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Greenhouse–icehouse transition in the Late Ordovician marks a step change in extinction regime in the marine plankton

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Two distinct regimes of extinction dynamic are present in the major marine zooplankton group, the graptolites, during the Ordovician and Silurian periods (486–418 Ma). In conditions of “background” extinction, which dominated in the Ordovician, taxonomic evolutionary rates were relatively low and the probability of extinction was highest among newly evolved species (“background extinction mode”). A sharp change in extinction regime in the Late Ordovician marked the onset of repeated severe spikes in the extinction rate curve; evolutionary turnover increased greatly in the Silurian, and the extinction mode changed to include extinction that was independent of species age (“high-extinction mode”). This change coincides with a change in global climate, from greenhouse to icehouse conditions. During the most extreme episode of extinction, the Late Ordovician Mass Extinction, old species were selectively removed (“mass extinction mode”). Our analysis indicates that selective regimes in the Paleozoic ocean plankton switched rapidly (generally in <0.5 My) from one mode to another in response to environmental change, even when restoration of the full ecosystem was much slower (several million years). The patterns observed are not a simple consequence of geographic range effects or of taxonomic changes from Ordovician to Silurian. Our results suggest that the dominant primary controls on extinction throughout the lifespan of this clade were abiotic (environmental), probably mediated by the microphytoplankton.

survivorship | extinction | plankton | graptolites | age selectivity

The importance of the marine plankton in both the carbon cycle and in the food web that supports the diversity of marine life is undisputed. However, the evolutionary dynamics of planktic species and the factors controlling their diversity and evolutionary turnover are still poorly known (1, 2). This is particularly so for the Paleozoic, where problems of preservation and sampling bias, and poor time resolution, have precluded detailed analysis. How does the marine plankton respond to environmental perturbations arising from climate change over geological time? How does background extinction differ from episodic and mass extinction in the pelagic realm? Is the risk of plankton species extinction dependent on the amount of time since the species originated (3)? These questions have important implications for macroevolutionary process, stability of marine ecosystems, and modern biodiversity conservation (3–5). Here, using a new global data set of unparalleled temporal resolution, we attempt to answer these questions.

The graptoloid clade (order Graptoloidea) constituted the main component of the early Paleozoic macrozooplankton from the beginning of the Ordovician to the Early Devonian (6). Graptoloids were colonial filter-feeding protochordates, generally ranging from a few millimetres up to ~200 mm in maximum dimension, which lived suspended in the water column in a range of depth zones. They have been used extensively for correlation and zonation (7–10), and the stratigraphic distributions of species are well documented. Thus, their observed stratigraphic ranges

commonly are inferred to be good approximations of their true ranges in time, and empirical graptoloid range data have been used as examples of, or tests for, macroevolutionary rates (3, 4, 11–13). Like most of the marine macroplankton, their evolutionary dynamics are interpreted to have depended closely on those of the microphytoplankton and bacterioplankton (13–16), the primary producers in the food web and which, in the modern oceans, are sensitive indicators of oceanic circulation, nutrient flux, and global climate (1, 17); in addition, they depended on physical properties of the water mass such as temperature and chemistry.

Most previous studies of taxonomic survivorship using the fossil record have been limited by the relatively coarse time resolution of the analyses, generally no better than 7- to 11-My time bins (5, 18–20). We use the constrained optimization (CONOP) global graptolite composite developed by Sadler et al. (10) that has been calibrated directly by radiometric dating and provides the basis for the Ordovician and Silurian global time scales (21). This composite has been constructed from >18,000 local records of the stratigraphic ranges of 2,045 species in 518 published stratigraphic sections distributed globally; it resolves 2,031 discrete temporal levels through the 74-My span of the graptoloid clade, yielding a mean resolution of 37 kya between levels (13). The first- and last-appearance events of all species in all sections have been used to optimally order, and proportionally space in time, the earliest first appearance and latest last appearance of each taxon using a simulated annealing optimization heuristic (10, 22) (see *SI Text, Construction of the Global Composite Sequence*). The raw extinction and origination rates of the 2,045 graptolite species have been

Significance

In the graptoloids, a major group of early Paleozoic plankton, extinction selectively removed young species during times of background (low intensity) extinction. Age-independent extinction was confined to high extinction rate spikes of short duration that were related to environmental perturbations. During the extreme Late Ordovician Mass Extinction, old species were selectively removed. Graptoloids provide a sensitive indicator of marine environmental change and suggest that age selectivity of extinction in oceanic pelagic ecosystems switched rapidly and repeatedly from one mode to another and back again, a pattern that can be detected only when temporal resolution and species turnover rates are exceptionally high.

