface. There is then a drop into the lower part of the Plenus Marls Member, a short-lived recovery and a further decrease to minimum values in Bed 8 of the Plenus Marls Member, with the almost complete loss of *Biscutum* and strong decline of *Zeugrhabdotus*. Nannofossil preservation is worse in the upper part of the section and some of this trend is probably a preservational effect. However, most other species do not show the same pattern, as might be expected if preservation were the sole control. Interestingly, the genera *Acaenolithus* and *Broinsonia* show a parallel distribution pattern (Fig. 3), and these genera have been interpreted as indicative of nearshore conditions (Hattner *et al.* 1980), and presumably thus of relatively eutrophic conditions.

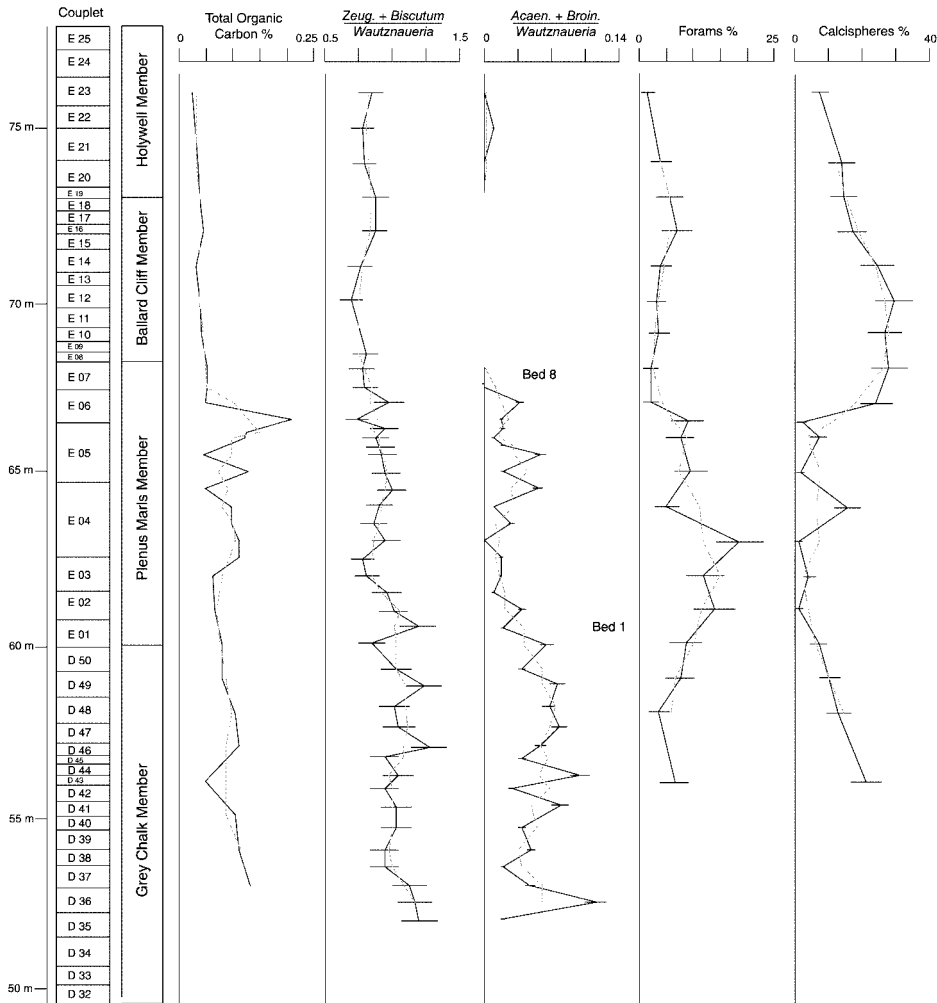
There is also a distinct increase in the abundance of the coccolithophorid *Eprolithus floralis* (Stradner 1962) Stover 1966 in the upper part of the Plenus Marls Member (Bed 7, couplet E6). Similar enrichments of *E. floralis* appear to be a general feature of the latter part of the C–T 'boundary interval' (Bralower 1988; Lamolda *et al.* 1994). The consistent enrichment in this species is both unusual and hard to interpret, since there is no clear model for its palaeoecology, but it provides good evidence that palaeoenvironmental change of some type was affecting the nanoflora.

