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THE STRATIGRAPHY OF MASS EXTINCTION

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Abstract: Patterns of last occurrences of fossil species are often used to infer the tempo and timing of mass extinction, even though last occurrences generally precede the time of extinction. Numerical simulations with constant extinction demonstrate that last occurrences are not randomly distributed, but tend to cluster at subaerial unconformities, surfaces of forced regression, flooding surfaces and intervals of stratigraphical condensation, all of which occur in predictable stratigraphical positions. This clustering arises not only from hiatuses and non-deposition, but also from changes in water depth. Simulations with intervals of elevated extinction cause such clusters of last occurrences to be enhanced within and below the interval of extinction, suggesting that the timing and magnitude of extinctions in these instances could be misinterpreted. With the possible exception of the end-Cretaceous, mass extinctions in the fossil record are characterized by clusters of last occurrences at these sequence stratigraphical horizons. Although these clusters of last occurrences may represent brief pulses of elevated extinction, they are equally likely to form by stratigraphical processes during a protracted period (more than several hundred thousand years) of elevated extinction rate. Geochemical proxies of extinction causes are also affected similarly, suggesting that many local expressions of mass extinction should be re-evaluated for the timing of extinction and its relation to environmental change. We propose three tests for distinguishing pulses of extinction from clusters of last occurrences produced by stratigraphical processes.

Key words: extinction, sequence stratigraphy, modelling.

THE evidence for a bolide impact at the end of the Cretaceous (Alvarez *et al.* 1980) and the recognition of periodicity in mass extinctions (Raup and Sepkoski 1984) spurred interest in the causes of mass extinction. The timing of last occurrences of species in stratigraphical columns soon became key evidence for inferring whether a mass extinction was sudden, pulsed or gradual (Huber 1986; Macellari 1986; Kauffman 1988; Marshall and Ward 1996). It was quickly realized that the Signor–Lipps effect complicates the timing of extinction, by which incomplete sampling causes abrupt extinction events to appear gradual in the stratigraphical record (Signor and Lipps 1982). Despite such complications, the stratigraphical pattern of last occurrences continues to be used to infer timing and tempo at other mass extinctions (Finney *et al.* 1999; Jin *et al.* 2000; Brookfield *et al.* 2003; Shen *et al.* 2011; Yan *et al.* 2013; Wang *et al.* 2014).

Although the Signor–Lipps effect is well known, it belies the complexity of patterns of last occurrences in the fossil record. In particular, numerical modelling (Holland 1995, 2000) and field studies (see review in Patzkowsky and Holland 2012) demonstrate that facies changes, changes in the rate of sedimentation, and hiatuses exert a control on the occurrence of fossils that frequently overwhelms that of sampling (Holland and Patzkowsky 1999). As a result, abrupt events may appear gradual in the stratigraphical record, gradual events may appear abrupt, and both gradual and abrupt events may appear pulsed. These effects of stratigraphical architecture apply not only to fossil occurrences, but also to geochemical proxies of environmental change, for which the actual history of geochemical change is obscured by the presence of hiatuses and variations in sedimentation rate, and in some cases, by facies changes (Ghienne *et al.* 2014).

Based on this understanding of the stratigraphical controls on the position of last occurrences, this paper will examine the stratigraphical pattern of last occurrences and what can be inferred from that pattern about the timing and tempo of extinction.

MODELLING THE SEQUENCE STRATIGRAPHICAL OCCURRENCE OF FOSSILS

By coupling models of evolution, marine ecology and sedimentary basin architecture, it is possible to generate realistic and testable models of the stratigraphical distribution of fossils (Holland 1995; Holland 2000; Holland and Patzkowsky 2002).

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The origination and extinction of species is readily simulated with random-branching models in which lineages are tracked through time (Raup 1985). At each time step, a species may branch to produce a new species, it may go extinct, or it may persist. In the simulations used here, the probability of both speciation and extinction is set to the Phanerozoic average of 0.25 per lineage million years (Raup 1991*a*). Starting diversity is set to 1000 species to make patterns of last occurrences more apparent.

The ecology of each species is fixed at its origination and is described by a Gaussian model (Fig. 1) that describes the probability of collection of that species with respect to water depth (Holland 1995, 2000; Patzkowsky and Holland 2012). Preferred depth (PD) is the water depth in which the species is most likely to be found and is equal to the mean of the Gaussian curve. Depth tolerance (DT) reflects the ability of the species to live in depths other than its PD, and it is the standard deviation of the Gaussian curve. Peak abundance (PA) is the probability of collection for the species at its PD, and it is the maximum of the Gaussian curve. Each species is randomly assigned values for PD, DT and PA according to limits based on modern and ancient species (Holland *et al.* 2001).

Sedflux (Hutton and Syvitski 2008) is used to simulate the stratigraphy of a sedimentary basin. Like most sedimentary basin models, Sedflux simulates sedimentation and erosion through time along an onshore to offshore transect. At each time step, relative change in sea level is calculated from changes in subsidence and eustasy. Sediment is introduced at one end of the basin and deposited across the basin according to realistic rules of sediment transport, a strength of Sedflux that distinguishes it from other basin models. Sedflux also incorporates compaction and isostatic deformation from the sediment load.

By coupling these three models, it is possible to simulate the origination and extinction of species with known ecological characteristics in stratigraphical columns across a sedimentary basin. From Sedflux, individual stratigraphical columns are extracted, and these record the water depth and thickness of accumulated sediment at one location through time. These columns are sampled uniformly at a vertical spacing of 0.5 m, and at each sampled horizon, each species is tested for whether it was extant at the time of deposition. If it was, the probability of collection is calculated based on its ecological characteristics and the water depth at that horizon. This probability is compared to a random number generated from a uniform distribution on (0, 1) to determine whether the species was collected at that horizon. This procedure is repeated for every species at every horizon to assemble the fossil record. From this, the number of last occurrences at every sampled horizon in that stratigraphical column is calculated.

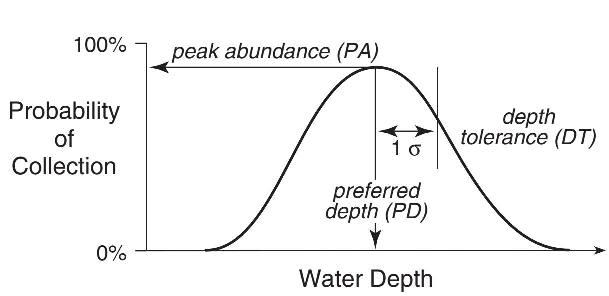

FIG. 1. Gaussian model of the probability of collection of a species as a function of water depth (after Holland 1995).

In the initial model, extinction rate is held constant to explore patterns in last occurrences when there is no mass extinction. In subsequent models, brief but non-instantaneous mass extinctions are simulated within different systems tracts to compare their expressions in the stratigraphical record.

A single basin simulation is used to illustrate the patterns in last occurrences that can occur, depending on sequence stratigraphical architecture and the timing of extinction. The aim is not to mimic any particular architecture, nor to model all possible architectures, but to simulate common patterns that can be used as principles for understanding the consequences of stratigraphical architecture. The basin simulation depicts 8 myr of deposition along a passive margin 200 km wide. Eustasy is simulated with a combination of third-order (1–10 myr, *sensu* Vail *et al.* 1977) and fourth-order (100 kyr to 1 myr) cyclicity. Four third-order cycles are present, each of 2 myr duration and 30 m peak-to-peak amplitude. Fourth-order cycles have a duration of 200 kyr and amplitude of 5 m. All parameterization files for the Sedflux run, as well as code for the simulation of the fossil record, are available in Holland and Patzkowsky (2015).

The stratigraphical record of this simulation is described using sequence stratigraphical concepts (Table 1). The simulation (Fig. 2) is dominated by the third-order cyclicity, with the internal stacking patterns of these sequences defined by fourth-order cycles. The lowstand systems tract (LST) is expressed as a series of fourth-order cycles that stack basinward and upward in a narrow zone near the downdip termination of each third-order cycle. The transgressive systems tract (TST) contains fourth-order cycles that step landwards and upwards, each traversing a distance of 50 km or more. The highstand systems tract (HST) is preserved as a couple of progradationally stacked fourth-order cycles near the updip termination of the third-order sequence. The falling-stage systems tract (FSST) is well developed as a series of seaward- and downward-stepping fourth-order cycles.

Representative stratigraphical columns were selected from this cross section to illustrate common stratigraphical patterns. Columns A and B display well-developed progradational stacking in the third third-order sequence,

TABLE 1. Glossary of sequence stratigraphical terminology, with concepts based on Van Wagoner *et al.* (1990), Hunt and Tucker (1992), Ainsworth (1994) and Catuneanu (2002, 2006).

Aggradational stacking	Parasequences or sequences that are stacked directly on top of one another, such that there is no long-term net landward or seaward drift in the position of facies belts.
Degradational stacking	A stacking pattern in which units stack seawards and downwards, that is down the depositional profile (Neal and Abreu 2009). Similar to progradational stacking, in which units stack seawards and upwards. Units within degradational stacking are bounded by surfaces of forced regression.
Depositional sequence	Sedimentary cycles bounded by subaerial unconformities and their correlative surfaces. Depositional sequences are often simply called sequences. The internal architecture of sequences is more complicated than that of parasequences and contains four systems tracts defined by stacking pattern and position within a sequence. In ascending order, these are the lowstand systems tract (LST), transgressive systems tract (TST), highstand systems tract (HST) and falling-stage systems tract (FSST). Within any given region, one or more systems tracts may be missing, owing to non-deposition or erosion. For example, depositionally updip settings typically lack FSSTs and LSTs.
FSST	The final and uppermost systems tract within a depositional sequence, characterized by degradational stacking.
Flooding surface	Sharp contact separating overlying deeper-water facies from underlying shallow-water facies. Surface may display minor erosion, fossil accumulations and firmground or hardground features.
HST	The third systems tract within a depositional sequence, characterized by aggradational to progradational stacking, and overlain by the FSST.
LST	The lowest systems tract within a depositional sequence, characterized by progradational to aggradational stacking, and overlain by the TST.
Parasequence	Sedimentary cycles bounded by flooding surfaces. Internally, parasequences typically have simple, shallowing-upward arrangements of facies bound through Walther's Law. Some parasequences have thin deepening-upward intervals at their base, and much more rarely, some parasequences may deepen upwards. Parasequences and sequences are not distinguished by thickness or inferred duration.
Progradational stacking	A stacking pattern in which successive parasequences or sequences are stacked upwards and seawards, producing a net upward shallowing.
Retrogradational stacking	A stacking pattern in which parasequences or sequences are stacked upwards and landwards, producing a net upward deepening.
Surface of forced regression	Sharp to somewhat erosional contact, separating overlying shallower-water facies (typically shoreface) from underlying deeper-water facies.
Systems tract	Linkage of contemporaneous depositional systems, which are three-dimensional assemblages of lithofacies. Systems tracts are defined by their position within sequences and by their internal stacking pattern.
TST	The second systems tract within a depositional sequence, characterized by retrogradational stacking, and overlain by the HST.

with column B containing a better record of the subsequent TST. Column C contains two well-developed surfaces of forced regression, one at the sequence boundary at the base of the second third-order sequence and one within the FSST of the following third-order sequence. Column D lacks any record of LST deposition, with the time of the LST represented by a hiatus at the sequence boundary.

