

## Sea-level change and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies

Andrew B. Smith, Andrew S. Gale, and Neale E. A. Monks

**Abstract.**—The association between mass extinction in the marine realm and eustatic sea-level change in the Mesozoic is well documented, but perplexing, because it seems implausible that sea-level change could actually cause a major extinction. However, large-scale cycles of sea-level change can and do alter the ratio of shallow to deep marine continental-shelf deposits preserved in the rock record both regionally and globally. This taphonomic megabias alone could be driving patterns of first and last occurrence and standing diversity because diversity and preservation potential both change predictably with water depth. We show that the Cenomanian/Turonian faunal event in western Europe has all the predicted signatures expected if taphonomic megabias was the cause. Grade taxa terminating in pseudoextinction and Lazarus taxa are predominantly found in the onshore facies that disappear for extended periods from the rock record. Before other mass extinctions are taken at face value, a much more careful analysis of biases in the rock record needs to be carried out, and faunal disappearances need to be analyzed within a phylogenetic framework.

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Accepted: 19 July 2000

### Introduction

Over the past 20 yr an enormous amount of effort has gone into documenting the size, duration, and selectivity of mass extinctions in an attempt to develop general theories about their cause and effect. As yet, an all inclusive theory of mass extinctions remains elusive and individual events are still largely explained on an ad hoc basis. However, ever since the work of Newell (1967), the association between periods of mass extinction in the marine realm and eustatic sea-level change has been commented upon. Of the 14 mass extinctions treated in detail by Hallam and Wignall (1997), all but one were associated with major transgressive events. By comparison, other possible correlatives, such as bolide impact or climatic change show much poorer match (MacLeod 1998).

Previous workers have sought to explain this correlation by searching for plausible oceanographic events triggered by sea-level change that might drive biological extinction. However, major sea-level change also alters the nature of the geological and fossil record (Jablonski 1980; Holland 1995) and it is important to distinguish between sampling ar-

tifact and biological pattern. Here we document the relative importance of oceanographic versus taphonomic processes in shaping biological diversity of macrobenthic invertebrates across the Cenomanian/Turonian boundary. This interval was identified by Sepkoski and Raup (1986) and Sepkoski (1986) as one of the largest extinction events in the Mesozoic, and it coincides with a second-order transgression (Haq et al. 1987) and oceanic anoxic event (Gale et al. 1999; Harries and Little 1999). Furthermore, this time interval benefits from having a highly refined biochronologic and cyclostratigraphic timescale, detailed sequence stratigraphic framework, and wide basinal outcrop coverage against which to document faunal change (Gale 1995; Sageman et al. 1997; Robaszynski et al. 1998; Gale et al. 2000).

### Sea-Level Change and Extinction

**Potential Mechanisms.**—Three oceanographic processes are commonly invoked to explain why sea-level change and mass extinction commonly coincide:

1. Sea-level change can severely alter the surface area of ecologically critical zones over

the continental shelves. At the time of the last glacial maximum 21,000 yr ago, the global surface area of continental shelf lying within the photic sea-bottom zone (defined as within ca. 60 m water depth) was only 18% of present-day levels (Schaff 1996). Extinction under this model is driven by increased competition for space and resources among the shallow benthic biota during lowstand.

2. Transgression is commonly associated with the expansion of the oxygen minimum zone onto the continental shelf, triggered by enhanced surface-water productivity as terrestrial-derived nutrients are brought into the system. The spread of dysoxic or anoxic conditions during maximum transgression is then envisaged as the principal cause of mass extinction (Hallam 1989; Wignall and Twitchett 1996; Hallam and Wignall 1997; Harries and Little 1999).

3. Sea-level rise can alter oceanographic circulation patterns, for example by causing the breakdown of shelf-margin fronts and the spread of stratified oligotrophic oceanic waters across large parts of the continental shelf during highstands (Hay 1995; Gale et al. 2000). The resultant lower surface-water productivity leads directly to extinction as starvation spreads through the food chain (Paul and Mitchell 1994).

Mechanisms 1 and 2 result in gradual extinction as deteriorating conditions over time put pressure on successive generations, because even the fastest transgression is orders of magnitude longer than the generation time of benthic faunas. Gale et al. (2000), for example, estimated that the end-Cenomanian transgressive systems tract had a duration of approximately 800,000 yr, based on cyclostratigraphy. Mechanism 3 is potentially instantaneous on a geological timescale, with the loss of a shelf-margin front occurring within the space of a single 21K Milankovitch-periodicity sediment bundle (Gale et al. 2000).

Each model makes a specific prediction about both the speed of the event and which portion of the benthic fauna will be most severely affected, and should thus be testable. Surface-area effects will cause preferential extinction among benthos living in the photic zone, anoxia will have the strongest effect on

outer-shelf and deep-water benthos, and stratification of shelf waters will cause highest levels of extinction among midshelf faunas.

*Problems.*—Despite the appeal of invoking sea level as a cause of extinction, there are strong reasons for questioning whether it plays a significant role.