The abundance of pithonellid calcispheres rises sharply through couplet E6 (Beds 6–8 of the Plenus Marls Member), coincident with a marked drop in the abundance of foraminifera (Fig. 4). Similar calcisphere enrichments have been recorded at this level from many other localities (Hart 1991; H. Willems pers. comm. 1999).

#### *Isotopic curves*

The  $\delta^{18}\text{O}$  curve (Fig. 1) shows a trend of progressive lightening values through the Grey Chalk and Plenus Marls members, which is reversed at the top of the Plenus Marls Member and lower part of the Ballard Cliff Member (Couplets E7–E12). Thereafter values fluctuate irregularly. The lightening trend was interpreted to reflect Late Cenomanian warming by Jenkyns *et al.* (1994); the 'peakiness' in the higher part of the section probably reflects the very irregular diagenetic cementation at these levels.

The  $\delta^{13}\text{C}$  curve (Fig. 1) is broadly similar to that published by Jenkyns *et al.* (1994), based on the Holywell section, with the major difference being that the relative expansion of the Plenus Marls Member at Beachy Head results in a more gradual build up of values between Beds 1 and 4. The positive excursion starts at the base of the Plenus Marls Member with values gradually increasing to a peak within Bed 3.  $\delta^{13}\text{C}$  values fall slightly through Beds 4–7, then rise to a plateau of high, but fluctuating, values through the Ballard Cliff Member.  $\delta^{13}\text{C}$  values then fall gradually in the lower part of the Holywell Member. This global  $\delta^{13}\text{C}$  excursion is widely interpreted as reflecting the burial of large amounts of organic carbon, associated with a rapid rate of sea-level rise during the Late Cenomanian (Jenkyns 1980; Jenkyns *et al.* 1994).



**Fig. 4.** Plots of palaeoproductivity indices against stratigraphic height through the latest Cenomanian–earliest Turonian. Total organic carbon and the abundance of selected calcareous nannofossils, foraminifera and calcispheres are plotted. Plenus Marls Member Bed 1 (couplets E1–E3) and Bed 8 (couplet E7) are highlighted for reference. Error bars on the nannofossil productivity indices represent  $\pm 10\%$ ; error bars on total foraminifera and calcisphere counts are  $\sqrt{n}$ . Zeug., *Zeugrhabdotus*; Acan., *Acaenolithus*, Broin., *Broinsonia*.

## Discussion

### *Faunal extinction or faunal replacement?*

Our data unequivocally identify two intervals (within Bed 1 and Beds 7–8 of the Plenus Marls Member) when the benthic community was undergoing rapid change (Figs 2, 3). Furthermore, at both intervals overall species diversity dropped (Fig. 2). Clearly both intervals record significant faunal events, but were these changes on a local scale, marking immigration/emigration of species as biofacies migrated over the shelf, or genuine regional-wide events that record the demise of benthic communities?

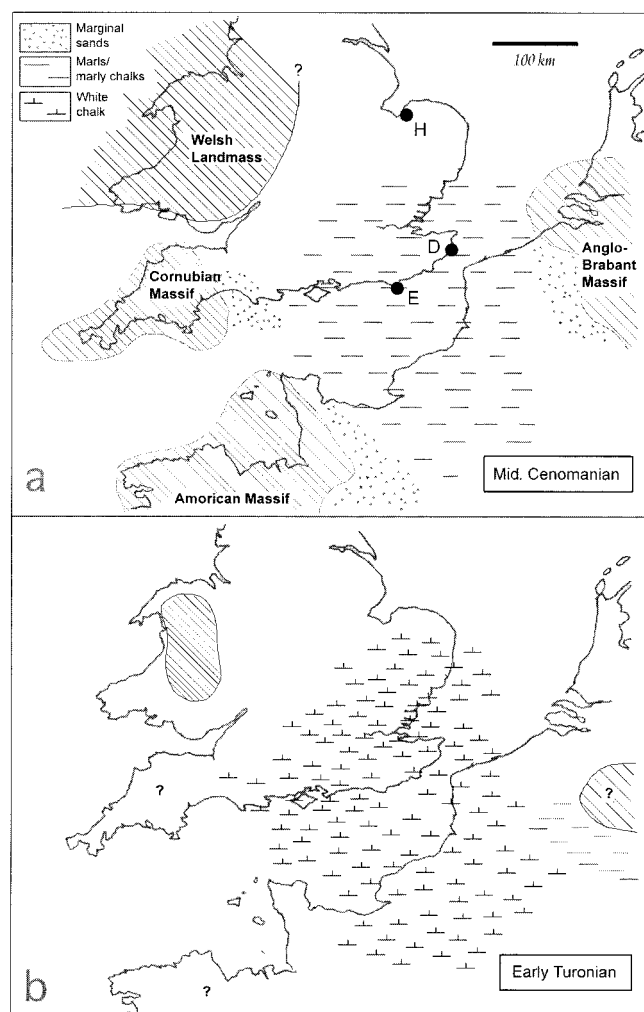
Two questions need to be answered. How widespread are the changes at these levels within the Anglo-Paris Basin, and what is the long-term fate of the clades that are affected; do they simply disappear temporarily or are they lost forever?