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smoothed with a 0.25-My moving window centered at each resolved level, providing, in effect, instantaneous rate curves, each with 2,031 control points. Extinction and origination rates, and the derivative measures such as faunal turnover (origination + extinction), have thus been estimated with a precision that is orders of magnitude better than in most previous studies of global extinction. Uncertainty bounds have been estimated by bootstrapping. Our data set spans the entire lifespan of the graptoloid clade; the uppermost part, in the earliest Devonian, is omitted from further analysis because species diversity is very low and analytical uncertainty becomes unacceptably large. For similar reasons, the basal 4 My of the clade history is not included in the analysis.

To test if extinction depends on species age, we use taxon survivorship of birth cohorts (23) (Fig. 1A) and AIC-based model selection (Figs. S1–S6). Birth cohorts are comprised of all species originating in a short interval of time; we use time bins of 0.25 million years, 0.5 million years, and 1 million years. A survivorship curve, produced by plotting the age of species in a cohort against the proportion of species still extant as the cohort decays over time, is exponential when the probability of extinction is uniform through the life of the cohort. In a semilog plot, this results in a linear distribution (3) (Fig. 1A, $\beta = 1$). Significant deviations from an exponential relationship indicate age dependency of extinction and yield curves in semilog space that are either convex up or concave up, which are approximated by Weibull distributions with shape parameters (β -values) greater than or less than unity, respectively (24). A concave-upward curve indicates a decreasing extinction probability with species age (Fig. 1A, $\beta < 1$). A convex-upward curve indicates increasing extinction probability with taxon age (Fig. 1A, $\beta > 1$). To produce Fig. 2C, on which each cohort is represented by a single point plotted at its β -value, we varied the cohort durations and start times in successive iterations using time bin durations of 0.25 million years, 0.5 million years, and 1 million years, and offsets of

bin start equal to one-fifth of the bin duration. This produces, in effect, a series of moving windows of different duration and boundary ages, and, for this reason, points shown are not statistically independent of each other. This approach, however, maps out patterns of survivorship that are robust to arbitrary variations in cohort size and start time, and robust results are indicated by clustering of points in the figure. In contrast, isolated points in the plot are idiosyncratic to a particular combination of bin duration and starting time, and are ignored during subsequent interpretation. Gaps in coverage indicate intervals where species richness is low and cohorts fail to meet the qualifying threshold of at least 20 taxa.

Results and Discussion

Graptoloid Extinction Rate Curve. The graptolite per lineage-million-years (Lmy) species-level extinction rate curve (Fig. 2B) fluctuates throughout the time series but nevertheless shows a step change that demarks two contrasting levels of intensity: (i) low amplitude and low median rate in the Floian to mid-Katian (“pK-Ordovician”) referred to as predominantly “background” extinction and (ii) a higher median rate with much greater variance in the late Katian to end-Silurian (“K-Silurian”), labeled “episodic” extinction. The transition between the two regimes is relatively sharp and takes place in the late Katian, when there was a coincident transition in global climate regime and in the marine carbon isotope ratios (25, 26). Following Cooper et al. (13), we treat these two parts of the extinction rate curve independently in setting threshold levels for identifying major extinction episodes. The threshold levels are somewhat arbitrary, and we have chosen the 75th percentile, equal to 0.72 species per Lmy in the pK-Ordovician and 1.46 species per Lmy in the K-Silurian (see Fig. 2). The graptolite extinction rate reached extreme levels of intensity (greater than 1.5 species per Lmy) repeatedly through the K-Silurian, including during the Late Ordovician Mass Extinction (LOME) (13, 27). These severe extinction episodes are interpreted to have been