First, although all three mechanisms outlined create extinction locally, they are unlikely to work over large regions because of the generally excellent dispersal capability of most marine fauna. Except in the case of low oceanic islands that may become completely drowned, increasing sea level will simply displace onshore-offshore habitats rather than eradicate them. So, for example, expansion of the oxygen minimum zone and spread of anoxia onto the continental shelf may cause local extinction, but many taxa will simply migrate into, or survive within, more oxygenated onshore settings. Even in the most extreme and best-documented ocean anoxic event, at the end-Cenomanian, there is no geochemical, sedimentological, or faunal evidence that anoxia spread into midshelf or inshore settings where biodiversity was highest (Gale et al. 2000). Similarly, starvation may affect broad areas of continental shelf as nutrient input is suddenly switched off, but there will remain zones of high productivity where, for example, river influx continues to provide a source of nutrients.

Second, there have been dramatic changes in sea level over the past two million years generated by sharp changes in ice volume at the poles, yet the effect of this on the survivorship of marine fauna has been negligible. Valentine and Jablonski (1991, 1993) showed that Quaternary sea-level instability was correlated with dramatic changes in the community structure and geographic range of mollusks along the eastern Pacific coastline of North America but resulted in “unexceptional” levels of extinction. Marine benthos in the recent past have simply migrated as sea levels have changed. Although Pleistocene sea-level change has been largely vertical, with little change in surface area of shelf seas (Jablonski 1985), it has driven marked changes in the surface area of ecologically critical zones (Schaff 1996).

Finally, Jablonski (1985) and Jablonski and Flessa (1986) have claimed that most families of marine benthic invertebrates are immune to sea-level change, because they have representatives living in oceanic island settings. Unlike faunas from broad continental shelves, oceanic island faunas may be less affected by surface-area effects and more buffered from productivity crashes, and may face fewer barriers to tracking sea-level rise and fall, or so it is argued. However, this has been disputed (Paulay 1990; Erwin 1993: p. 241) and for most settings oceanic island faunas are probably just as susceptible to sea-level-induced extinction as continental-shelf faunas.

Thus, although there are plausible mechanisms for generating local extinction, evidence suggests that sea-level change alone could not cause a sizable mass extinction of continental-shelf benthos on a broad regional or global scale.

#### Sea-Level Change and the Onshore-Offshore Record

Sea-level change has a further major effect on marine faunal diversity by exerting a strongly selective bias on the preservation of depth-related facies in the sediment record. The biases are now being interpreted in terms of sequence stratigraphy, but the basic principles can be traced back to Barrell (1917) and were emphasized by Jablonski (1980). Brett (1995, 1998), Patzkowsky and Holland (1999), and Holland (1995, 1999) have highlighted how crucial it is to understand basinal depositional patterns before interpreting diversity patterns.

In inner-shelf settings where accommodation is limited, there is a strong bias toward selective preservation of deposits formed within transgressive systems tracts (TST). Highstand, and most especially lowstand, deposits are only rarely preserved in such settings because of the pervasive nature of erosion associated with both sequence boundaries and transgressive ravinement surfaces (Loutit et al. 1988). Moreover, during major sea-level rises (second- and third-order sequences of Vail et al. 1991), deeper-water facies spread onto the inner shelf during transgression. As shallow-water deposition is displaced

onto the cratonic interiors, where there is minimum accommodation space, thin and often condensed successions are "perched" on cratons. These are highly susceptible to erosional destruction during subsequent lowstands, and as a result, the outcrop area of shallow shelf sediments can be predicted to decrease sharply during major transgressive events.

This is clearly evident in the Cenomanian-Turonian deposits of northwestern Europe. The sequence stratigraphic framework for the Anglo-Paris basin is now well established (Robaszynski et al. 1998) and consists of a series of five overlapping sequences deposited under a regime of progressively increasing water depth. We have used the 1:50,000 and 1:63,360 geological map series of England and France to quantify the surface-area outcrop of onshore, midshelf, and outer-shelf facies over time. For each map we assigned an environmental setting both at outcrop and, where known, from borehole data. This demonstrates a reduction and eventual loss of onshore sedimentary facies as sea level progressively rose (Fig. 1). It is important to realize that it is not simply that onshore sedimentary environments of this age exist somewhere and have not been explored. Shallow-water deposits of early- to mid-Turonian age have been completely eradicated from the sedimentary record of western Europe, through the subsequent 100 million years of net sea-level fall.

This change in the ratio of shallow- to deep-water deposits over time is crucial for two simple reasons:

1. *Diversity of commonly fossilized benthic macroinvertebrates is strongly depth related.* The relationship between marine biodiversity and water depth remains surprisingly poorly understood and there remain many uncertainties (see Gray et al. 1997). On the basis of counts of taxa from sediment recovered from cores or grabs, it was originally believed that species diversity increased with depth to around 2000 m (e.g., Grassle and Maciolek 1992). However, Gray et al. (1997) presented more extensive data, which showed that in unconsolidated sediments comparable species diversity exists in shallow- and deep-water settings. Nonetheless, the key point to bear in mind is that this habitat (level-bottom soft