*Synchronicity of change.* Jefferies (1962, 1963) convincingly demonstrated the synchronicity of faunal change within the Plenus Marls Member by demonstrating the lateral persistence of individual beds across the Anglo-Paris Basin. Within current limits of resolution, the major change in fauna took place more or less simultaneously across southern England and NW France (Robazynski *et al.* 1998).

However, faunal change may have occurred slightly earlier in the East Midlands Shelf, along the SW border of the North

Sea Cleveland Basin. We have carried out a similar faunal analysis of the Cenomanian succession in the comparatively deeper-water setting of the Hunstanton region in Norfolk, UK (see below, Fig. 5). Here, as in the Plenus Marls Member at Eastbourne, there is a switch from a moderately diverse fauna to a depauperate fauna dominated by pycnodontid and inoceramid bivalves, but this takes place at a level towards the top of the Middle Cenomanian *A. jukesbrownei* Zone (unpublished data held by the senior author). This highly depauperate fauna continues until immediately beneath the sub-plenus erosion surface where diversity rises very slightly before dropping once again in the Plenus Marls and Ballard Cliff members correlative levels. Thus the most important faunal break, and the one similar in aspect to that seen above Bed 7 of the Plenus Marls Member in the Anglo-Paris Basin, took place at the preceding sequence boundary, approximately 1 million years earlier, in the Cleveland Basin.

*Extinction and pseudoextinction.* In theory it should be relatively easy to distinguish between faunal disappearances that represent migration and local extinction events, from those that mark true extinction events. After all, if migration were the cause, one would expect to find the taxon in question in younger rocks of appropriate facies somewhere else. However, in practice the situation is much more difficult, because factors large enough to effect major changes in the distribution



**Fig. 5.** Palaeogeography of the Anglo-Paris Basin and adjacent massifs during the Mid-Cenomanian (a) and the Early Turonian (b). During the Mid-Cenomanian (a) relatively large areas of emergent massifs supplied clastic material to adjacent seas; shallow water sands accumulated on the basin margins, and clay-rich chinks in the central basin. The sands supported a very diverse shallow marine benthos. During the major transgression of latest Cenomanian and Early Turonian time, the massifs were extensively submerged (b), drastically reducing the source areas, and oceanic white chalks spread across the region. No shallow marine sands of this age are preserved anywhere and were probably eroded from the interiors of massifs by post-Cretaceous erosion. E, Eastbourne; D, Dover; H, Hunstanton.

of facies belts over the continental shelf, and thus instigate migration, also significantly alter the distribution of facies that end up being preserved in the sedimentary record. Nowhere is this more clearly demonstrated than with the great transgression of the late Cenomanian.