THE STRATIGRAPHICAL EXPRESSION OF CONSTANT EXTINCTION

To understand the stratigraphical expression of mass extinction, it is necessary to begin with the distribution of last occurrences when there is no mass extinction.

If the stratigraphical record was uniform, with unchanging facies, constant preservation and constant sedimentation with no appreciable hiatuses, last occurrences would be uniformly distributed through a stratigraphical column if extinction rate was constant. Two decades of sequence stratigraphical research demonstrate that such a stratigraphical record is exceptionally rare for shallow-water marine systems (Catuneanu 2006).

When extinction rate is held constant, numerical simulation shows that the distribution of last occurrences is markedly non-uniform (Figs 3–5). In the most distal of these columns (Fig. 3), two clusters of last occurrences are present near the stratigraphically condensed base of the column with one cluster at the transgressive surface (0 m) and the other at the maximum flooding surface (1 m). In both cases, last occurrences are concentrated

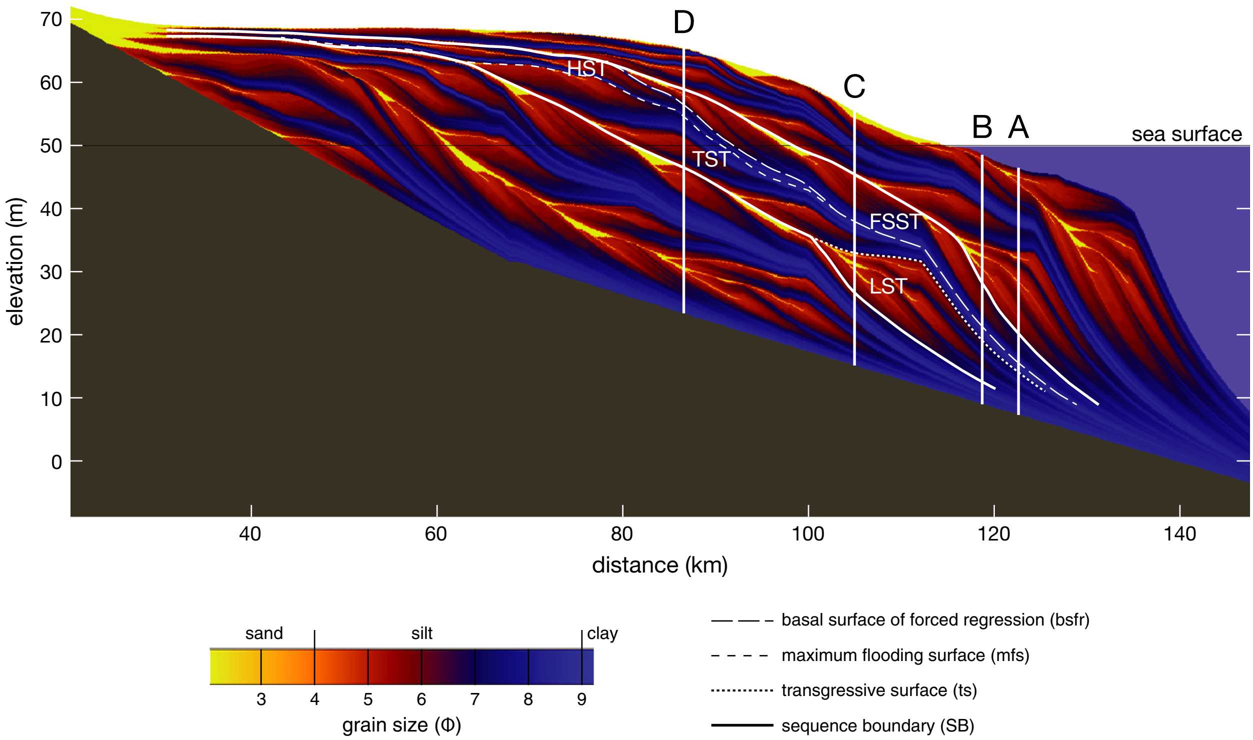

FIG. 2. Modelled onshore–offshore cross section of the sedimentary basin produced by Sedflux and used throughout this study. One of the four simulated third-order sequences is delineated, along with the surfaces that bound its systems tracts. *Abbreviations*: FSST, falling-stage systems tract; HST, highstand systems tract; LST, lowstand systems tract; TST, transgressive systems tract. Colour online.

primarily by stratigraphical condensation, demonstrated by the relative thickness of these systems tracts compared to equivalent systems tracts of equal duration higher in the section.

Depositional rates increase upcolumn, as indicated by the increased thicknesses of many of the systems tracts, but depositional rates are locally low near maximum flooding surfaces (9 and 31 m). As a result, the importance of stratigraphical condensation in generating clusters of last occurrences can vary markedly within a stratigraphical column. Similarly, the large facies changes near the two maximum flooding surfaces (9 and 31 m) favour the appearance of deep-water species, which abruptly disappear with the rapid shallowing into overlying facies. Many of these deep-water species go extinct before the next occurrence of deep-water facies higher in the column, causing their last occurrences to be clustered at the maximum flooding surface.

Depositional rates are extremely rapid in the LST in the middle of the column (13–26 m), causing the number of last occurrences to be low throughout this interval. The number of last occurrences rises near the top of all columns, and this is largely an edge effect of the end of the simulation, but it is a situation often faced by outcrop studies. For example, in any column measured in the field, species will appear to have last occurrences in that column that only reflect the upper limit to the measured stratigraphical column.

In a slightly more landward location (Fig. 4), the patterns of last occurrences are overall similar, but with a new variation. Shortly above the cluster of last occurrences at the maximum flooding surface (12 m) is a second interval of elevated last occurrences (13–15 m). This second interval corresponds to a thin interval of rapid shallowing within the FSST. The last occurrences in this interval are not driven by stratigraphical condensation, as depositional rates are high, but are driven entirely by rapid facies change. This interval of shallowing represents the last occurrences of all those relatively deep-water (i.e. >15 m) species that went extinct before such depths were achieved again (at 32–34 m). Thus, rapid facies change works to concentrate last occurrences at both flooding surfaces and forced regressions. Flooding surfaces tend to preserve last occurrences of shallower-water species, and surfaces of forced regression tend to preserve last occurrences of deeper-water species (Holland 2000).

A third column illustrates the controls on last occurrences in a more landward setting (Fig. 5). This column also contains the basal cluster (1 m) controlled by condensation and abrupt shallowing, as well as a mid-column cluster at the maximum flooding surface (16 m). Two new clusters correspond to sequence boundaries (24 and

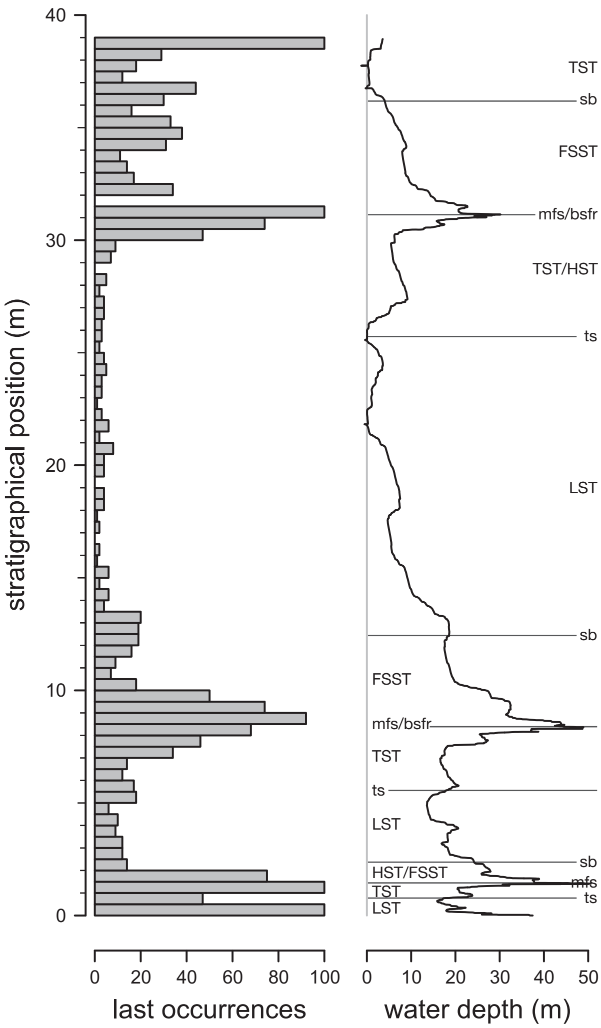

FIG. 3. Modelled first and last occurrences at location A (see Fig. 2), when there is no mass extinction. Sampled horizons are 0.5 m thick. Sequence architecture indicated over plot of water depth through the stratigraphical section. In some cases, systems tracts cannot be distinguished at this scale (e.g. HST/FSST) and the surface separating them is not shown. *Abbreviations*: bsfr, basal surface of forced regression; FSST, falling-stage systems tract; HST, highstand systems tract; LST, lowstand systems tract; mfs, maximum flooding surface; sb: sequence boundary; ts, transgressive surface; TST, transgressive systems tract.

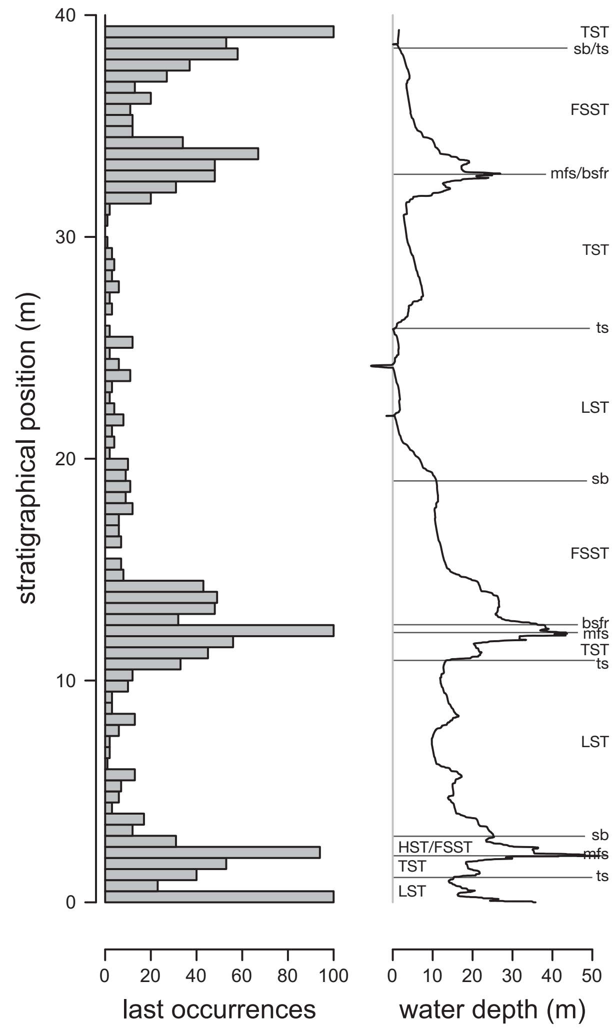

FIG. 4. Modelled first and last occurrences at location B (see Fig. 2), when there is no mass extinction. See Figure 3 for key to sequence stratigraphical architecture.