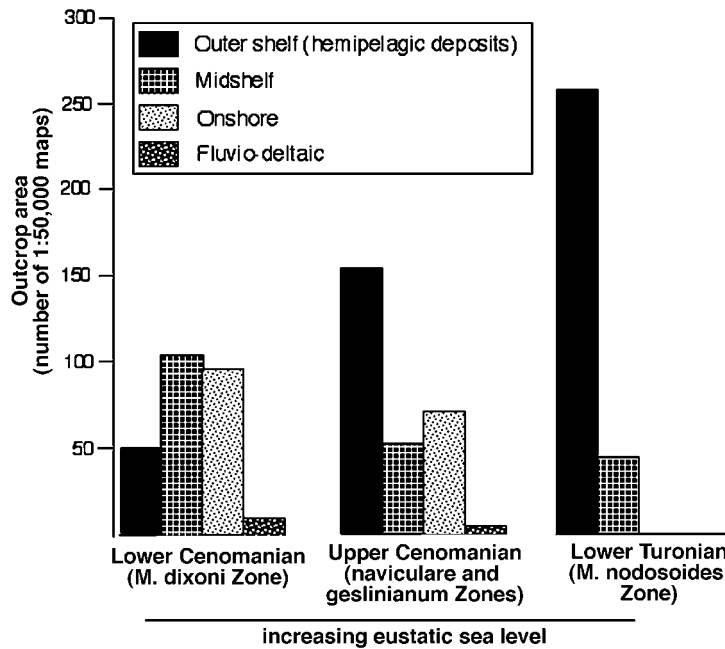


FIGURE 1. Surface outcrop area of strata classified into hemipelagic, midshelf, littoral, and fluvio-deltaic deposits in the Cleveland, Anglo-Paris, Aquitaine, and Vautonian Basins of England and France. Surface area is determined as the number of geological survey maps (out of 1428) in which deposits of these types crop out, and is calculated for three geological time intervals.

substratum) represents just one of many marine landscapes. In onshore settings ecological landscapes are very much more diverse, with estuaries, coastal sand flats, mud flats, rocky shores, cobble bottoms, kelp forests, mangroves, reefs, and seagrass beds, each with its own biota; by comparison the deep-sea environment is monotonously uniform (though with small-scale heterogeneity). It is therefore intuitive that, if the one environment that can be compared quantitatively between coastal and deep-water settings has comparable species diversity, then onshore diversity must greatly outweigh deep-water diversity simply because of the environmental heterogeneity it encompasses (Gray et al. 1997).

That shallow-water macrofaunas are more diverse is borne out by a number of empirical surveys. For example, across the modern continental shelf of Crete, macrobenthic diversity, abundance, and biomass of macrobenthos were all found to decrease with increasing depth (Karakassis and Eleitheriou 1997). Similarly, echinoid species diversity is highest in less than 20 m, dips between 20 m and 80 m, and then rises to a second peak at around 100

m water depth off the coast of Japan (Fig. 2). Below about 125 m, diversity drops significantly. The shallow-water peak is due to the diversity of algivore and epipsammic feeders, whereas in deeper water carnivores and deposit feeders dominate.

2. *Preservational potential is controlled by sedimentary regime, which is strongly depth related.* Not only does diversity change with depth but preservation potential of faunas is also affected, although there remain few data. Sediment accumulation rate must be the single most important factor in determining preservational potential of organisms. Within any given environment a suite of taphonomic processes act to destroy the skeletal remains of organisms. These vary in importance and effectiveness according to environment, and result in a range of high- to low-grade taphonomic assemblages (see Parsons and Brett 1991). Both longer residence time at the sediment surface and higher water energy enhance mechanical and biological erosion, and thus best preservation is typically to be found in onshore, but not high-energy nearshore environments. For example, Kidwell and Baumiller (1990) ex-

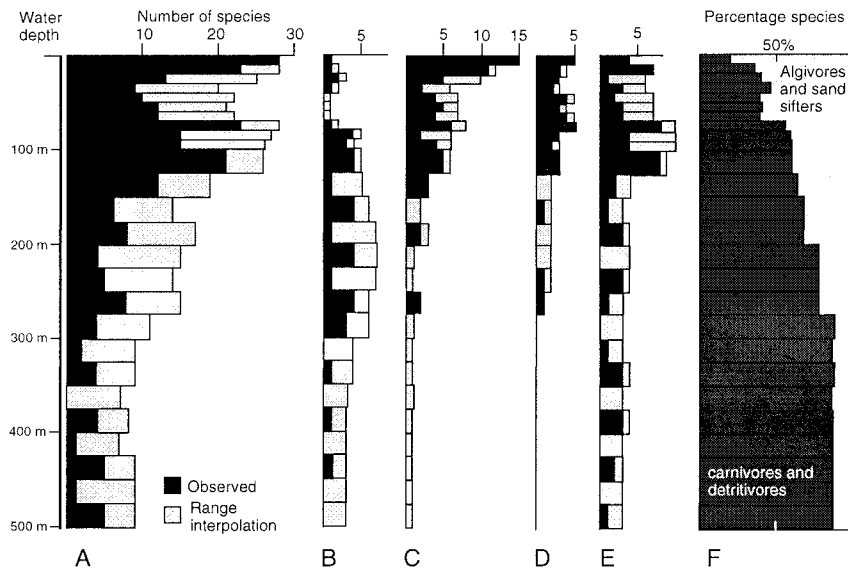


FIGURE 2. Diversity of echinoid species with water depth off Sagami Bay, Japan (data from Shigei 1986). A, Total species diversity. B, Carnivores (cidaroids). C, Algivores and grazers. D, Epipsammic feeders (clypeasteroids). E, Selective deposit feeders (spatangoids). F, Changing proportion of trophic groups with depth. In A–E, solid bars = observed number of species within each depth bracket, light stipple = number of species with range interpolation (species known from both shallower and deeper settings are counted as present even though none have been collected at that particular depth bracket).

amined the degree of disarticulation of echinoids in different settings and predicted the best environment for preservation lay between 20 m and 50 m water depth.