During the early Cenomanian, sediments with faunas from mid- and inner-shelf settings outcrop extensively around the marginal parts of the basin (e.g. Devon, Sarthe) (Fig. 5). However, the Lower and Middle Turonian outcrops in the Anglo-Paris Basin are developed exclusively in mid- to deep-water chalk facies, and there is no surviving record of sediments representing more onshore environments (Fig. 5), even though such deposits were presumably laid down around the basin margins. Inshore deposits at times of high sea level,

being 'perched' high on the cratonic interiors, are the most susceptible to loss through erosion during subsequent regressive phases. As sea level has fallen by around 100 m since reaching an all-time high in the late Cretaceous (Haq *et al.* 1987; Komintz *et al.* 1998), it is not surprising that only mid- to deep-water shelf lithofacies survive from the Turonian highstand interval.

Since shallow-water shelly marine invertebrate biotas are, in general, much more species rich than contemporary deeper-water biotas (due to habitat heterogeneity in shallow water settings), any significant reduction in the relative proportion of outcrops preserving shallow-water faunas could lead to an apparent decrease in diversity. So the switch from a stratigraphic record composed predominantly of inshore to mid-shelf deposits of Cenomanian age to one of purely deep-water deposits of Turonian age could, by itself, explain the apparent drop in diversity that is registered by the fossil record in the Anglo-Paris Basin.

Distinguishing between the disappearance of taxa through extinction, and non-sampling in the fossil record (pseudo-extinction) requires phylogenetic data. If inadequate sampling is causing the majority of disappearances, then most taxa should reappear, either unchanged (Lazarus taxa) or in a slightly modified form (sister taxa), when appropriate facies reappear in the rock record. If extinction is the cause then neither it nor any descendant species from it will be found in younger rocks. Because background extinction will continue to affect biotas during any gap in the fossil record, it is expected that some genuine extinction will take place over time, even if the gap is entirely due to sampling artifact. The important thing is the relative dominance of the two categories.

There are 67 genera of calcite-shelled macroinvertebrates present in the latest Cenomanian of Eastbourne (Fig. 3). Although most of these disappear from the Turonian of the Anglo-Paris Basin, only four (6%) can be regarded as genuine lineage extinctions, i.e. lineages that have no post-Cenomanian representatives or derived sister groups. A similar situation probably exists for benthic foraminifera, although here we are hampered by the lack of a phylogenetic framework. Most of the disappearances from the Eastbourne section are at species level, and related taxa appear further up the section. Only the planktonic foraminiferan genus *Rotalipora* probably represents a genuine extinction at generic level.

The implication from this is that the vast majority of Cenomanian genera, although not sampled during the subsequent Turonian anywhere in the Anglo-Paris Basin, survived in basin margin refugia that are no longer represented in the sedimentary record. The latest Cenomanian thus represents a period when faunal ranges underwent major reorganization rather than a period of mass extinction.

#### *Anoxia as a kill mechanism*

The idea that the latest Cenomanian extinction was brought about through an expansion of the oxygen minimum zone and the spread of dysoxic conditions across much of the shelf has been championed by many workers (e.g. Schlanger 1981; Jarvis *et al.* 1988; Elder 1989; Hart 1996; Caus *et al.* 1997). Evidence for a decrease in bottom water oxygenation through the latest Cenomanian succession of the Anglo-Paris Basin is based on the inverse relationship seen between rising  $\delta^{13}\text{C}$  values and decreasing microbenthic diversity (Jarvis *et al.* 1988, fig. 31), which was established from the succession at Dover, Kent, some 100 km to the east of our study area.

There are three strands to the argument put forward by Jarvis *et al.* (1988) and others: (i) that there is a marked decline in benthic foraminifera diversity associated with dysoxia, (ii) that deep-dwelling planktic foraminifera suffered more intense extinction than shallow water forms, indicating that dysoxia rose into the water column and (iii) that the shift in  $\delta^{13}\text{C}$  ratio was the product of local (i.e. eastern North Atlantic shelf margin) high productivity. We challenge all three assumptions.

A progressive decrease in the diversity of benthic foraminifera and ostracods through the Plenus Marls Member was interpreted by Jarvis *et al.* (1988) as evidence of falling sea-floor oxygenation, and illustrated by cartoons showing the stepwise disappearance of 'less tolerant' species (Jarvis *et al.* 1988, fig. 34). We do not contest that there was a decrease in diversity in microfauna through this interval, and indeed demonstrate that a similar pattern of progressive impoverishment exists at Eastbourne. What we do contend is that this decline in diversity had anything to do with decreasing oxygenation levels. Macrofauna, trace fossils and sedimentary geochemistry all argue against any lowering of bottom water oxygenation in mid-shelf environments of SE England.