36 m). In depositionally landward settings, the subaerial unconformity at the sequence boundary represents a progressively longer hiatus. Facies above and below both of these sequence-bounding unconformities are similar, indicating that the accumulation of last occurrences here is governed solely by the duration of the hiatus. As the duration of the hiatus at the sequence boundary grows in increasingly landward settings, an increasing number of species have no fossil record and therefore no local last occurrence. As a result, the cluster of last occurrences at a sequence boundary may shrink in a landward direction, especially as hiatuses become substantially longer.

In summary, four stratigraphical processes generate clusters of last occurrences even when extinction rate is held constant, and these clusters have predictable sequence stratigraphical positions. Low rates of stratigraphical accumulation form clusters of last occurrences typically occur in depositionally downdip settings and in association with major flooding surfaces in the TST and near the maximum flooding surface. Flooding surfaces generate clusters of last occurrences of relatively shallower-water species, and flooding surfaces recording greater amounts of facies change are generally limited to the TST (Van Wagoner *et al.* 1990; Catuneanu 2006). Surfaces of forced regression produce clusters of last occurrences of relatively deeper-water species and are typically limited to the FSST. Surfaces of forced regression

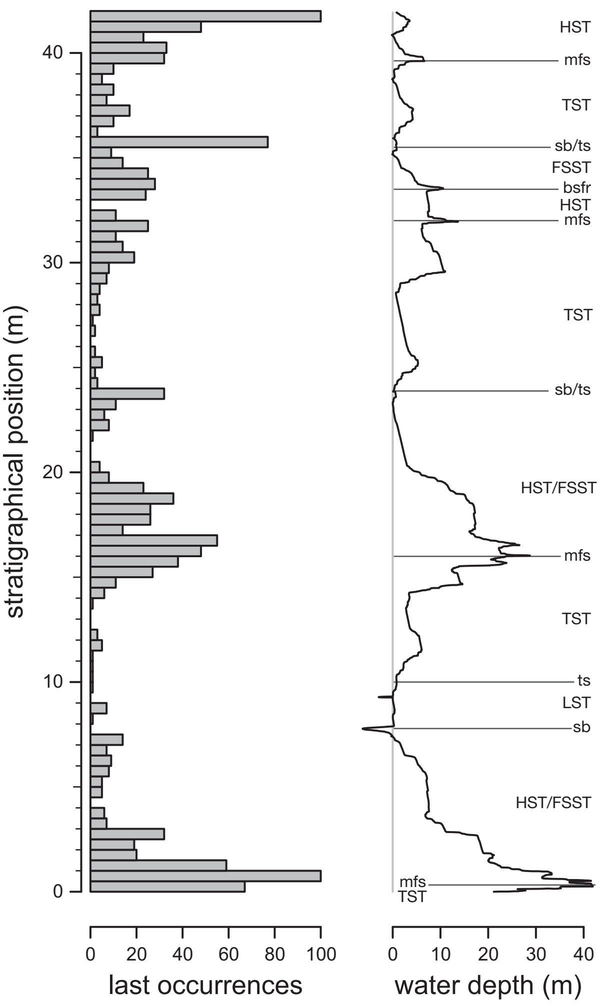

FIG. 5. Modelled first and last occurrences at location D (see Fig. 2), when there is no mass extinction. See Figure 3 for key to sequence stratigraphical architecture.

may also occur in the early LST and late HST, particularly for high-amplitude, short-period cyclicity (Hunt and Tucker 1992; Ainsworth 1994; Catuneanu 2006). Hiatuses at sequence-bounding unconformities cause clusters of last occurrences solely through non-deposition, and are more common in depositionally updip locations (Van Wagoner *et al*. 1990; Catuneanu 2006).

THE STRATIGRAPHICAL EXPRESSION OF MASS EXTINCTION

Three scenarios of a brief mass extinction are simulated. Each takes place within a particular systems tract that is characterized by a distinctive stratigraphical architecture and corresponds in most cases to a particular type of relative sea-level change. The mass extinction is simulated by a peak extinction rate 25 times higher than the background extinction rate. The mass extinction is modelled with duration of 500 kyr, with extinction rate increasing linearly from the background to the peak rate in the first 250 kyr, and falling linearly to the background rate in the subsequent 250 kyr.

The first scenario considers the case of mass extinction during a slow relative rise in sea level, such as during the LST or HST. Both systems tracts are characterized by progradational stacking of parasequences with weakly developed flooding surfaces. Because the LST is better developed in this basin simulation than the HST, a mass extinction is simulated only within the LST.

The second scenario depicts a mass extinction during a rapid relative rise in sea level, as in the TST. This systems tract is characterized in siliciclastic systems by retrogradational stacking of parasequences defined by well-developed flooding surfaces, typically with substantial deepening.

The third scenario portrays a mass extinction during a relative fall in sea level, that is within the FSST. The FSST is unique in that it is characterized by internal cycles separated by surfaces of forced regression rather than flooding surfaces. The FSST is commonly absent in depositionally updip areas, and the time represented by the FSST is included in the hiatus at the sequence boundary.

For each of these scenarios, the timing of a mass extinction in a particular systems tract is coincidental; there is no suggestion that the change in sea level caused the mass extinction. The possibility that there is a causal link between diversity changes and factors governing the stratigraphical record (such as sea level) is known as common cause (Peters and Foote 2002). If common cause occurs, such as if extinction is tied to habitat area, extinction patterns would be non-random among taxa. Such selective extinction is not simulated here, owing to the complex and case-dependent relationship between sea level and changes in habitat area (Holland 2012, 2013; Holland and Christie 2013). Even so, habitat-selective extinction would amplify most of the signal in the models presented here.

Scenario 1: extinction during slow relative rise in sea level

A mass extinction within the LST elevates the numbers of last occurrences throughout the LST (12–25 m, Fig. 6) relative to the no-mass-extinction model (Fig. 3). Sampling effects alone (i.e. the Signor–Lipps effect) ought to cause a downward smearing of last occurrences, and that pattern is present in this model. Without the Signor–Lipps effect, the number of last occurrences ought to climb steadily from the onset of extinction (13 m) to the peak of extinction (19 m). Instead, the number of extinctions is relatively flat through this entire interval. Some of this downward smearing of the extinction is also attributable to the shallowing that occurs within this interval and the gradual loss of deeper-water species.

In addition, the number of last occurrences is also elevated near the maximum flooding surface (8 m; Fig. 6). Abrupt shallowing above the maximum flooding surfaces drives this increase relative to the no-mass-extinction model (Fig. 3). Any deep-water species that occurs near the maximum flooding surface that goes extinct within the mass extinction is forced to have its last occurrence near the maximum flooding surface. Thus, the downward smearing of a mass extinction is more than simply the result of Signor–Lipps sampling effects: surfaces and intervals of major facies change will accumulate last occurrences. Importantly, such surfaces can give the impression of additional pulses of extinction prior to the actual extinction. Furthermore, in this simulation, the cluster of last occurrences at the maximum flooding surface exceeds that of any horizon within the time of mass extinction, including the peak of the mass extinction. Read at face value, this column (Fig. 6) would be interpreted as peak extinction near 8 m, followed by progressively declining extinction rates up to 20 m. In other words, a literal reading of the stratigraphical record would mislead in both the timing and temporal pattern of extinction.

In a more updip setting, where the LST is absent, the time corresponding to the LST is contained entirely within the hiatus at the sequence-bounding unconformity (Fig. 7). A cluster of last occurrences is present at the

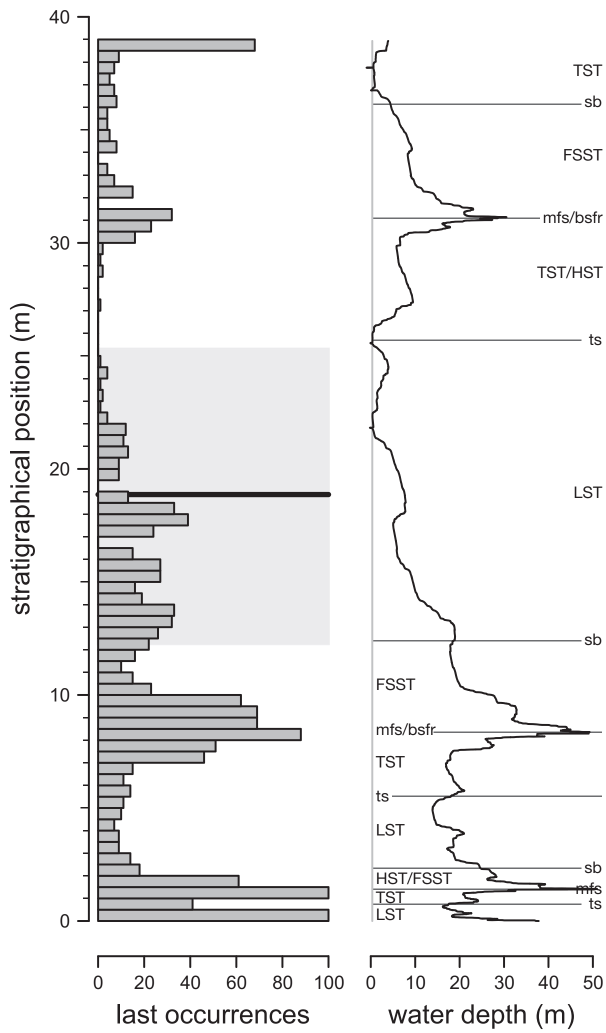

FIG. 6. Modelled first and last occurrences at location A (see Fig. 2), when there is a mass extinction in the LST, a time of slowly rising relative sea level. See Figure 3 for key to sequence stratigraphical architecture. Grey shading indicates time of elevated extinction, with peak extinction shown by bold black line (19 m).