Skeletal diagenesis also varies with water depth. In modern deeper marine environments, seawater becomes undersaturated with respect to aragonite. This leads to a strong depth signal in the preservation of many molluscan taxa, such as ammonites, as is clearly evident in the Cenomanian/Turonian event (Fig. 3).

#### The Distribution of Lazarus Taxa and Pseudoextinctions

Major platform drowning events, like the Cenomanian/Turonian event, alter the surface area of ecologically critical zones represented across the continental shelf and result in large-scale lateral displacement of habitats. This by itself can cause extinction, at least locally, but it also creates gaps in the fossil record by shifting onshore sedimentary facies with their high-diversity faunas farther onto the cratons where their chance of being preserved is less. Even if such deposits are not destroyed entirely, the overall reduction in

“searchable” surface area of shallow-water deposits that is created would cause sampled diversity to change through a simple species/area effect (the larger the surface area available the more species are found [Rosenzweig 1995]). Therefore, even if no biological extinction took place, platform drowning would be expected to create an apparent decline in the diversity of predominantly shallow-water clades, whereas the increased surface area of offshore facies introduces a low diversity of new taxa from deeper-water settings previously undersampled in the geological record. It is therefore critical that we distinguish losses that are attributable to biological extinction from those that arise purely from sampling. To do this a phylogenetic framework is essential.

If large-scale taphonomic biases are acting on the fossil record, then clades with major gaps in their fossil record (Lazarus taxa of Jablonski 1986) should be distributed predictably in relation both to major sea-level cycles and to their onshore-offshore distribution. We predict that the fossil record of shallow-water taxa should contain major gaps at times of



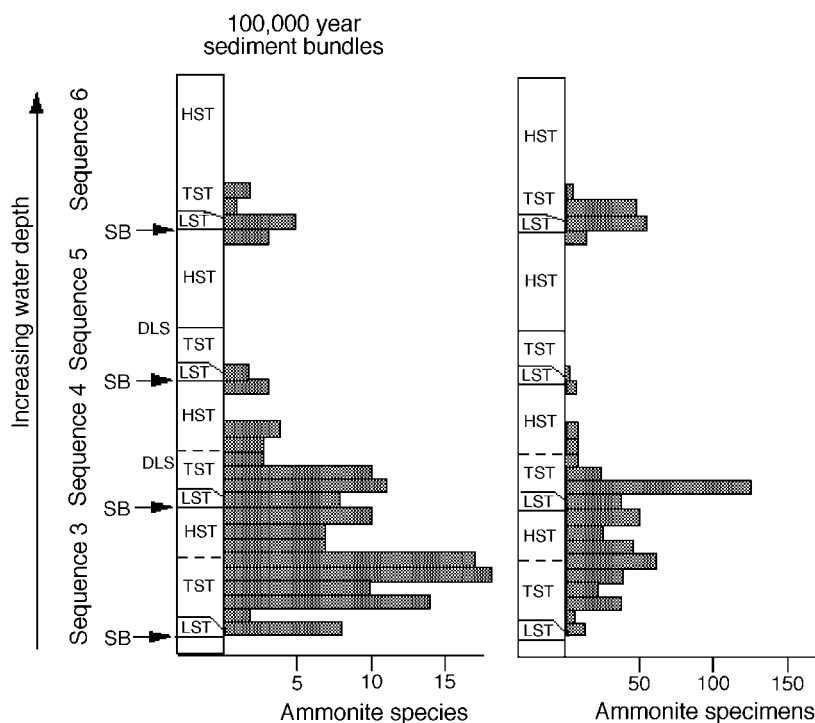


FIGURE 3. Ammonite diversity in the Cenomanian of Sussex, England. Ammonite species and specimen numbers are plotted for 100,000-yr intervals (five chalk-marl sedimentary couplets) through four sequence bundles based on collections made at Southerham and Eastbourne, Sussex, England. Water depth increases with each sequence. Notice how ammonites are preserved only in the shallowest parts of the higher sequence bundles. Sequence stratigraphy follows Robaszynski et al. 1998. DLS = downlap surface; HST = highstand systems tract; LST = lowstand systems tract; SB = sequence boundary; TST = transgressive systems tract.

platform flooding, whereas offshore taxa should have major gaps at lowstand intervals.

So long as species on either side of a taphonomic gap are recognized as belonging to the same clade, no real problems are created. However, lineages that are not sampled for some considerable period in the fossil record rarely remain unchanged but continue evolving and acquiring new characters. Historically, taxonomists have commonly used gaps in the fossil record to separate a derived portion of a clade from its plesiomorphic "ancestral" grade (Smith 1994). Consequently, a second prediction of our model is that pseudoextinctions will also be concentrated in shallow-water faunas that disappear during platform flooding events and in deep-water faunas during lowstands. Because taxic diversity is greater onshore, the pseudoextinctions at platform drowning events should be more numerous and thus pose much more of a problem.

Phylogenetic information is thus essential

for the correct interpretation of taxonomic disappearances that coincide with major sequence stratigraphic boundaries.