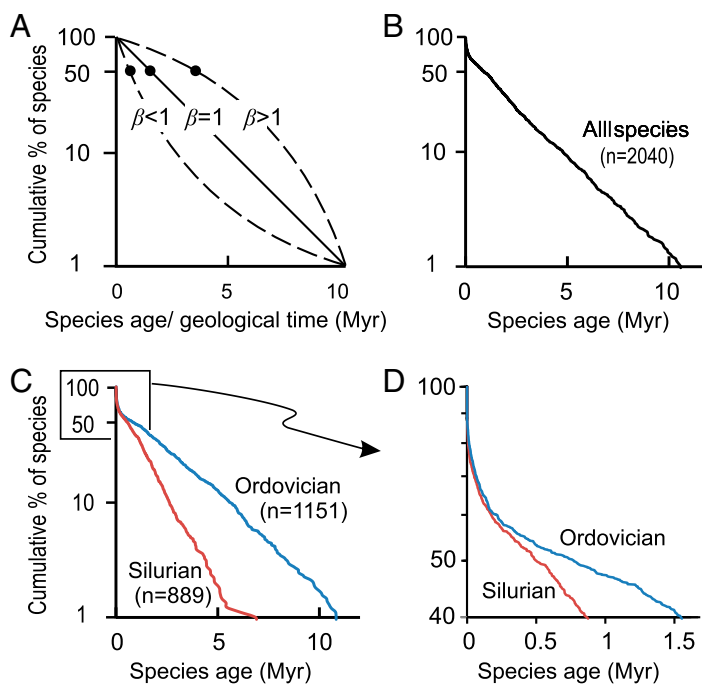


Fig. 1. (A) Semilog plot showing idealized taxon survivorship curves for a cohort commencing at 0 My; $\beta = 1$, linear survivorship curve indicating exponential decay rate (constant extinction probability); $\beta < 1$, decreasing decay rate, extinction probability decreases with taxon age; $\beta > 1$, increasing decay rate, extinction probability increases with taxon age. Black dots indicate median cohort age in each curve. (B–D) General age structure curves for all species (B) and for all Ordovician and all Silurian species (C and, detail, D). The life expectancy of a Silurian species is half that of an Ordovician species.