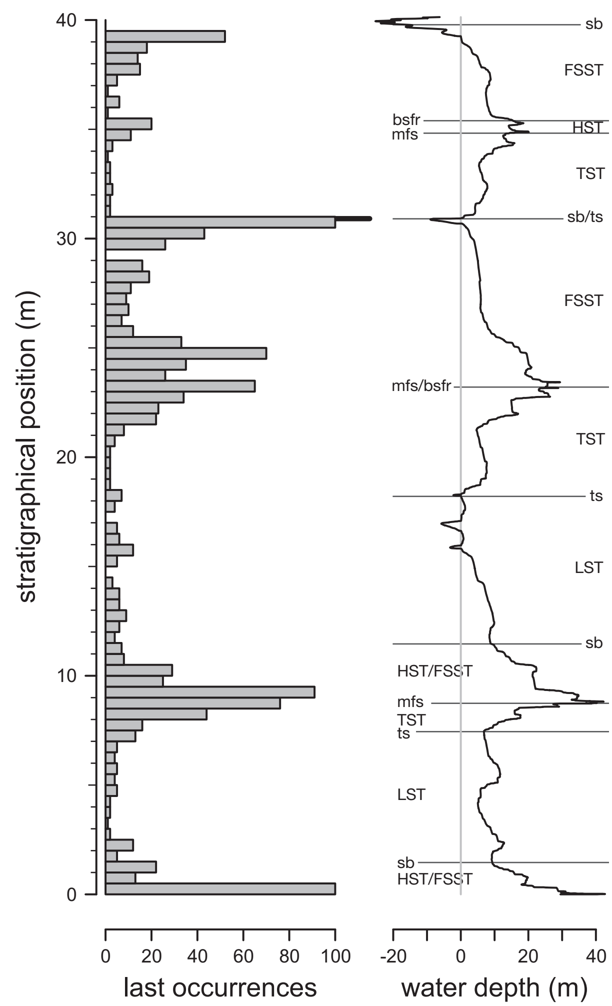

FIG. 7. Modelled first and last occurrences at location C (see Fig. 2), when there is a mass extinction in the LST, a time of slowly rising relative sea level. See Figure 3 for key to sequence stratigraphical architecture. Peak extinction occurs at 31 m.

unconformity (31 m), but these last occurrences all predate the time of extinction, which is not recorded by sediment at this locality. Geochronological dating of this surface would reveal the age of the rocks beneath the unconformity, not the time of extinction. Two additional clusters of last occurrences are also present several metres beneath the unconformity. The upper cluster (25 m) corresponds to a surface of forced regression within the FSST, and the lower cluster (23 m) corresponds to a stratigraphically condensed interval at the maximum flooding surface and the beginning of the FSST. The numbers of last occurrences are elevated in both of these horizons as a result of rapid facies change, and the lower cluster is also the result of slow rates of deposition.

Farther updip, the extinction is still contained within the sequence-bounding unconformity, and it is manifested as a cluster of last occurrences at that surface (36 m, Fig. 8). In addition, the number of last occurrences rises steadily from 28 m towards the unconformity (36 m). In this more updip location, the hiatus at the unconformity is longer than at column C and includes greater portions of the FSST and TST, in addition to the entire LST. As a result, the cluster of last occurrences at the sequence boundary (36 m) represents not only species that went extinct during the mass extinction interval, but also some species that went extinct before and after the mass extinction. Geochronological dating of this surface, however, would produce a date that precedes the time of extinction. This more updip location also lacks the strong condensation, and facies changes present near the maximum flooding surface at column C, and as a result, it lacks the double cluster in last occurrences present in column C.

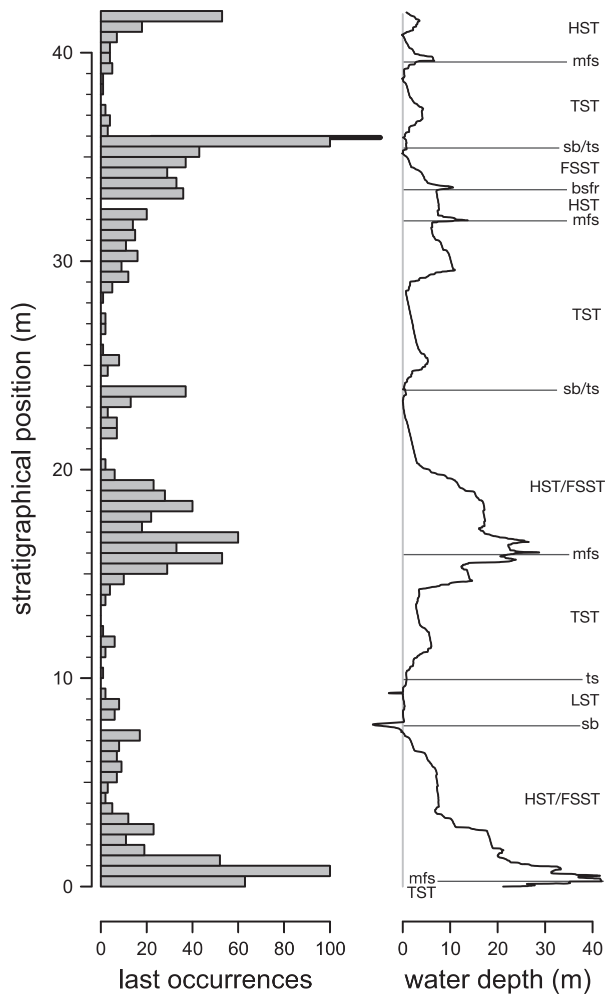

FIG. 8. Modelled first and last occurrences at location D (see Fig. 2), when there is a mass extinction in the LST, a time of slowly rising relative sea level. See Figure 3 for key to sequence stratigraphical architecture. Peak extinction occurs at 36 m.

Scenario 2: extinction during rapid relative rise in sea level

A mass extinction within the TST in a stratigraphically downdip position produces a simple pattern with a cluster of last occurrences corresponding to the time of peak extinction (30 m, Fig. 9). Stratigraphical condensation at the top of the TST, coupled with strong facies change near the maximum flooding surface, will somewhat exaggerate the magnitude of this cluster. Geochronological dating of this cluster would accurately measure the time of peak extinction. This cluster of last occurrences is preceded by an interval of steadily rising numbers of last occurrences (25–30 m), reflecting the steady rise in extinction rates. Stratigraphical condensation at the top of TST obscures that the extinction peak was also followed by an extended decline in extinction rates. Relatively rapid deposition and a lack of surfaces of abrupt facies change in the underlying LST (13–25 m) prevent the formation of clusters of last occurrences below the extinction interval.

In a depositionally more updip location in which the LST is absent and replaced by a sequence-bounding unconformity (31 m, Fig. 10), the main cluster of last occurrences immediately precedes the time of extinction and is recorded in the latest part of the FSST. Geochronological dating of these last occurrences would produce a date that is older than the time of peak extinction; that is, it would result in a date of the youngest FSST deposits at this location. In locations farther updip in which the sequence-bounding hiatus includes greater portions of the FSST and TST (not shown), the main cluster of last occurrences includes greater numbers of species that went extinct prior to the mass extinctions. At location C (Fig. 10), the main cluster of last occurrences is followed by declining numbers of last occurrences, which reflects the decline in extinction rates through the TST (31–34 m). As in the LST extinction (Fig. 7), a double cluster of last occurrences several metres below the main cluster of last occurrences is produced (23 and 25 m).

Scenario 3: extinction during relative fall in sea level

Extinction during the FSST produces a strong cluster of last occurrences that coincides with the time of peak mass extinction (36 m, Fig. 11). Elevated numbers of last occurrences are also produced throughout the time of extinction (33–36 m), a pattern enhanced by the relative thinness of the FSST at this location. A strong cluster at the base of the FSST coincides with rapid shallowing at the basal surface of forced regression (33 m), with the consequent last occurrence of deeper-water species that go extinct later in time. The top of the underlying TST also contains elevated numbers of last occurrences (29–33 m), and many of these are caused by relatively uncommon deeper-water species that go extinct later in time. The effects of the extinction are also felt at the sequence boundary nearly 10 m below the extinction horizon (24 m), causing a 40% increase in the number of last occurrences at that surface.

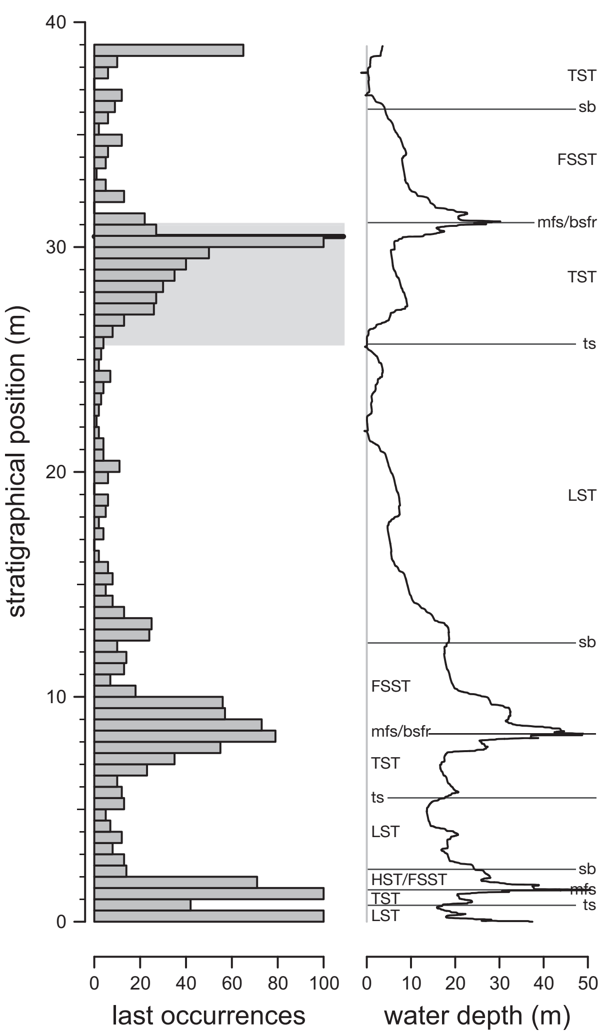

FIG. 9. Modelled first and last occurrences at location A (see Fig. 2), when there is a mass extinction in the TST, a time of rapidly rising relative sea level. See Figure 3 for key to sequence stratigraphical architecture. Peak extinction occurs at 31 m.

In depositionally downdip settings, such as locations C, B and A (not shown), similar patterns result. The primary difference in these locations is that the main cluster of last occurrences tends to occur near the base of the FSST, owing to strong condensation and facies changes near the base of the FSST.

Summary of mass extinction model patterns

From all of these models, several common patterns emerge. First, clusters of last occurrences are expected in the stratigraphical record, even when extinction rate is constant. Increases in the rate of extinction can also produce clusters of last occurrences, but such clusters are typically enhanced by abrupt changes in facies, hiatuses or stratigraphical condensation.

Second, where rates of deposition are rapid, no cluster of last occurrences may develop (e.g. Fig. 6). For a cluster of last occurrences to develop in such settings, the extinction interval must be brief and extinction rate must be substantially elevated above background levels.