#### The Cenomanian/Turonian Event As a Product of Sampling Bias, Not Mass Extinction

The Cenomanian/Turonian event is almost universally accepted as one of the largest mass extinctions of the Mesozoic (Sepkoski 1986; Hallam and Wignall 1997; Harries and Little 1999), yet it is our contention that the nature and pattern of taxic disappearance observed in western Europe are entirely in keeping with this event being primarily taphonomic in origin. Sea level rose rapidly during the Cenomanian to reach a high in the early to mid Turonian (Haq et al. 1987; Robaszynski et al. 1998). This resulted in platform drowning and there is a successive shift toward deeper-water facies dominating the rock record (Fig. 1). Recorded diversity in the lower Cenomanian of

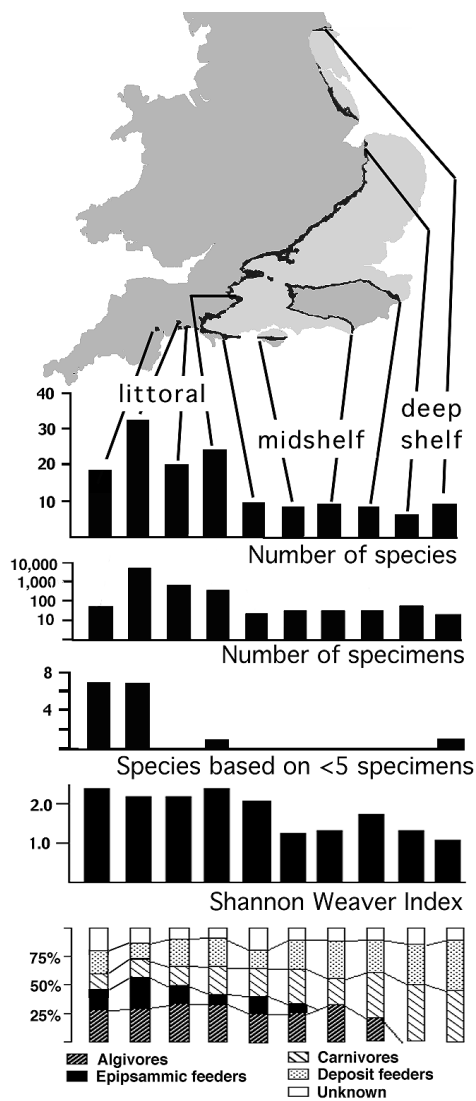


FIGURE 4. Variation in species numbers, specimen numbers, rarity, diversity, and trophic composition for echinoid faunas across the continental shelf in the lower Cenomanian of the United Kingdom. Faunas are based on collections made by A. S. Gale, A. B. Smith, and C. R. C. Paul, and by C. W. and E. V. Wright.

Western Europe is very much greater than that in the lower Turonian, but is this because of mass extinction or because the lower Cenomanian record contains extensive sedimentary facies deposited in 20–100 m water depth (where both diversity is higher and preservation potential better) whereas the lower Turonian record is almost exclusively one of deeper-water shelf facies? Analysis of the faunal losses in terms of environmental distri-

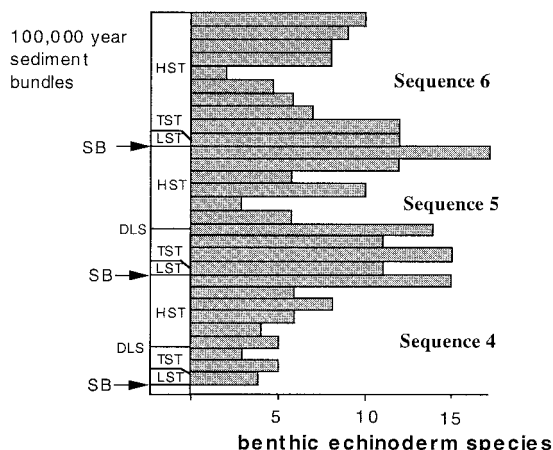


FIGURE 5. Echinoderm diversity through sequence stratigraphic units 4, 5, and 6 of Robaszynski et al. (1998) plotted for 100,000-yr time intervals (based on inferred Milankovitch cyclicity evident in the sediment). Data comes from Eastbourne, Sussex, England, a mid-shelf setting.

bution and whether they represent extinction or pseudoextinction is crucial.

We have undertaken a detailed study of echinoid diversity and abundance across a shelf transect in the mid Cretaceous of England. This demonstrates that diversity and abundance of echinoids varied across the shelf with depth during the early Cenomanian, exactly as predicted from the modern fauna (Fig. 4). Onshore settings have higher species diversity, higher absolute numbers of species, and also higher abundance of individuals, presumably at least partially a result of enhanced preservation potential. Rare species (based on five or fewer individuals) are also most common in shallow-water settings. Shallow-water faunas are dominated by algivorous regular echinoids and bulk-sediment-swallowing cassiduloids, whereas deeper-water faunas are dominated by selective deposit feeders (holasteroids and spatangoids) and carnivore/scavengers (cidaroids), exactly matching the pattern seen today.

Within single sections, variation in species numbers and abundance corresponds closely with sequence stratigraphy and inferred water depth. In a midshelf environment highest diversity is found to peak around sequence boundaries and lowest diversity coincides with highstand system tracts (Fig. 5).