**Macrofauna.** Periodic hypoxia and anoxia generated by short-lived phytoplankton blooms can lead to periodic mass mortalities of the marine benthos, and a well-established pattern of structural change to benthic invertebrate communities occurs as hypoxia increases in shallow marine settings (e.g. Pearson & Rosenberg 1978; Diaz & Rosenberg 1995). With decreasing levels of dissolved oxygen species diversity falls, as does species biomass. Species abundance, however, initially rises, marking the rise to dominance of specialist taxa able to thrive in mildly hypoxic conditions, before falling rapidly.

Both species richness and abundance decline through the Plenus Marls Member, with the most marked drop occurring at Bed 8 (couplet E7). However, this is not the signal expected from increasing hypoxia. Through much of the Plenus Marls Member the macrofauna remains as diverse as in the preceding Grey Chalk Member, and is composed of typical shallow-water taxa of the period. At the start of the Ballard Cliff Member faunal diversity does drop significantly, and just a few species dominate. But the forms that rise to major dominance are echinoderms (a goniasterid asteroid and a cidarid echinoid), animals that are not especially tolerant of low oxygen conditions (Lawrence 1987). Factors other than oxygenation are likely to be driving the change in the fauna.

**Trace fossils.** Jarvis *et al.* (1988) suggested that the abundance of the trace fossil *Chondrites* in the Plenus Marls Member was a result of a decrease in bottom water oxygenation. This argument was based on the paper of Bromley & Ekdale (1984) which showed that *Chondrites* is more tolerant of low oxygen conditions than other ichnogenera. However, Bromley (1996, p. 222) has since qualified this statement, saying that 'it follows that if *Chondrites* is found alone, cutting primary fabric and representing a low percent of bioturbation, then dysoxic bottom waters are likely'. As the ichnofossil assemblage is diverse, with *Chondrites* clearly cross-cutting older traces, and there is no evidence of any primary lamination in the Plenus Marls Member, it is likely that these beds were deposited in fully oxygenated conditions.

**Sedimentology.** In the highest part of the Plenus Marls Member (Beds 7 and 8) and up through the Ballard Cliff and

Holywell members, shallow scours 1–2 m across and 10–20 cm deep are relatively common. These are each floored by a hardground, and contain many small (0.5–2.0 cm) white chalk intraclasts. Similar intraclasts are also found scattered through the chalks and marls of the Ballard Cliff and Holywell members. These features demonstrate the existence of strong bottom currents capable of considerable erosion. Since evidence of current activity is characteristically absent from dysoxic facies (Tyson & Pearson 1991) we conclude that dysoxic conditions are unlikely to have developed over prolonged periods during this interval.

**Degree of pyritization.** The degree of pyritization directly reflects the oxygenation of bottom waters at the time of deposition (e.g. Raiswell *et al.* 1988). Although we could apply this technique to only two horizons in the Plenus Marls Member (Beds 4 and 6, couplets E5 and E6) because of technical reasons, both had levels of pyritization that fall well within the 'fully aerobic' category of Raiswell *et al.* (1988). Geochemical evidence therefore points to the Plenus Marls Member being deposited under normal levels of oxygen.

**Planktic foraminifera and oxygen levels in the water column.** The disappearance of successive species of the planktic foraminiferan *Rotalipora* in Bed 1 of the Plenus Marls Member (*R. greenhornensis*) and at the top of Bed 3 (*R. cushmani*), followed by the subsequent loss of all planktics except *Hedbergella* in Beds 6–8, was interpreted by Jarvis *et al.* (1988) as a response to progressive expansion and intensification of an oxygen minimum zone through the water column. According to their interpretation, the vertical rise of low oxygenated water initially excluded the deepest dwelling planktic genus (*Rotalipora*) and later all others dwelling at intermediate depths. However, evidence exists to suggest that *Rotalipora* was neither deep dwelling nor oxygen sensitive. This genus is common in organic-rich sediments of the Hartland Shale in the Western Interior Basin, USA, in beds deposited in 100 m or less water depth and in a regime where there was a strongly developed oxygen minimum zone (Hay *et al.* 1993). Recent work on the local extinction of *Rotalipora cushmani* from an expanded succession in the Tarfaya Basin, Morocco (Luderer & Khunt 1997) has shown that the disappearance of this species coincides with a negative  $\delta^{18}\text{O}$  event, and thus with lowered salinity or (more probably) raised temperature. It may be that the disappearance of *Rotalipora* and other planktic foraminifera is related to changing temperature rather than oxygenation levels.