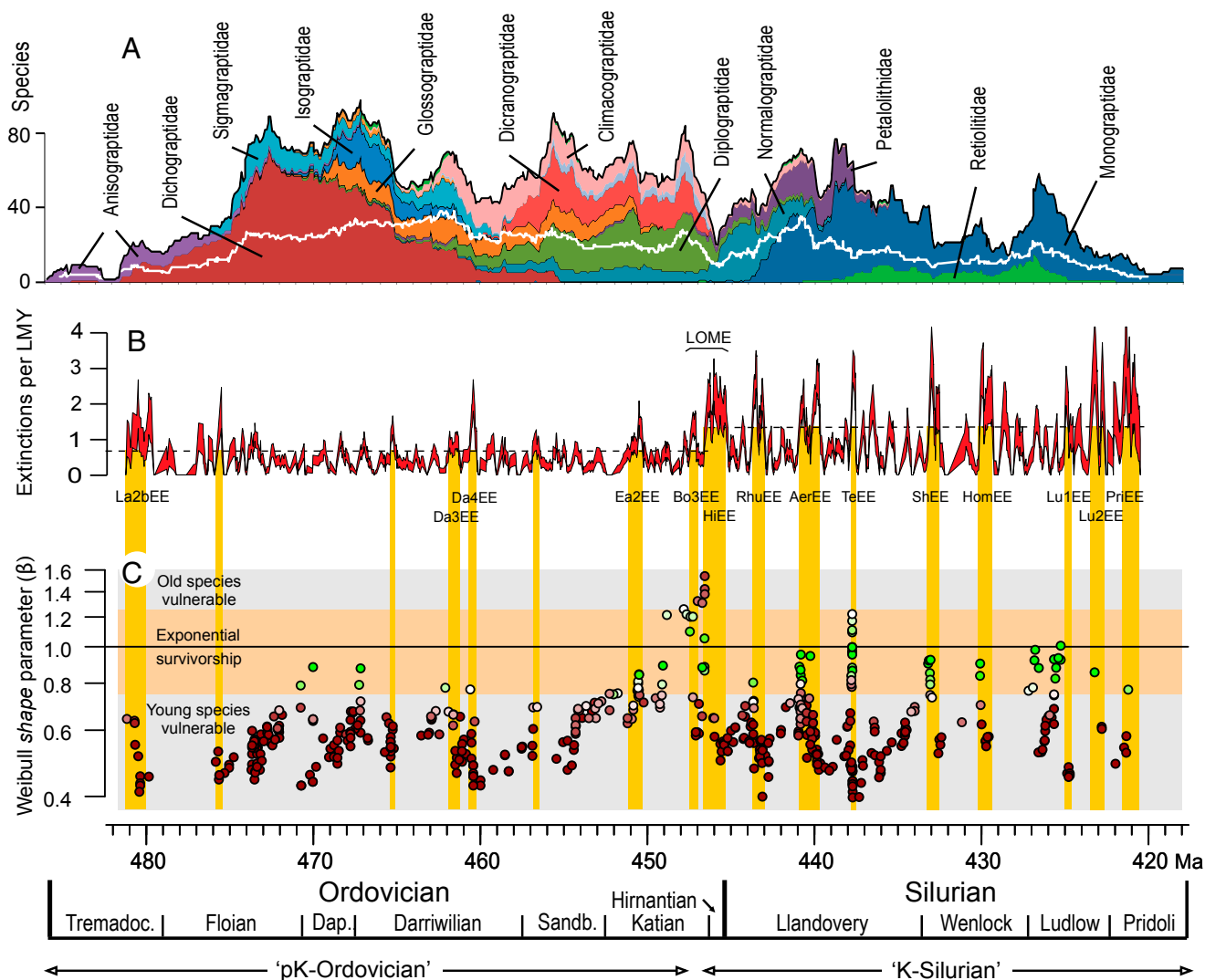


Fig. 2. (A) Graptoloid standing species richness, main families shown. The white line is level-by-level generic richness. (B) Extinction rate (extinctions per lineage-million-years), 0.25-My moving window, centered at each level in the composite. The band represents ± 1 SE from bootstrap means (1,000 iterations) of median values for each 0.25-My bin. The main extinction episodes, those exceeding the 75th percentile for each period (dashed lines) are: La2bEE, Lancafieldian 2; Da3EE, Darriwilian 3; Da4EE, Darriwilian 4; EaEE, Eastonian; BoEE, Bolindian; HiEE, Hirnantian; RhuEE, Rhuddanian; AerEE, Aeronian; ShEE, Sheinwoodian; HomEE, Homerian; Lu1EE, Ludfordian (early); Lu2EE, Ludfordian (late); and PriEE, Pridolian. (C) Weibull shape (β) value for each cohort survivorship curve is plotted at the median age, in geological time, of the last appearances of its constituent species. Red points, Weibull model preferred; green points, exponential model preferred; the darker the tone, the greater the AIC weight of the preferred model. Age bands with clusters of green points indicate fields with cohorts in which extinction is not dependent on species age; 498 points are shown.

triggered by abiotic, environmental perturbations of the graptolite ecosystem related to rapid changes in the marine climate (13, 28, 29). The link between Ordovician–Silurian evolutionary dynamics of the marine fauna and global climatic events is well supported (30–36), especially for the LOME and the Sheinwoodian climatic–evolutionary events and their accompanying perturbations in the carbon cycle. The clade survived these catastrophic extinction rates, among the highest recorded for any marine group (11), by virtue of the correlated, equally intense, spikes in origination rate (13); extinction otherwise would have been sufficient to almost extinguish the clade in less than a million years. The high species turnover rate reflects the exceptionally short median life span of a graptoloid species—0.89 My in the pK-Ordovician and 0.48 My in the K-Silurian. In comparison with other groups (means only are available), ammonites (~ 1 My) are comparable but planktonic foraminifera [6–9.5 My (37) or ~ 12 –15 My (11)] have much longer mean durations than graptoloids (0.65–1.00 My).