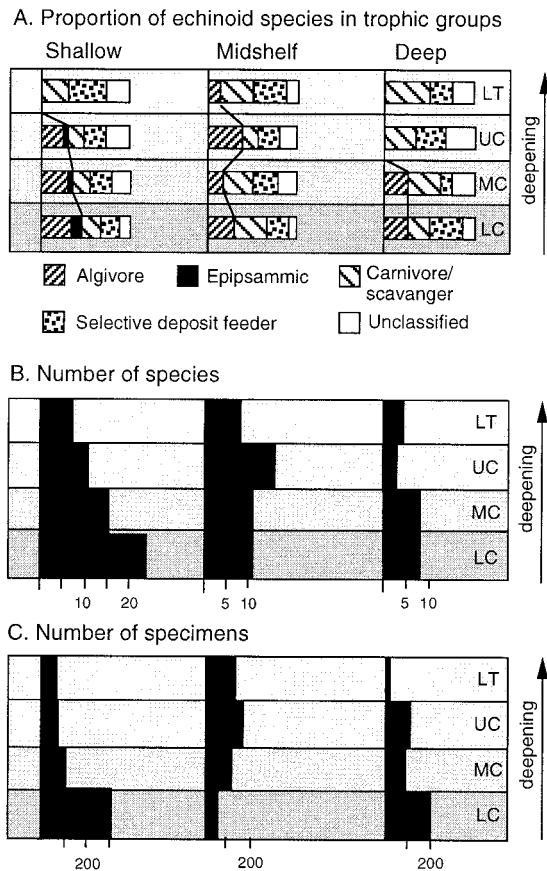


FIGURE 6. Changes in sampling diversity, species diversity, and trophic structure of echinoids through the Cenomanian transgression, based on collections made from the Cenomanian–early Turonian of south Devon (inshore), Eastbourne (midshelf), and Hunstanton (outer shelf). LC = lower Cenomanian; MC = middle Cenomanian; UC = upper Cenomanian; LT = lower Turonian.

Furthermore, in each setting—shallow, mid-shelf, and outer-shelf—there is a progressive loss in both species diversity and numbers of specimens with each sequence bundle as water depth increases. In each case, the faunal signature observed is of replacement of shallower-water taxa by deeper-water taxa (Fig. 6). Eventually, with the breakdown of shelf-margin fronts in the *juddii* Zone, a new fauna spread rapidly across the mid and deep shelf. This lower Turonian fauna has been puzzling because of its cryptic origin (Busson and Cornée 1996). Under our model it represents an outer-shelf and upper-slope fauna, already specialized for those presumably oligotrophic

settings, that has expanded its range onto the shelf.

Through this period a succession of taxa disappear from the fossil record, generally coincident with maximum flooding surfaces in each sequence bundle. That these losses are predominantly due to undersampling is apparent from the distribution of Lazarus gaps and pseudoextinctions at generic level.

As predicted above, Lazarus taxa are overwhelmingly found in shallow-water settings (Fig. 7), which in England are confined almost exclusively to the early Cenomanian. In France and Germany, however, restricted areas of shallow-water deposits continue into the middle and late Cenomanian, and many of the taxa absent from England can be found continuing in these inner cratonic settings. All, however, have disappeared completely from the record by the start of the Turonian. Lazarus taxa start to return with the reappearance of onshore settings in the latest Coniacian to early Santonian of the Craie de Villedieu, Sarthe, France; others return in the onshore settings of the early Maastrichtian of France and the Benelux countries. Cassiduloids in particular are an excellent guide in the Cretaceous to shallow-water conditions, and they completely disappear from Europe between the late Cenomanian and mid Coniacian. The absence of the onshore genus *Hyposalenia* is even more extreme, in that it remains unsampled between the mid Cenomanian and the early Danian. Clearly, onshore habitats existed that have not been preserved in the fossil record.

Cladistic analysis has been used to identify sister-group relationships and to distinguish extinction from pseudoextinction. In the case of cassiduloids (Fig. 8), although all genera disappear worldwide in the early to mid Turonian, there are no genuine biological extinctions. Sister species reappear in the Coniacian to Maastrichtian, either still assigned to the original genus or under the guise of a new generic name. Pseudoextinctions are also almost exclusively confined to taxa restricted to onshore settings in the early Cenomanian of England, as predicted (Fig. 7). The derived sister group is often only trivially differentiated from its antecedent grade. Thus, *Pygopistes*