**$\delta^{13}\text{C}$  excursion as evidence of regional upwelling.** Jarvis *et al.* (1988) hypothesized that high productivity in the eastern North Atlantic produced by a major upwelling event during the Late Cenomanian–Early Turonian led to the expansion and intensification of the oxygen minimum zone, the  $\delta^{13}\text{C}$  excursion, and the extinction peak. Their assumption was that the  $\delta^{13}\text{C}$  excursion seen in the chalks of NW Europe was a product of local (i.e. North Atlantic margin) upwelling and a high productivity front and the resulting sequestration of  $^{12}\text{C}$ -rich organic matter in black shales on the upper continental slopes.

In fact the  $\delta^{13}\text{C}$  excursion is not regional but global. The detailed similarity between  $\delta^{13}\text{C}$  curves from widely scattered localities such as Colorado, USA, Eastbourne, UK, and Tarfaya, Morocco (Gale *et al.* 1993; Khunt *et al.* 1990) imply a global rather than regional change in  $\delta^{13}\text{C}$ . Although various

authors have suggested that local influences have affected the timing and magnitude of the  $\delta^{13}\text{C}$  excursion in the latest Cenomanian, the examples cited arose from inaccurate biostratigraphic correlation (Hilbrecht & Hoefs 1986; Bralower 1988), or are entirely hypothetical (see discussion in Jenkyns *et al.* 1994). There is thus no fundamental genetic relationship between the  $\delta^{13}\text{C}$  curve at any given site and local productivity, development of an oxygen-minimum zone or any other environmental parameter. Indeed, the global  $\delta^{13}\text{C}$  signal may well be registered in terrestrial organic matter and even in calcretes (e.g. Koch *et al.* 1992).

*Seasonal dysoxia?* Seasonal dysoxia occurs extensively in modern environments such as the Arabian Sea (e.g. Banse 1984; Naqvi 1987) and is controlled by strong variation in seasonal flux of organic matter in the water column and on the sea floor. Could a comparable seasonal effect have existed in the Late Cenomanian–Early Turonian succession at Eastbourne but not be preserved in the pervasively bioturbated chalk sediment record? The possible occurrence of seasonal dysoxia/anoxia in the geological record can be tested in several ways. Firstly, Oschmann (1993) demonstrated that the synchronisation of animal life cycles with  $\text{O}_2$ -fluctuation cycles occurred commonly in ancient shelf environments. Examples of this include specialist species of bivalves with extended planktic larval stages which only achieve maturity and colonise the sea-floor during oxygenated phases. The diversity and relatively high abundance in the Plenus Marls and Ballard Cliff members of macrofossil taxa for which this strategy would be impossible makes seasonal dysoxia very unlikely, as does the presence of large, relatively slow-growing animals such as the regular echinoid *Hirudocidaris*.

Secondly, the orbital precession cycle operates principally by moderating seasonal effects. Since precession is demonstrably the dominant orbital signal in the Late Cenomanian–Early Turonian succession at Eastbourne (Gale *et al.* 1999a), rhythmic couples should record any seasonal fluctuation in oxygen levels. No such signal is evident in these pervasively bioturbated rhythmic chalks with very low TOC values.

#### *Palaeoceanographic change and the oligotrophication of continental shelf settings*

If the Late Cenomanian–Early Turonian faunal change in the marine shelf environment occurred primarily through immigration/emigration and a reorganization of faunal distributions rather than mass extinction, and if there is little evidence that dysoxia played any part in this replacement, what is the likely mechanism responsible for creating biotic change at the C–T boundary? In our view, surface water productivity holds the key. Benthic diversity is coupled to pelagic diversity and abundance in modern oceans, albeit in a complex way (e.g. Graf 1992; Rosenberg 1995). Thus a key factor controlling benthic biodiversity in the geological past must be palaeoproductivity in the overlying water column.