Birth Cohort Survivorship Analysis. The great majority of cohorts throughout the Ordovician and Silurian periods (423 out of 498 measured values) are best fit by Weibull distributions with $\beta < 1$, and most of these have $\beta < 0.75$. For these cohorts, extinction risk decreases with taxon age. Most cohorts with $\beta > 0.75$ are of Katian or younger age and are confined largely to very short time intervals with elevated extinction rate (Fig. 2). This pattern, combined with the contrast in extinction intensity described above, defines a distinctive extinction regime that distinguishes the K-Silurian from the pK-Ordovician. The probability of finding the observed correspondence of $\beta > 0.75$ with extinction episodes by chance is $\ll 0.001$ (one-tailed test based on randomizing the age of cohorts 10,000 times and calculating the proportion of cohorts with $\beta > 0.75$ that lie within our extinction episodes). For most of these cohorts with $\beta > 0.75$, an exponential fit is favored, except for a number of cohorts at ~ 447 Ma, for which a Weibull distribution with $\beta > 1.2$ is favored and extinction risk increases with taxon age.

The clustering of points indicates that the observed highly non-random distribution is robust to variations in both time bin duration and start time.

We further tested the robustness of our results as follows (details in *SI Text, Tests for Sensitivity and Bias in the Analyses* and *Tests for Bias in the Data* and Figs. S5 and S7). The analysis was repeated after removing the shortest-ranging species (12% of the total) and, again, after first combining the ranges of consecutive congeneric species for which the last appearance of one was coeval with the first appearance of the other; these tests showed that neither undersampling nor pseudoextinction are likely to influence the observed pattern significantly.

Patterns of survivorship revealed by our analyses are not detected at the genus level (Fig. S8A). The generally low β -values are recovered by species-level analyses at the temporal resolution of stages (average duration 4.6 My) and biostratigraphic zones (average duration 1.1 My), but the fine-scale structure visible in our results is entirely (stages) or largely (zones) invisible at these resolutions (*SI Text, Genus, Stage, and Zone Resolution Analyses* and Fig. S8B).

Discussion

From these results, we infer that the background mode of survivorship for graptoloid species was extinction risk that decreased with taxon age ($\beta < 0.75$). At any given time, extinction risk was higher for new species than for old species, reflected in the excess of short-lived species above the expectation of constant extinction (Fig. 1D). This applied during both times of relatively low background extinction rate in the pK-Ordovician and times of more volatile, but not peak, extinction rate in the K-Silurian. It also applied during times of adaptive radiation of the graptoloid clade, in the Floian Age, and refilling the same eospace in the Llandovery Epoch after the LOME diversity crash (13). A negative dependence of extinction on taxon age, previously reported in marine, mainly benthic, genera (5), is here shown to also apply to marine zooplanktic species. This finding points to the importance of abiotic factors in driving extinction; old species and genera tend to be more widely distributed and represented by more local populations, rendering them less susceptible to environmentally driven extinction (38–40), although Finnegan et al. (5) found that additional, unexplained, factors were involved for their data. Note that survivorship trajectories for short-lived taxa (taxon durations < 0.2 My) are identical in the pK-Ordovician and K-Silurian (Fig. 1D); the shorter median duration of K-Silurian taxa therefore results from fewer long-lived species than in the pK-Ordovician, rather than from a surfeit of short-lived species.

The age-independent fields represent brief excursions into selectively neutral territory ($0.75 < \beta < 1.3$), in which extinction risk was essentially random with respect to taxon age. They lie within, or close to, major graptoloid extinction episodes (Fig. 2) that previously have been linked to environmental changes (13, 29, 35). For this reason, it seems plausible that the age-independent fields resulted ultimately from abiotic processes rather than the kinds of biotic interactions that were initially proposed as part of Van Valen's (3) "Red Queen hypothesis" to help explain age-independent survivorship. Thus, during both background and episodic extinction, extrinsic, abiotic factors appear to be the primary drivers in graptoloid evolution.