Third, stratigraphical architecture commonly generates additional clusters of last occurrences stratigraphically below the time of extinction. Such additional clusters are at stratigraphically predictable horizons: major flooding surfaces (such as those in the TST), well-developed surfaces of forced regression (in the FSST), sequence-bounding unconformities and stratigraphically condensed intervals, which are commonly best developed near the maximum flooding surface. In some cases, stratigraphical architecture can give the illusion of a double pulse (e.g. Fig. 11) or even a triple pulse of extinction (e.g. Figs 7, 10).

Fourth, the main cluster of last occurrences is commonly older than the time of peak extinction rate. As a result, geochronological dating of clusters of last occurrences will result in a date of the stratigraphical surface, such as a flooding surface or sequence boundary, not the time of extinction. Previously, such dates would have been within error of the time of extinction, but remarkable advances in the precision of radiometric dates (Bowring *et al.* 2006; Shen *et al.* 2011) now make it possible that the time of extinction would lie outside the confidence interval for the radiometric date.

Last, the classical simple backward smearing of a mass extinction in the Signor–Lipps effect is an uncommon pattern. Such a pattern would be expected only in the case of an absence of well-developed flooding surfaces and surfaces of forced regression, an absence of facies control of faunas, an absence of sequence-bounding unconformities and a lack of significant variation in sedimentation rates. Two decades of sequence stratigraphical research indicates that such conditions are rare in shallow-marine settings.

THE STRATIGRAPHICAL ARCHITECTURE OF MASS EXTINCTIONS

The stratigraphical expression of mass extinction is considerably more complicated than any expectation that last occurrences might directly reflect times of extinctions or that they might be simply smeared downward through a stratigraphical section as in the Signor–Lipps effect. Given that clusters of last occurrences are the expectation, even when extinction rate is constant, a sceptic could argue that all clusters of last occurrences are solely the result of stratigraphical architecture and that there have been no mass extinctions. We do not advocate that view, as extinction rate has clearly varied over time (Foote 2003). Instead, we argue that intervals of elevated extinction rate are expressed through stratigraphical processes that generate clusters of last occurrences and that these clusters do not directly reflect changes in extinction rate. We examine several marine mass extinctions below. For each, we discuss the scenarios of extinction timing and tempo that are consistent with observed patterns of last occurrences and stratigraphical architecture.

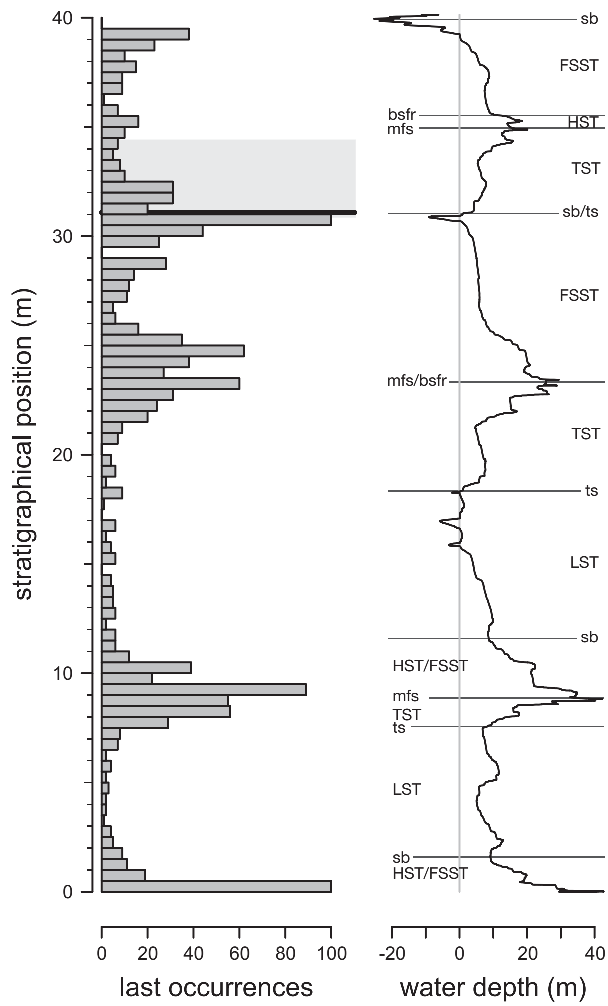

FIG. 10. Modelled first and last occurrences at location C (see Fig. 2), when there is a mass extinction in the TST, a time of rapidly rising relative sea level. See Figure 3 for key to sequence stratigraphical architecture. Peak extinction occurs at 31 m.

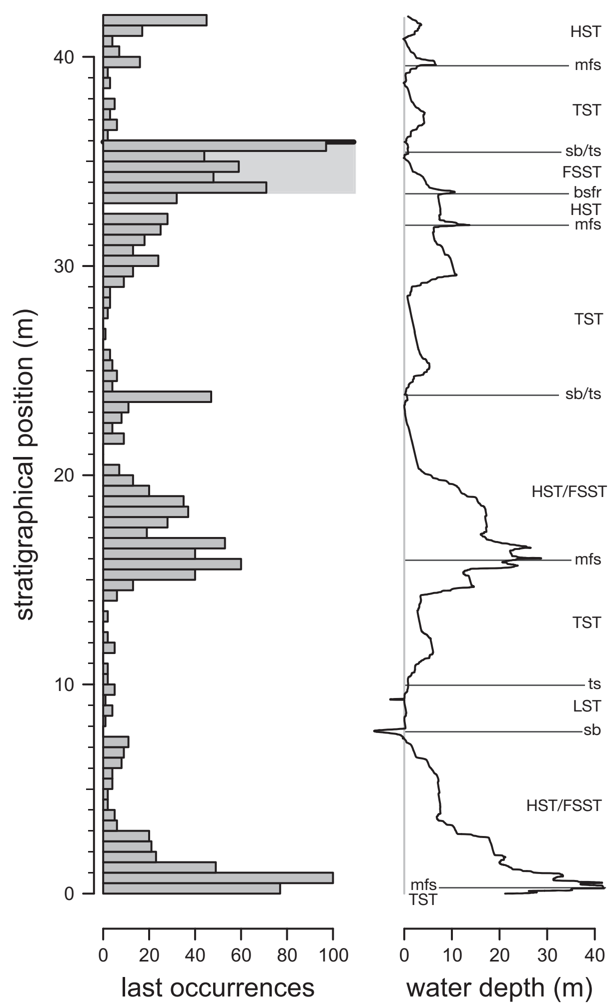

FIG. 11. Modelled first and last occurrences at location D (see Fig. 2), when there is a mass extinction in the FSST, a time of falling relative sea level. See Figure 3 for key to sequence stratigraphical architecture. Peak extinction occurs at 36 m.

Cambrian biomeres

The Cambrian and Lower Ordovician record several major extinctions known as biomeres (Palmer 1965, 1984; Westrop and Cuggy 1999; Adrain *et al.* 2009). These extinctions involve the abrupt termination of many shallow-water trilobite lineages, a reduction in the number of biofacies across the shelf, and the immigration and origination of new lineages seeded from deeper-water taxa (Stitt 1977; Palmer 1984; Westrop and Ludvigsen 1987; Westrop and Cuggy 1999). In many locations, the extinction is closely associated with an unconformity (Palmer 1984) or a major flooding surface at the top of a protracted shallowing-upward succession (Palmer 1984; Westrop and Ludvigsen 1987). A hardground is often present at or very close to the biomere boundary (Palmer 1984). Last occurrences of abundant shallow-water species are clustered at the biomere boundary, with a few last occurrences leading up to the boundary (Palmer 1984, figs 5A–B, 12B). In some cases, a flooding surface 1–2 m below the boundary also has a cluster of last occurrences (Palmer 1984, fig. 5C).

The stratigraphical architecture of prolonged shallowing-upward, capped by a major flooding surface that commonly bears a hardground, strongly suggests a HST, capped by a combined sequence-bounding unconformity and transgressive surface. Such architecture, common to cratonic settings and updip portions of passive margins (Van Wagoner *et al.* 1990; Catuneanu 2006), implies that the time representing the missing FSST and LST is contained within the hiatus at the sequence boundary. These missing systems tracts would have been deposited downdip, although subsequent patterns of uplift and exposure may not have exposed these rocks.

Although the presence of a cluster of last occurrences at the uppermost strata beneath the flooding surface might indicate a mass extinction at that point in time, it is also consistent with other scenarios. For example, any extinction within the FSST or LST would also produce a cluster of last occurrences in the same horizon (Figs 7, 8, 11), even if the extinction was prolonged rather than abrupt. Furthermore, because the extinction is marked by a replacement of shallow-water faunas, it is also possible that the extinction occurred in the early TST (similar to Fig. 10, but with extinction limited to the early TST) and that the loss of shallow-water faunas may have occurred when deeper-water deposits were present over most of the current outcrop area.

Late Ordovician extinction

The Late Ordovician mass extinction is the one of the most severe mass extinctions in Earth's history, and it is second only to the end-Permian in its intensity (Raup 1991*b*). The stratigraphical pattern of last occurrences is well documented and may be expressed as one or two clusters of last occurrences.

A single cluster of last occurrences is typically found in cratonic locations that lie in a depositionally updip setting. Such clusters are found at surfaces that are both a well-developed subaerial unconformity and a major flooding surface (Finney *et al.* 1997, 1999).

A pair of clusters of last occurrences is generally found in settings that are depositionally downdip or marginal to cratons, and these have led to the widespread interpretation of the end-Ordovician extinction as a two-phase extinction event (Brenchley and Newall 1984; Finney *et al.* 1999; Sheehan 2001; Brenchley *et al.* 2003; Delabroye and Vecoli 2010; Ghienne *et al.* 2014; Harper *et al.* 2014). The first of these phases coincides with an abrupt shift from deeper-water facies to shallower-water facies near the base of the *Normalograptus extraordinarius* graptolite Biozone. This first phase primarily affected nektonic and planktonic forms (particularly chitinozoa and graptolites), as well as some shallow-water and deep-water shelf species. The second phase coincides with a major flooding surface, with deep-water mudstones overlying typically shallow-water carbonates. In some cases, this flooding surface is developed on a subaerial unconformity (Finney *et al.* 1997). This second phase occurs within the *Normalograptus persculptus* graptolite Biozone and primarily affected conodonts and shallow-water benthic taxa.

The pattern of a double cluster of last occurrences arises commonly in the simulations, both when a mass extinction is present (Figs 8, 11) and when there is no increase in extinction rate (34 and 36 m, Fig. 6). That extinction rate was elevated in the latest Ordovician is clear; the question is what extinction scenarios are consistent with the observed stratigraphical pattern of last occurrences.