Our study demonstrates that there were two short intervals during which the marine benthos underwent rapid change; in Bed 1 and Bed 8 of the Plenus Marls Member (Fig. 2). We believe that well-documented palaeoceanographic events at the time explain both, although the two events are unrelated.

Faunal change within Bed 1 of the Plenus Marls Member immediately follows a sequence boundary representing a fall in sea level. Although many taxa passed through this

interval, certain groups were strongly affected, most notably passive suspension feeders (corals and crinoids) and surface deposit feeders (holasterid echinoids). These changes are not accompanied by a change in surface water productivity (as measured by our productivity indices), but do coincide with a marked increase in siliciclastic input which may have been responsible for the disappearance of certain trophic groups. Diversity recovers rapidly in higher beds with lower siliciclastic content.

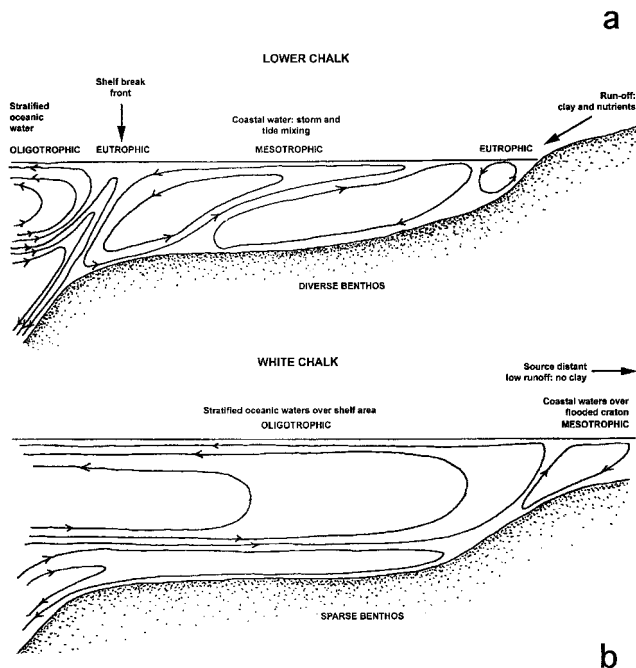
The second change, towards the top of the Plenus Marls Member, coincides with a decrease in siliciclastic content and the onset of white chalk deposition. All three of our palaeoproductivity indicators point to a major change in surface water ecology at this time. Nannofossil evidence suggests a progressive reduction in surface water productivity through the upper part of the Plenus Marls Member, and the increased abundance of calcispheres in couplet E6 (Bed 7), and the reciprocal decrease in relative abundance of foraminifera, marks a significant change in surface water conditions. From our knowledge of nannoplankton palaeoecology and extant calcareous dinoflagellates, we infer these changes record a shift from moderately highly productive (mesotrophic) to distinctly oligotrophic surface waters.

Hay (1995) suggested that the spread of white chalk facies onto the shelves and into flooded continental interiors was brought about by the collapse of shelf-break fronts during the high sea-level stand of the Late Cretaceous. Our observations support his view, and events at the C–T boundary fall into place if we consider them as recording a switch from mesotrophic to oligotrophic oceanographic conditions caused by rising sea level and the breakdown of shelf-edge fronts.

At the present day, the boundaries between shelf seas and open oceans are marked by zones of mixing called shelf-break fronts (Summerhayes *et al.* 1995). These separate the continental shelf regions (generally less than 200 m deep), which are characterized by oceanographers as ‘brown and green water’, from the stratified ‘blue water’ of open oceans. Tidal mixing in shelf regions results in extensive nutrient recycling between the sea-floor and surface waters, generating eutrophic (inshore) to mesotrophic (mid-shelf) conditions. By contrast, outer shelf and open oceanic waters are stratified and the photic zone nutrient-starved, generating oligotrophic conditions. In these settings productivity is largely restricted to a narrow band at the base of the photic zone. High productivity is, however, found at shelf-break fronts since these are zones where deep-ocean waters rich in nutrients are brought up to the photic zone through upwelling.