An alternative interpretation of these neutral excursions during the K-Silurian is that they could reflect simply a quantitative consequence of the overall intensification of extinction (38). If this were the case, then we would expect to see a significant positive association between extinction rate and β during the K-Silurian, but, in fact, this relationship is negligible (Spearman rank-order correlation coefficient: $r_s = 0.071$; $P = 0.10$; see *SI Text*). Indeed, by eye, we see that there are many times of elevated extinction that are marked by vulnerability of young species. To further test this, we used logistic regression to characterize

the relationship between taxon age and survival within cohorts (cf ref. 5) and compared the slopes of these regressions to their corresponding extinction rates. Contrary to the idea that intensification of extinction itself weakens selectivity during the K-Silurian, the correlation between extinction rates and regression coefficients is small and nonsignificant (details in *SI Text*). We therefore conclude that the excursions to selectively neutral extinction during the K-Silurian, identified herein, cannot be explained as a simple consequence of elevated extinction intensity alone.

During the extreme perturbation of the LOME (447–445 Ma), β -values > 1.3 indicate positive dependence of extinction risk on taxon age: Old species became vulnerable to extinction and were selectively removed. The change in age selectivity mode suggests that, like the selectively neutral fields, the LOME did not result simply from scaled up background extinction (39, 41). The LOME marks the largest depletion in species diversity (77% loss) in the history of the clade and the complete, or near-complete, removal of many long-standing families, genera, and species, including the Diplograptidae, Climacograptidae, and Dicranograptidae (27, 28). It was associated with major positive excursions in the carbon isotope ($\delta^{13}\text{C}_{\text{carb}}$) ratio (25, 29, 42), global continental glaciation (43, 44), changes in oceanic circulation, water mass properties, and microphytoplankton populations (42, 45), and the deep-water graptoloid biotope was severely degraded or destroyed (13, 29). The main surviving group after the LOME, the cold-adapted normalograptids (46), diversified rapidly in the early Silurian, driving a rapid recovery in species richness of the clade. Our findings suggest that the LOME was a unique event that marks the transition to a new regime in which frequent extinction episodes disturbed the age structure of the entire clade, prevented the accumulation of long-lived species in the Silurian, and reduced the median species duration to half its Ordovician value (Fig. 2B). It is not clear whether the positive dependence of extinction risk on taxon age during the LOME indicates that a novel extinction mechanism was operating during this event or whether it represents simply an extreme expression of the processes operating during other severe extinction episodes. One possible mechanism for the high β -values is that when environmental change is severe and rapid enough, old species that were adapted to a previous environment become maladapted in the new environment, compared with newly evolving species, and are selectively removed (4).

The LOME caused an almost complete turnover in the graptoloid clade, raising the possibility that the contrast in extinction rate from Ordovician to Silurian might result from this turnover and be an intrinsic property of the taxonomic groups themselves rather than the result of extrinsic environmental factors. Only one family, the Normalograptidae, is represented by a significant number of species in both the Ordovician and Silurian. Interestingly, the median duration of an Ordovician normalograptid species (1.20 My) is significantly longer than that of a Silurian species (0.33 My; Mann Whitney-U, two tailed, $P = 0.02$). Therefore, the change in extinction regime takes place within a single family and suggests that the higher extinction probability of Silurian species is not due simply to changed taxonomic composition (updated from ref. 47).

Notably, the high temporal resolution of the present data set reveals that changes in age selectivity associated with extinction episodes were short lived and sharp (Fig. 2), and the graptoloid survivorship regime returned rapidly (within 0.5 My) to its background state after each extinction episode, even though diversity itself was much slower to recover (e.g., ~ 5 My in the case of the LOME).

Previous studies of taxonomic survivorship, which dominantly consider benthic marine genera and are resolved to time units of 7- to 11-My duration or longer, generally show extinction to be negatively age-dependent (i.e., $\beta < 1$) and negatively correlated with geographic range (5). The planktic foraminifera, in contrast, generally show taxon age to be positively related to extinction

$[\beta > 1$ (4, 24, 48, 49)]; Doran et al. (49) found, for the planktic foraminifera, significant positive age dependency of extinction in the long recovery periods following mass extinctions. The graptolites seem to show features of both these patterns. Through most of their history, extinction risk decreases with taxon age, as seen in the benthos. In contrast, during many extinction episodes, graptolite extinction probability is independent of taxon age. Extinction risk that increases with taxon age, as observed in the planktic foraminifera, is confined, in the graptolites, to a single short interval of extreme environmental stress (the LOME).