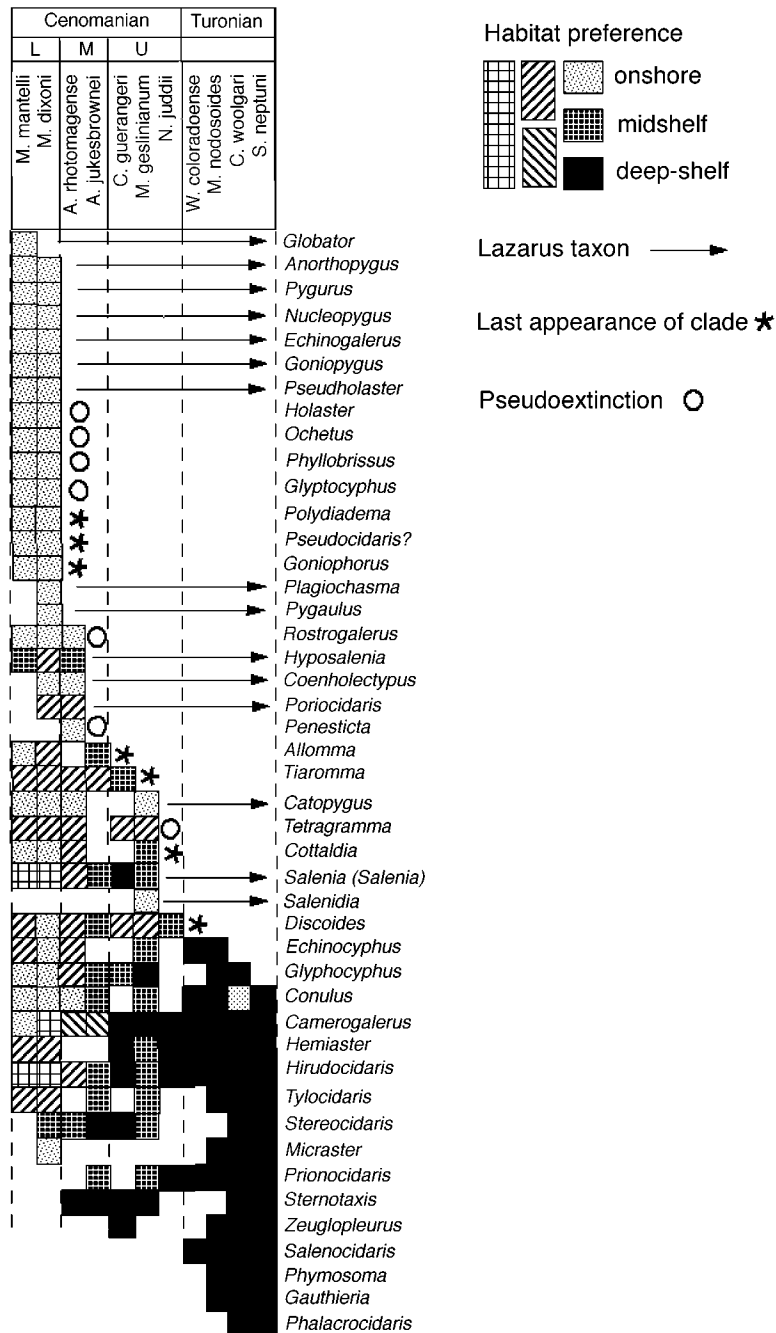


FIGURE 7. Distribution of extinctions and pseudoextinctions among Cenomanian–Turonian echinoids of southern England at generic level, classified according to water depth distribution. Note that pseudoextinctions and Lazarus taxa are predominantly restricted to taxa in onshore settings, whereas true extinction is slightly more prevalent in midshelf settings.

differs from its Cenomanian sister group, *Pygaulus*, only in having its apical disk positioned more toward the anterior, while *Oolopygus* is distinguished from its Cenomanian

sister group, *Penesticta*, in having single not double pores in its phyllodes. Neither represent a biologically or ecologically significant change.