The Cenomanian Lower Chalk represents a time of relatively shallow water across much of the Anglo-Paris Basin (i.e. 50–100 m water depth). In such relatively shallow shelf seas there would have been effective tide and wave mixing and an adequate supply of sediments and associated nutrients via runoff from hinterland sources (Fig. 6a). This resulted in muddy sediments with moderate (mesotrophic) productivity, which supported a diverse fauna of echinoids, bivalves and brachiopods. A shelf-edge front maintained a barrier from oceanic conditions, and pure nannofossil chalks at this time accumulated only along the continental slope to the west of the UK.

The great transgression of the Late Cenomanian initially caused only a moderate and gradual decrease in species richness, as increasing distance between sea-floor and surface waters reduced levels of nutrient recycling and decreased surface productivity. However, a critical water depth was



**Fig. 6.** Reconstruction of shelf profile in southern England and west of the UK during time of deposition of (a) the Lower Chalk (Cenomanian) and (b) the highest Plenus Marls Member (Bed 8) and the basal White Chalk Formation (latest Cenomanian and Early Turonian). For most of the Cenomanian (a) a well-defined shelf break front separated stratified, oligotrophic oceanic water from tidally and storm-mixed mesotrophic coastal waters. The latter supported a diverse benthos including many deposit feeders and algivores, and was fed with clay and nutrients by runoff from hinterland sources (see Fig. 5). In the Late Cenomanian (b) (*M. geslinianum* and *juddii* zones) a major sea-level rise ultimately resulted in collapse of the shelf break front and the spread of oligotrophic, stratified oceanic waters onto the shelves. This collapse is recorded in the upper part of the Plenus Marls Member as a sharp decrease in productivity proxies and benthic diversity that continues through the lower part of the White Chalk Formation. Additionally, submergence and distancing of source areas following the Late Cenomanian transgression resulted in a sharp cut-off of clastic supply, reflected in the deposition of purer nannofossil chalks.

eventually reached, coinciding with the time of Plenus Marls Member Beds 7/8, at which point the shelf-edge front broke down and oceanic waters spread over much of the continental shelf of north-western Europe (Fig. 6b). The ensuing oligotrophic conditions resulting from sea-level rise and stratification over large parts of the continental shelf caused a major productivity crash and had almost immediate effect on the marine benthos. As a result many of the detritivores, all of the algivores and a large proportion of filtration and suspension feeders disappeared. The total abundance of foraminiferans also fell, with a concomitant rise in the calcispheres (mostly pithonellids) by about 15%. Since sea-level rose in a series of pulses during the Cenomanian (Robaszynski *et al.* 1998), the spread of stratified waters onto the shelf may have begun earlier in the deeper waters of the Cleveland–North Sea Basin.

The crash in benthic diversity was thus driven by changes in surface water productivity generated through normal oceanographic processes. Extensive local extinction presumably took place through starvation, but, given the wide dispersal capabilities of most marine invertebrate larvae, the vast majority of

species must have been able to disperse to more eutrophic, onshore environments as sea-level gradually rose. Sea-level change by itself is unlikely to be able to generate extinction of marine invertebrates (e.g. Jablonski 1985), although the enhanced competition for space that resulted must have put pressure on some species. Busson & Cornée (1996) have emphasized that the origin of the replacement fauna appearing in the earliest Turonian is largely cryptic. Under our interpretation, it represents a community previously confined to the upper shelf slope that expanded across the shelf following breakdown of the shelf-break front and the spread of oligotrophic oceanic conditions.

Unfortunately for palaeontologists, this sea-level rise also created a huge bias in the sedimentary record, and we have almost no outcrop remaining that represents Turonian onshore eutrophic to mesotrophic settings in NW Europe. The drop in base level since the peak transgression in the Early Turonian has removed virtually all evidence of these more onshore Late Cretaceous deposits through erosion, leaving only a record of the deeper mid-shelf environments and their lower diversity faunas. Thus the reduction in benthic macro-invertebrate diversity near the C–T boundary evident in the fossil record is probably more a reflection of a significant switch in the nature of the surviving sedimentary record than a record of true extinction.

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