An outstanding question remains: Why is survival age-dependent? Presumably, the causal agent is a correlate of species age, such as increasing organismal fitness (which we cannot test) or some aspect of the “ecological footprint” of a species, such as geographic range, that is commonly observed to increase with species age (40 and references therein). To assess the possible role of geographic range, we assigned each species occurrence to an equal-area map cell of $\sim 5 \times 10^4$ km² and measured the geographic range of each species in each time interval (i.e., not aggregated over its lifetime) as the number of cells in which it is found. Given uncertainties with paleogeographic reconstructions, we based these assignments on present-day coordinates; because most species are confined to single paleocontinents, cell occupancy in paleocoordinates generally agrees well with that based on modern coordinates (50). We then carried out logistic regressions of survival with respect to range (see *SI Text*). Consistent with previous studies, range enhances survival; median regression coefficients are 0.26 ± 0.031 for the entire time series and 0.27 ± 0.036 for the K-Silurian. Selectivity with respect to range during the K-Silurian appears to be somewhat stronger with increasing extinction intensity (correlation between extinction rate and regression coefficient: $r_s = 0.28$; $P = 0.009$).

Importantly, although geographic range and age both predict survival, age is not merely a proxy for range. Range and age correlate positively but not very strongly (median r_s within intervals: 0.20 ± 0.019 for the entire time series; 0.10 ± 0.017 for the K-Silurian). Moreover, the effect of age on survival is virtually the same in a simple logistic regression as in a multiple logistic regression incorporating both age and range. The linear relationship between multiple (B_{mult}) and simple (B_{simp}) age coefficients is given by $B_{mult} = 0.94 B_{simp} - 0.034$ ($r^2 = 0.93$). Thus, species age evidently contributes to survival above and beyond its possible contribution to geographic range. The reason for this remains unresolved.

Conclusions

Our results suggest that, in planktic groups such as the graptolites, where species turnover rates and temporal and taxonomic

resolution are all high enough, age selectivity of extinction is seen to be tightly linked with, and highly responsive to, extinction episodes associated with severe changes in marine climate. We recognize three alternative, and qualitatively distinct, modes of selectivity: background extinction mode, where extinction rates are low and newly evolved species are most vulnerable; high extinction mode, where extinction rates are elevated and all species are equally vulnerable; and mass extinction mode, where extinction rates are extreme and old species are the most vulnerable. Graptoloids provide a sensitive indicator of marine environmental change and suggest that selective regimes in oceanic pelagic ecosystems switched rapidly from one mode to another and back again. The reversion to background evolutionary turnover rates and mode, following environmental perturbations, was rapid even in cases where the full ecosystem recovery took several million years. The distinctive dynamics revealed here suggest the existence of a threshold in the severity of environmental change in the marine environment below which young species of zooplankton were selectively removed and above which old species became increasingly vulnerable to extinction. This threshold was crossed repeatedly in the Late Ordovician to end-Silurian icehouse climate.

Methods

The CONOP analysis was performed using the software CONOP9, as reported elsewhere (10). The initial ordinal composite was scaled using mean rock thickness separating event levels in the local sections after all these sections had been rescaled to mitigate the effects of their different accumulation rates (for procedures and protocols, see ref. 10 and *SI Text*). The resultant scaled composite was then age-calibrated by means of 23 radiometrically dated volcanogenic beds that are present in local graptolite-bearing sections and integrated into the global graptolite composite. All subsequent analyses were undertaken in R (51). Survivorship analysis of successive birth cohorts used a maximum likelihood, model-fitting approach and the corrected Akaike Information Criterion (AICc; see ref. 52) for model selection. For each observed cohort distribution of species durations, we identified the best-fitting exponential and Weibull distributions, determined which of these two had the overall best fit to the data, and recorded the best-fit Weibull shape parameter (β). These analyses accounted for the fact that the exponential distribution is a special case of the Weibull, and used the method of Hirose to reduce bias in the maximum likelihood estimation of the Weibull β -parameter (53) (see *SI Text* for details).

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