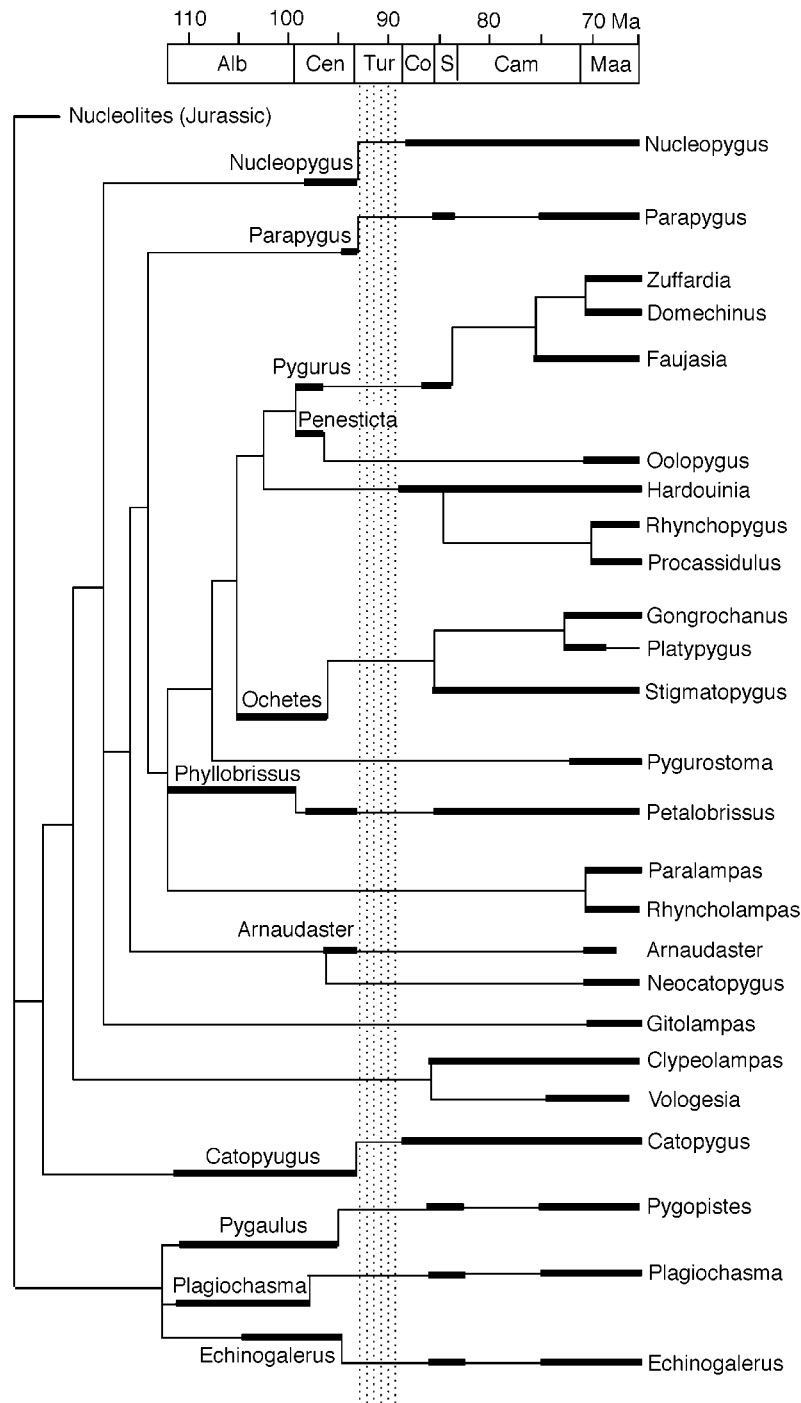


FIGURE 8. Cladogram of Late Cretaceous cassiduloid genera calibrated against their stratigraphic records. Characters are as listed in Smith (in press) and the data matrix is available on request. Cenomanian taxa are treated as possible ancestors to derived clades if they have one or fewer autapomorphies. Each name is a terminal taxon in the analysis. Parsimony analysis was conducted using the program PAUP (Swofford 1999). A heuristic search algorithm with 100 random-addition replicates found 139 trees of length 132 steps with a CI of 0.41 and RI of 0.76. Characters were then reweighted according to their rescaled consistency index and the search repeated. This found 60 equally parsimonious trees, and the strict consensus of those is what is calibrated against the stratigraphic record. Stippled zone indicates time interval when cassiduloids are absent from Europe.

There is also an extremely strong depth signature to the distribution of ammonites and other aragonitic-shelled mollusks in the Cenomanian–Turonian. Diversity and abundance are strongly linked to clay content in the sediment; the generally good preservation in the early stages of the Cenomanian transgression in more onshore settings gives way to very sporadic preservation, coinciding with early transgressive systems tracts at the base of sequence stratigraphic units 5 and 6. Peak diversity of ammonites is found in the early sequence packages and decreases markedly as water depth increases and clay content decreases (Fig. 3).

There are of course a number of true extinctions at generic level that do take place at this time. The environmental distribution of these suggests that either surface-area effect or starvation took its toll on the marine benthos, but we can rule out anoxia as a cause because none are in deep-water settings where the effects of anoxia would have been strongest. However, because shallow-water taxa such as *Hyposalenia* disappear from the geological record for such a long interval of time, it is possible that these true extinctions are also scattered through time rather than all being concentrated at the end-Cenomanian.

#### Summary and Wider Implications

The coincidence between platform flooding events in the Cretaceous with the three peaks of extinction recognized by Sepkoski and Raup (1986) is intriguing. In the Cretaceous there were three platform drowning events: in the Aptian, Cenomanian, and latest Maastrichtian–Danian (Haq et al. 1987). In each case a high-diversity shallow-water echinoid fauna is replaced by a long interval of restricted taxonomic diversity. We, like others before us, have argued that eustatic sea-level rise by itself can have only a minor part in creating extinctions. Here we point out that platform drowning changes the nature of the sedimentary record, altering the relative proportions of shallow- to deep-water shelf sediments that end up being preserved. This in turn directly controls sampled diversity, because both diversity and preservation potential vary with depth.

Most workers interested in mass extinction have either ignored or simply dismissed sampling and taxonomic artifact as irrelevant. Harries and Little (1999), for example, documented biotic change both at the Cenomanian/Turonian boundary and during the early Toarcian. They felt confident that, by taking a regional approach and showing that the same pattern exists across a wide geographic area, they had overcome sampling problems. However, the same sea-level signature is present in all their outcrops and there is every reason to believe that their pattern simply records the overall loss of shallow-water facies from the fossil record. They also used raw taxic data without phylogenetic correction, claiming that the appearances of new genera derived from extinct survivors represent “macroevolutionary events.” That might be true if environmental sampling were uniform before and after, but it is not, and cladistic analysis is needed to tease apart taxa that appear and disappear through sampling artifact from genuine lineage terminations.

There is a growing awareness that the sequence stratigraphic framework exerts a primary control on the nature of the fossil record (Holland 1995, 1999; Brett 1995, 1998). Authors working in this area have assumed that facies bias present in one region can be overcome by tracking shallow-water facies depositionally updip at times of progressive deepening. However, our study shows that this may not always (or perhaps not even often) be possible, because second-order cycles of deepening-upward and downlap on a 10–30-million-year timescale create major biases in the rock record. The preservation of outcrops representing onshore facies, with their diverse faunas, is not uniform through time, and this has major implications for analyses of diversity, origination and extinction in the fossil record.

Many years ago Jablonski (1980) emphasized the dangers of mistaking apparent versus real effects of sea-level change. His warning has not been heeded and the megabiases in the fossil record continue to mislead paleontologists. We contend that the Cenomanian/Turonian events record sampling artifact rather than true biological crises. We suspect

that many other mass extinctions coincident with major flooding events (e.g., Rhaetian/Hettangian and early Toarcian) will also turn out to contain a strong signal generated by megabias in the sedimentary record.

### Acknowledgments

We are very grateful to A. I. Miller, S. M. Holland, and L. Parks for their helpful reviews of this paper. This research was funded by National Environment Research Council grant GR3/11322.

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