Although a double cluster of last occurrences could indicate two phases of extinction, it is also consistent with a single prolonged period of extinction whose expression is manifested stratigraphically into two discrete clusters of last occurrences (e.g. Fig. 11). In particular, the observed pattern of last occurrences through the Late Ordovician is consistent with a protracted interval of extinction spanning the FSST, LST and earliest TST before the end of the Ordovician (Finney *et al.* 1999). Such an extinction would be expected to produce two clusters of last occurrences. The first would correspond to the basal surface of forced regression in the FSST, and the second would lie at the transgressive surface, the first major flooding surface following the LST (Fig. 11). The first of these clusters would be dominated by the disappearance of deeper-water planktonic taxa, and the second dominated by the loss of a broad suite of shallow-water taxa. Both of these patterns have been documented for the Late Ordovician extinction (Finney *et al.* 1999).

In depositionally updip areas, the time representing the FSST, LST and early TST is typically contained within the hiatus at the sequence-bounding unconformity. As a result, all last occurrences become clustered immediately under this surface, resulting in the single cluster of last occurrences seen in these settings (Figs 7–8).

Most studies of the Late Ordovician extinction have regarded hiatuses as being uncommon and of short duration, unless they can be biostratigraphically documented. In contrast, one recent sequence stratigraphical study of classic Late Ordovician exposures on Anticosti Island and the Anti-Atlas Mountains has suggested that both regions contain significant hiatuses and condensed sections, as well as substantial cyclic changes in depositional environments (Ghienne *et al.* 2014). Such an architecture would force a substantial reappraisal of the chronology in this interval, not only of fossil occurrences but also of geochemical proxies of environmental change.

Late Devonian diversity crisis

The Late Devonian is one of the five largest diversity declines in the Phanerozoic (Raup and Sepkoski 1982; Sepkoski 1986), although recent analyses suggest that the diversity decline was primarily the result of decreased origination rather than elevated extinction (Bambach *et al.* 2004). Late Devonian faunal changes occur in three separate episodes, with the Taghanic event at the end of the Givetian, the Kellwasser event at the end of Frasnian and the Hangenberg event at the end of the Famennian (House 1985). Of these, the Kellwasser or Frasnian–Famennian event is the largest.

In depositionally updip areas, the sequence architecture of the Kellwasser event consists of a sequence-bounding subaerial unconformity merged with a major flooding surface (Chen and Tucker 2003, 2004). In many areas, the flooding surface is marked by a shift from relatively shallow-water carbonate deposits to significantly deeper-water organic-rich mudstone and shale (McGhee 1996; Hallam and Wignall 1997). In depositionally downdip areas, in which the FSST and LST are preserved, the event separates into two clusters of last occurrences, with one at the base of the FSST and the other at the transgressive surface atop the LST (Hallam and Wignall 1997; Chen and Tucker 2003). In these depositionally downdip areas, the lower cluster records the loss of relatively deeper-water pelagic species, and the upper cluster records the loss of shallower-water species, as is also seen in the Late Ordovician extinction.

The common expression of the Kellwasser event as a single surface recording both sea-level fall (the sequence-bounding unconformity) and sea-level rise (a major flooding surface) has led to disagreements over whether the event was caused by the fall or the rise in sea level (McGhee 1996; Hallam and Wignall 1997). Regardless of identifying the causal agents involved, both types of surface are sites where last occurrences would be expected to be concentrated. For subaerial unconformities, the hiatus is responsible for the clustering of last occurrences, but for major flooding surfaces, abrupt deepening and stratigraphical condensation are the primary agents of clustering. Indeed, one of the characteristics of the Kellwasser event is that the extinction was felt much more severely by shallow-water faunas, and a clustering of last occurrences of shallow-water species is the expectation at a major flooding surface. This stratigraphical pattern of last occurrences is consistent not only with a pulse of extinction timed with the flooding surface, but also with a more protracted interval of extinction in which last occurrences of shallow-water species become clustered at the flooding surface. If extinction rate was not elevated during the Late Devonian as has been argued (Bambach *et al.* 2004), all of the clusters of last occurrences would be solely the result of stratigraphical processes.

End-Permian extinction

With an estimated 96% species extinction (Raup 1979), the end-Permian is the most severe biotic crisis of the Phanerozoic, and it is one of the two most extensively studied extinction events. Detailed study of the boundary was long hampered by a substantial hiatus in most regions (Erwin 1993; Hallam and Wignall 1997), but discoveries of good boundary sections in China (Hongfu *et al.* 2001; Shen *et al.* 2011), India (Nakazawa *et al.* 1975; Brookfield *et al.* 2003; Algeo *et al.* 2007) and Italy (Broglio Loriga *et al.* 1986; Wignall and Hallam 1992; Farabegoli *et al.* 2007; Posenato 2010) have greatly increased understanding of this event.

In South China, the Permo-Triassic boundary is well exposed along an onshore to offshore transact from the Emeishan Volcanic Plateau to the Western Upper Yangtze Platform (Shen *et al.* 2011). The extinction has been best studied at the global boundary stratotype at Meishan (Hongfu *et al.* 2001), where the Permo-Triassic boundary is placed in bed 27 and the maximum extinction interval interpreted as beds 24–28 (Shen *et al.* 2011). The inferred extinction interval is approximately 0.5 m thick (Hongfu *et al.* 2001) and represents an estimated 200 $\pm$ 100 kyr (Shen *et al.* 2011; Wang *et al.* 2014). The inferred extinction interval and system boundary are closely associated with a series of major flooding surfaces within the TST, which records a rapid upward transition from bioclastic micrite to calcareous mudrock (Hongfu *et al.* 2001). Last occurrences are distributed through the interval from bed 24e to bed 29a (Hongfu *et al.* 2001), and several species of foraminifera, brachiopods, bryozoans and ammonoids persist shortly above the extinction interval, but disappear in the lowermost Triassic. Other studies argued that the pattern of last occurrences indicates two pulses of extinction (Song *et al.* 2013, Clarkson *et al.* 2015).

In Italy, the end-Permian extinction is closely associated with a series of flooding surfaces within the TST through the Tesero and lowermost Mazzin Members of the Werfen Formation. The interval immediately below the lowest of these flooding surfaces is complicated, where the 2-m Bulla Member of the Bellerophon Formation contains at least two subaerial unconformities (Farabegoli *et al.* 2007). Several conodonts and molluscs that disappear in the extinction interval reappear 14–22 m higher in the section in a shallowing-upward interval (Farabegoli *et al.* 2007). The basal *parvus* zone of the Triassic is substantially thicker in Italy (21 m) than it is at Meishan (0.08 m), implying that the earliest Triassic at Meishan is highly condensed.

In India, the main extinction horizon lies approximately 2 m below the Permo-Triassic boundary at the Guryul Ravine section (Algeo *et al.* 2007). Both the inferred extinction horizon and the boundary lie at major facies changes in the lowermost Khunamuh Formation, and both horizons appear to be significant flooding surfaces. The system boundary at this section has been interpreted as a second extinction horizon (Algeo *et al.* 2007). The main extinction horizon is underlain by a 2.7-m-thick, sharp-based and internally complex unit (bed 46) in the uppermost Zewan Formation, which consists of sandy grainstone and quartz sandstone (Brookfield *et al.* 2003). The base of this unit has been variously interpreted as recording rapid shallowing (Brookfield *et al.* 2003) or a flooding surface (Algeo *et al.* 2007). The *parvus* zone overlying the end-Permian boundary is quite condensed at Guryul Ravine, where it is 1.5 m thick, compared to 21 m in Italy.

It is undeniable that the end-Permian extinction is real, but the interpretation of the stratigraphical pattern of last occurrences is considerably complicated by the sequence stratigraphical architecture. In all three well-studied areas, the main cluster of last occurrences is associated with one or more major flooding surfaces within the TST. In Italy at least, two subaerial unconformities are present less than 2 m below the main cluster of last occurrences, and a similar stratigraphy may be present in India. In both India and South China, basal Triassic strata are highly condensed relative to Italy. This combination of factors – one or more major flooding surfaces, stratigraphical condensation and possible subaerial unconformities – provides ample means to concentrate last occurrences. It is likely that the appearance of the end-Permian extinction is considerably altered by stratigraphical architecture, with the extinction taking place over a substantially longer period within the TST than generally thought. That facies play an important role in the occurrence of faunas in these sections is demonstrated by the recurrence of several conodont and mollusc species in Italy, 14–22 m higher in the section. Constrained optimization of 18 fossiliferous sections from across South China and northern peri-Gondwana also indicates that facies control plays an important role in the timing of last occurrences of taxa in any single section. This constrained optimization also indicates a deterioration in conditions nearly 1.2 myr before peak extinction (Wang *et al.* 2014), corroborating that the extinction event was more prolonged than a simple reading of last occurrences in any one section would indicate.

End-Triassic extinction

Although the end-Triassic extinction is commonly regarded as one of the big-five extinction events, its importance as a global event has been questioned (Hallam 2002) as has the importance of extinction relative to reduced origination as the cause of the diversity decline (Bambach *et al.* 2004). Like many of the extinctions already discussed, the boundary interval includes surfaces that are typical locations where last occurrences are stratigraphically clustered.

The sequence stratigraphy of the Triassic–Jurassic boundary has been studied in southwest Britain (Hesselbo *et al.* 2004), where several different definitions of the boundary been proposed. Most boundary definitions lie within the ~3-m-thick Lilstock Formation, split roughly evenly into a lower Cotham Member and an upper Langport Member. The lower part of the Cotham Member is interpreted as a FSST, capped by a subaerial unconformity (Hesselbo *et al.* 2004). The upper part of the Cotham Member and the entire Langport Member are interpreted as the lowest part of the TST, containing several significant flooding surfaces (Hesselbo *et al.* 2004). The Langport Member has an unusual conglomeratic bed that was originally interpreted as palaeokarst (Wignall 2001), but more recently as a series of debris flows during the early TST (Hesselbo *et al.* 2004).

The various boundary definitions that have been proposed primarily reflect differences of opinions over which taxonomic groups should be used to define the boundary, but the fact that most of these definitions lie within a narrow interval characterized by a subaerial unconformity and major flooding surfaces again suggests that many of the last occurrences lie at particular surfaces as a result of facies changes, hiatuses and stratigraphical condensation. Differences in preferred facies among taxa are a likely cause for their last occurrences lying at different horizons and therefore the disagreements on where the boundary should be placed. As argued for other extinctions, it is entirely plausible that the end-Triassic extinction was more protracted and that its expression in outcrops may seem more punctuated as a result of stratigraphical architecture. Indeed, Hallam (2002) argued on similar grounds that the end-Triassic extinction occurred over a longer period of time, and he specifically pointed to strong facies relationships of species as a particular problem in understanding the true tempo of the extinction.

Cenomanian–Turonian extinction

The effects of sequence stratigraphical architecture have been well documented for the Cenomanian–Turonian extinction (Gale *et al.* 2000; Smith *et al.* 2001). These studies have shown that the last occurrences of species across this boundary in western Europe are tightly coupled to progressive deepening across a series of major flooding surfaces and that these last occurrences are predictable based on the known facies occurrences of these species. Furthermore, many species are absent in the deepest-water portion of the section, yet reappear as 'Lazarus taxa' higher in the section when shallow-water facies returned to the region, similar to the pattern reported from the Italian Permo-Triassic sections.

Gale *et al.* (2000) pointed out that broad regions have a similar stratigraphical architecture and therefore display similar faunal patterns. Thus, the presence of widespread similar faunal patterns cannot be taken as evidence that last occurrences represent times of extinction, because faunal patterns will necessarily be similar if a similar stratigraphical record is being sampled. They also pointed out that one test of facies control, finding extinction taxa in shallow-water strata immediately above the Cenomanian–Turonian boundary, may not be possible because such strata have been eroded away completely during subsequent periods of uplift.

From these faunal and stratigraphical patterns, Gale *et al.* (2000) argued that the Cenomanian–Turonian faunal change is only a stratigraphical artefact, not a biological crisis. Such an interpretation is an extreme one, and it may not be the only possible interpretation. It may also be possible that there was elevated extinction rates during this time, but that these elevated rates occurred during a period in which major flooding surfaces formed, resulting in the appearance of a short-lived discrete episode of faunal turnover. Regardless of which of these two interpretations is correct, the conclusion is the same: last occurrences are strongly controlled by stratigraphical architecture and cannot be simply read as times of extinction.

End-Cretaceous extinction

The end-Cretaceous extinction is one of the best-understood extinctions, owing largely to the now well-established hypothesis of a bolide impact as its cause (Schulte *et al.* 2010). The stratigraphical pattern of occurrences of marine invertebrates has also been studied in detail at several places, including Seymour Island (Macellari 1986) and Zumaya, Spain (Ward 1990; Marshall and Ward 1996).

Six species of ammonoids on Seymour Island have their last occurrence at or very close to the Cretaceous–Palaeogene boundary, but five others have last occurrences up to 60 m below the boundary. Although the sequence stratigraphy of this section has not been interpreted, the lithological columns of Macellari (1986) suggest that the Cretaceous–Palaeogene boundary lies near a maximum flooding zone capping a 300-m-thick TST. Although ammonites are more abundant in the more distal facies in these columns, there is no obvious evidence of any sequence stratigraphical reason for the clustering of ammonite last occurrences at the Cretaceous–Tertiary boundary.

The stratigraphical distribution of ammonites and inoceramid bivalves has been studied intensively at Zumaya, Spain (Ward 1990; Marshall and Ward 1996). Thirteen species have their last occurrence at the Cretaceous–Palaeogene boundary, and 19 ammonoids have their last occurrences scattered through the column, up to 220 m below the boundary. Six inoceramids have their last occurrences in a zone 120–180 m below the boundary. As on Seymour Island, ammonoids are more abundant in some facies than in others. For example, a marl 1.5–8 m below the boundary is nearly barren of ammonoids, and similar marls lower in the section (e.g. 92–115 m below the boundary) have few ammonoids. The sequence stratigraphy of the Zumaya section has not been interpreted, so it is difficult to evaluate stratigraphical controls on ammonoid last occurrences. An abrupt facies change at the Cretaceous–Palaeogene boundary to a limestone unlike any lower in the column makes it difficult to evaluate whether the absence of ammonoids in lowermost Palaeogene strata is facies controlled.

Even with the difficulties of interpreting the sequence architecture of these two columns, their stratigraphical architecture is unlike all the previously discussed extinction horizons in that they are not associated with either a sequence-bounding subaerial unconformity, a basal surface of forced regression, or a major flooding surface in the TST. The clustered last occurrences of ammonites at the Cretaceous–Palaeogene boundary do not appear predictable from sequence stratigraphical architecture and are consistent with an abrupt extinction event.

In some sections that are more depositionally updip than Seymour Island and Zumaya, the Cretaceous–Palaeogene boundary is associated with the early TST (Donovan *et al.* 1988). At the Braggs locality (Alabama, USA), the Cretaceous–Palaeogene boundary lies 0.9 m above a subaerial unconformity at a sequence boundary, and 2.1 m below the maximum flooding surface. Three flooding surfaces are present within the TST here, and all display elevated iridium levels, owing to stratigraphical condensation. Thus, depositionally updip sections of this boundary expectedly display a strong relationship to sequence architecture. More downdip sections suggest that the timing of the last occurrences is not closely coupled to sequence architecture and therefore that the last occurrences likely reflect the extinction itself, not surprising given the rapidity of the end-Cretaceous extinction mechanism.

DISCUSSION

A pervasive pattern in the fossil record

With the exception of the end-Cretaceous extinction, all of the big-five mass extinctions, as well as the Cambrian biomeres and the Cenomanian–Turonian extinction, have similar stratigraphical expressions. Where only depositionally updip sections are available, all are characterized by a single major cluster of last occurrences that is closely associated with a major flooding surface within the TST. This surface records a substantial increase in water depth and is likely an interval of stratigraphical condensation. In many cases, this surface also coincides with a sequence boundary, with a hiatus that reflects the duration of the subaerial unconformity. Where depositionally downdip sections are available, such as for the Late Ordovician and the Late Devonian, a double cluster of last occurrences is present. The first and lower of these clusters is dominated by the last occurrence of relatively deeper-water taxa and coincides with a surface of forced regression within the FSST or at the base of the LST, which record a stratigraphically abrupt decrease in water depth. The second and higher of these clusters records the last occurrences of relatively shallow-water taxa and lies at a major flooding surface.

Other extinction events also occur in a similar context. For example, the Late Ordovician M4/M5 extinction of eastern Laurentia occurs at a combined sequence boundary and transgressive surface (Holland and Patzkowsky 1996, 1998, 2004; Patzkowsky and Holland 1996, 1999). The Pliensbachian–Toarcian extinction in the Cleveland Basin of Yorkshire is closely associated with a major flooding surface within the TST (Danise *et al.* 2013). Of the 11 turnover events identified from the Siluro-Devonian of the Appalachian Basin in the USA, five coincide with a sequence boundary and six occur near or at major flooding surfaces within the TST (Brett and Baird 1995). Similarly, the boundaries of Ecologic-Evolutionary Units (Boucot 1983) and Subunits (Sheehan 1996) commonly occur in similar positions. Ammonite replacements within the Lower and Middle Jurassic of Germany also show a repeated association with major flooding surfaces (Bayer and McGhee 1985; McGhee *et al.* 1991). The association of extinction and faunal turnover events with these surfaces is a pervasive pattern in the fossil record. Such a setting for faunal change has long led to uncertainty over the timing and cause of extinction, in particular whether the extinction is associated with 'regression' (by which most authors mean sea-level fall) or transgression (Hallam 1989). The difficulty is that such events correspond to the point of maximum stratigraphical overprint, a horizon that is associated with a hiatus, a major facies change and stratigraphical condensation, all of which concentrate last occurrences.

For all of these extinctions, the stratigraphical pattern of last occurrences has more than one possible interpretation. Although these clusters might represent short-lived episodes of increased extinction rate, their stratigraphical context is also consistent with a longer period of elevated extinction rate, with clustering of last occurrences driven primarily by some combination of subaerial hiatuses, marked deepening at a major flooding surface, rapid shallowing at a surface of forced regression and stratigraphical condensation. It is also possible for at least some of these events that the cluster of last occurrences is entirely the result of stratigraphical architecture and that no increase in extinction rates is required to explain the pattern (Gale *et al.* 2000; Smith *et al.* 2001), although we doubt that this is generally true. Even so, given the demonstrated abilities of sequence stratigraphical processes to cluster last occurrences even when extinction rates are not elevated, last occurrences should not be tacitly assumed to be equal to times of extinction.

For any particular event, there is typically a strong global consistency in its preservation. For example, the end-Permian extinction commonly occurs within a long hiatus in depositionally updip areas and at a pronounced flooding surface in depositionally downdip areas. Similarly, Cambrian biomere events are commonly preserved at a major flooding surface atop a thick progradational stack of carbonates. Such similarities reflect strong correlations among regions in the preserved stratigraphical record, owing to the position of eustatic sea level and the similarity of subsidence rates and accumulation rates. Only by examining sections in other settings will different stratigraphical expressions be revealed. For example, the Late Ordovician extinction was originally thought to be a single event until the discovery of depositionally downdip sections revealed a double cluster of last occurrences within the latest Ordovician (Finney *et al*. 1999). Continued exploration revealed that this double cluster was geographically widespread, at least within sections that were similarly depositionally downdip (Sheehan 2001; Brenchley *et al*. 2003; Delabroye and Vecoli 2010; Ghienne *et al*. 2014; Harper *et al*. 2014). Rather than showing that such an extinction had two pulses, these additional sections reflect the continued study of stratigraphically similar settings.

If mass extinctions were generally more prolonged than a direct reading of the stratigraphical record would indicate, it should not be surprising that so many mass extinctions have a similar stratigraphical expression. Third-order (i.e. duration of 1–10 myr) cyclicity is pervasive through the stratigraphical record (Haq *et al*. 1987; Van Wagoner *et al*. 1990; Catuneanu 2006). There is therefore a strong possibility that any prolonged mass extinction would span at least in part the falling stage through TST of a third-order sequence. As a result, last occurrences clustered by sequence stratigraphical processes would be expected to be a common expression of mass extinction.

Such an interpretation that last occurrences commonly predate the time of mass extinction is consistent with previous studies that suggest that last occurrences generally predate the time of species extinction (Holland and Patzkowsky 2002). This discrepancy in age, known as range offset, is commonly on the order of hundreds of thousands to a million years for benthic invertebrates (Holland and Patzkowsky 2002). Even for abundant and widespread planktonic microfossils, range offset is commonly hundreds of thousands of years (Dowsett 1988; Miller *et al*. 1994; Spencer-Cervato *et al*. 1994; Schneider *et al*. 1997; Kucera 1998; Kucera and Kennett 2000). Range offset is typically large enough that range offset now commonly exceeds the precision of geochronological methods (Holland and Patzkowsky 2002). In short, last occurrences should not be treated as times of extinction.

Recognizing true pulses of extinction

There are several ways to test whether a cluster of last occurrences was produced by a brief episode of increased extinction rate, a longer period of elevated extinction rate with stratigraphically concentration of last occurrences, or stratigraphical processes with no change in extinction rate.

The most direct way of recognizing that a cluster of last occurrences truly represents a brief episode of extinction is obviously when the cluster does not correspond to a subaerial unconformity, a surface of forced regression, a flooding surface or a condensed interval. This may not be as simple as it sounds.

For example, it has been argued that Cambrian biomere events do not coincide with flooding surfaces because the cluster of last occurrences lies within an interval of limestone, several centimetres below the switch to mudstone (Palmer 1965). In many cases, a flooding surface is overlain by one or more relatively bioclastic beds that precede the switch to deeper-water mudstone. Although such beds could be lithologically similar to the underlying limestone, they would be genetically related to the overlying mudstone. Furthermore, these beds would often be included lithostratigraphically with the underlying limestone, underscoring that lithostratigraphical boundaries often do not coincide with sequence stratigraphical surfaces (Donovan 1993).

Similarly, subaerial unconformities are notoriously difficult to detect (Galloway 1989), owing to poor and localized development of features related to subaerial exposure and erosion, as well as the removal of those features during subsequent transgression. As a result, subaerial unconformities are commonly overlain and underlain by the same lithology and therefore often lie within a single lithostratigraphical unit (Donovan 1993).

Although nearly all of the mass extinctions examined here are closely associated with one or more significant sequence stratigraphical surfaces, the end-Cretaceous extinction does not appear to be. This is particularly true on Seymour Island, although the section there may not be described in sufficient detail to understand its sequence architecture. A pronounced lithological change is present at the Cretaceous–Palaeogene boundary at Zumaya, but its sequence stratigraphical interpretation is not apparent. Thus, it appears that the cluster of last occurrences at the end of the Cretaceous is the strongest candidate for a truly short-lived episode of extinction.

The second way to test the cause of a cluster of last occurrences is to examine sections depositionally updip or downdip and compare the patterns of last occurrences. For example, if a cluster of last occurrences at a major flooding surface represents a pulse of extinction, the species that disappear at that surface should not be present above that surface anywhere. By working depositionally updip, it may be possible to observe where the shallow-water facies underlying the flooding surface at the original locality now lie above the flooding surface. If that facies contains the species whose last occurrences were below the flooding surface at the original location, those last occurrences were clustered by stratigraphical processes, not by a pulse of extinction. Likewise, if species have last occurrences at a surface of forced regression, one must search for that deeper-water facies in locations that are depositionally downdip, but above the surface.

This search depositionally updip or downdip may not always be possible. For example, depositionally updip regions necessary to test the Cenomanian–Turonian last occurrences have been removed by erosion and are no longer available (Smith *et al.* 2001). Similarly, lowstand deposits are often buried in the subsurface and are inaccessible. For many flat-topped carbonate platforms and shelves, lowstand deposits are confined to a narrow belt, making their exposure unlikely (Giles *et al.* 1999). On many modern coastal plains, depositional strike is often parallel to structural strike, meaning that only a narrow window along depositional dip is exposed.

Depositionally updip or downdip areas may be accessible, but in different sedimentary basins. For example, Late Ordovician dicranograptid, diplograptid and orthograptid graptolites thought to have gone extinct persist on the Yangtze Platform into the *N. extraordinarius* Biozone, higher than expected (Mitchell *et al.* 2007). Similarly, normalograptid species associated in most places with the post-extinction interval occur on the Yangtze Platform in the lower Hirnantian. Although the Yangtze Platform has been interpreted as a refuge region (Mitchell *et al.* 2007), these patterns of occurrence are also consistent with the Yangtze Platform preserving a depositionally downdip setting not seen in most other basins.

A similar persistence of faunas occurs above the Ptychaspid Biomere in New York, USA, where several trilobites are present in strata that biostratigraphically postdate the biomere boundary (Landing *et al.* 2011). The Ritchie Limestone in which they occur is a highly bioturbated mollusc-rich unit interpreted as an inner-shelf facies. As in the Ordovician example, the authors interpreted these trilobite occurrences as a refugium, but it is also possible that this represents a depositionally downdip setting that demonstrates the existence of these species later than their last occurrences at the widespread flooding surface would suggest.

The third way to test whether extinction was elevated in a particular time interval is to estimate the extinction rate itself. This would be done by first identifying two environmentally equivalent intervals of rock, one below the inferred extinction and one above. Minimally, these two intervals would need to represent the same lithofacies. Because faunas are often more sensitive indicators of environment than lithofacies (Holland *et al.* 2001), the post-extinction interval should contain species that co-occurred in the pre-extinction interval with species inferred to have gone extinct. Such a use of environmental-control taxa is similar to the concept of taphonomic-control taxa (Bottjer and Jablonski 1988). From these two intervals, the percentage extinction can be calculated as the percentage of species present in the lower interval that are not present in the higher interval. This can be compared to the expected percentage extinction over the elapsed time between the two intervals, given the Phanerozoic average extinction rate (Fig. 12), similar to the approach of Raup (1978) for the Permo-Triassic boundary.

This approach requires good age estimates, but advances in radiometric dating make this feasible in many places. Even where such dates are not available, it may be possible to place sufficient bounds on elapsed time to know whether the extinction rate is larger than the Phanerozoic average or larger than the background rate for that portion of geological time. Ivany *et al.* (2009) adopted a similar approach and used it to show that turnover within the Devonian Hamilton Group of New York was lower than expected for the Devonian.

It is presently unclear what these modelling results imply for global compendia of last occurrences, in particular, whether spurious global peaks in last occurrences are possible or even likely. The hope would be that global compendia would be based on a sufficiently large number of sedimentary environments and basins to cancel out any regional sequence stratigraphical effects. Knowing whether this is true awaits analyses of global environmental and provincial coverage for individual extinction events. In addition, global compendia tend to be at the level of the genus rather than the species, but these models are also likely to be largely applicable at the genus level. Genera may be monospecific, sometimes commonly so, making a genus-based model the same as a species-based one. Species within genera also often have similar ecological distributions (Ludvigsen *et al.* 1986), suggesting that genus-level patterns might be similar to those modelled here.

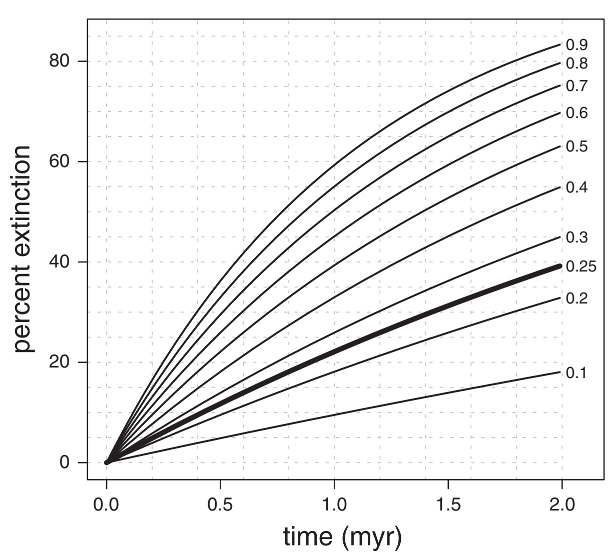

FIG. 12. Expected percentage extinction as a function of elapsed time and extinction rate. Extinction rates ranging from 0.1 to 0.9 per myr are indicated along the right, with the Phanerozoic average rate (Raup 1991*a*) of 0.25 indicated in bold.

Although extinction is the focus of this study, many of these model results would also apply to originations during recovery from mass extinction. The same processes that cause last occurrences to accumulate in particular horizons will do the same for originations. As a result, delayed and pulsed first occurrences are to be expected, even if the recovery was immediate and not pulsed.

Stratigraphical architecture and geochemical proxies of environmental change

The geochemical history of strata preserves a valuable record of environmental change during mass extinctions, and geochemical proxies are increasingly applied to the study of mass extinction. For example, carbon isotopes can reveal changes in carbon cycling that can be used to infer changes in organic carbon burial, productivity and changes in atmospheric pCO_2 concentrations (Kump and Arthur 1999; Bachan *et al.* 2012). Sulphur isotopes can be used to infer euxinic conditions in the marine environment (Grice *et al.* 2005), and boron isotopes can reveal changes in ocean pH and acidification (Clarkson *et al.* 2015).

Stratigraphical processes of sediment accumulation mean, however, that these proxies will not preserve a straightforward chronology of environmental change. For example, variations in sedimentation rate will expand the apparent history during times of rapid deposition and condense it during times of slow deposition. Hiatuses will remove entire sections of this history. Furthermore, some proxies may be subject to variation among facies, such that stratigraphical changes in facies complicate matters in that the vertical record of a proxy will reflect not only changes through time, but also changes in the sampled environment (Panchuk *et al.* 2006).

These processes can considerably complicate the preserved record of a geochemical proxy, hampering correlations between regions (Ghienne *et al.* 2014) but also complicating the understanding of environmental change during a mass extinction. Even so, it is important to stress that hiatuses, variations in sedimentation rate and the effects of facies change are all predictable given a knowledge of the sequence stratigraphical architecture of a stratigraphical column or region. As is true for the fossil record, the analysis of geochemical proxies must explicitly account for the stratigraphical record that is sampled.

CONCLUSIONS

Last occurrences of fossil species generally predate the times of extinction and cannot typically be directly used to infer the timing or tempo of extinction episodes. Numerical simulations of the fossil record demonstrate that last occurrences of fossil species will tend to cluster at sequence-bounding subaerial unconformities, surfaces of forced regression within and bounding the FSST, major flooding surfaces within the TST and intervals of stratigraphical condensation, such as the maximum flooding surface and other major flooding surfaces. Such clustering arises not only from hiatuses and non-deposition, but also by changes in water depth. Times of elevated extinction will cause such clusters of last occurrences to be enhanced at and below the interval of extinction; however, the classic Signor–Lipps pattern of simple backward smearing of last occurrences is an uncommon one in these simulations. Stratigraphical architecture also modifies the preserved history of geochemical proxies of environmental change.

Most mass extinctions in the fossil record have a similar stratigraphical expression. In depositionally updip settings, most extinction events are recorded as a single cluster of last occurrences that is closely associated with a major flooding surface, which in some cases is combined with a sequence-bounding subaerial unconformity. Where depositionally downdip sections are available, two clusters of last occurrences are present, with a lower one at a surface of forced regression and an upper one at a major flooding surface, again, possibly combined with a sequence-bounding subaerial unconformity. Although such clusters of last occurrences may indicate discrete pulses of extinction, they are equally consistent with a more prolonged extinction that is stratigraphically sharpened into clusters of last occurrences. The sole exception to this pattern is the end-Cretaceous extinction, which does not appear to coincide with any sequence stratigraphically significant surface.

Three tests are available for determining whether clusters of last occurrences reflect pulses of extinction or stratigraphical architecture and for testing whether extinction rates were elevated across an interval of clustered last occurrences. First, clusters of last occurrences not associated with subaerial unconformities, surfaces of forced regression, flooding surfaces and condensed intervals are likely to reflect a pulse of extinction, such as at the end-Cretaceous. Second, depositionally updip and downdip sections, where available, can be used to test whether a cluster of last occurrences represents true times of extinction. Third, by comparing environmentally similar deposits above and below a potential mass extinction episode, the percentage extinction could be calculated and compared to background rates to test for elevated extinction.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.1mg27

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