Deviation from Red Queen behaviour at stratigraphic boundaries: evidence for directional recovery

N. A. DORAN[1], A. J. ARNOLD[1], W. C. PARKER[1] & F. W. HUFFER[2]

[1]*Department of Geology, 108 Carraway Building, Florida State University, Tallahassee, FL 32306-4100, USA*

[2]*Department of Statistics, 214 OSB, Florida State University, Tallahassee, FL 32306-4330, USA (e-mail: Doran@gly.fsu.edu)*

Abstract: Boundary-defining events influence the evolutionary behaviour of post-extinction survivors. The Cox proportional hazards model takes into account the varying background extinction rates characteristic of boundaries and enables survivorship analysis of post-boundary behaviour. Survivorship results from the Middle Cretaceous to recent planktonic foraminifera reveal two intriguing observations. First, they indicate significantly age-dependent extinction probabilities in populations of species following two boundaries: Cenomanian–Turonian (C–T) and Cretaceous–Tertiary (K–T); the survivors are short lived and show rapid turnover. Characteristics that might mediate this macroevolutionary behaviour are clearly distinct from those that precede the extinction. We hypothesize that the rapid taxonomic turnover during post-extinction macroevolutionary recovery is driven by the lingering expression of 'passport' characteristics, where the primary adaptive value was during the preceding extinction. Second, age-dependency of extinction oscillates through time. Many survivorship curves averaging long-term data have exponential or near-exponential form: suggesting a lack of age-dependence consistent with the Red Queen hypothesis. The boundary events discussed here, analysed in higher-resolution 15 Ma subsets, demonstrate perturbation of some post-extinction populations toward positive age-dependence, and are followed by long intervals suggestive of recovery. Red Queen behaviour, when measured over very long time-spans, appears to be the time-averaged result of these boundary-generated oscillations between short-term positive age-dependence and longer-term return to nearly age-independent Red Queen behaviour.

It is unavoidable that the characteristics which survivor species carry with them through a mass extinction must necessarily be the same characteristics that mediate recovery – a fact so simple as to be a truism were its implications not so far-reaching. The implications for our understanding of adaptation are particularly compelling. Adaptation is such an integral aspect of the evolutionary process that its role often goes unquestioned – so much so that it can be tempting to begin an evolutionary study with the *a priori* assumption that organisms' adaptations reflect a harmonious relationship with the environment in which we find them. However, the survivors of an extinction, although they may (fortuitously or otherwise) have 'passport' (the 'passport' concept was developed from earlier work of A. J. Arnold, but is named here for the first time) characteristics that allowed them to pass through an event, may not necessarily reflect optimal adaptation to the post-extinction setting in which these survivors find themselves. These survivor species may

even be less well adapted to the post-extinction world than their recently extinct relatives would have been had they survived. In this sense, a passport characteristic, like a true passport, may lose its utility once the boundary has been passed.

Extinctions and their causes have received a great deal of attention – far out of proportion to the brevity of the events that they record. Conversely, biotic recovery from extinction, although it can span tens of millions of years (Arnold *et al.* 1995*b*; Erwin 2001), receives far less attention than such long recovery times would invite. We might speculate that this is because the post-extinction biota is viewed as depauperate and therefore of diminished interest; but, whatever the reasons, it is important to remember that it is not the victims of extinction but the survivors that shape subsequent diversification.

It is sometimes held that opportunists pass through boundaries and eventually dominate the recovery biota. Studies on the K–T and E–C

events have suggested that recovery is a much more complicated issue. Extinction survivors may include a range of survival characteristics, including residence in protected habitats, broad adaptive ranges, dormancy, larval stages, and many others (Kauffman 1984; Keller 1986a, b, 1988, 1989a, b; Hansen et al. 1987; Hansen 1988; Kauffman & Walliser 1988; Harries et al. 1996; Jablonski 2002). One mechanism of survival involves intrinsic biological factors, such as a proclivity for rapid speciation based on factors related to population structure or generation time. Lineages that show rapid speciation may leave distinctive patterns of survivorship during their recovery.

A lingering question also relates to the magnitude of extinctions. Are mass extinctions distinct departures from normal background levels of diversity fluctuation, or are they simply the most extreme end members of a continuous distribution of diversity fluctuations, different in degree but not in kind? In other words, is there anything special about mass extinctions other than the fact that we notice them because of their magnitude? In spite of a great deal of discussion, the issue is still unresolved (e.g. Boyajian 1986, 1991; Jablonski 1986, 1989, 2001; Thackery 1990; Hubbard & Gilinsky 1992; Raup 1994; Kirchner & Weil 2000). Our results suggest that some boundary extinction events can be distinguished from background diversity fluctuations, but that the distinction is expressed most clearly by the nature of recovery rather than by the magnitude of the extinction itself.

The Red Queen Hypothesis is based on Van Valen's (1973) Law of Constant Extinction – a counterintuitive but widespread observation that species within ecologically homogeneous taxa tend not to increase (or decrease) their immunity to extinction through time; instead, taxonomic survivorship curves show a constant probability of extinction regardless of species longevity. This observation is judged to be counterintuitive because longer-lived species might be expected to have more time to adapt to the abiotic environment, thereby acquiring a resistance to extinction that their shorter-lived relatives cannot. To explain this observation, Van Valen advanced the Red Queen Hypothesis, which holds that ever-changing biotic interaction between species requires that they continually evolve to avoid extinction, and that species do not develop increased immunity from extinction, because the remainder of the biota is continually evolving in response. Thus, later members of a lineage may be adaptively superior to their ancestors, but their fitness (and species

survivorship) remains unchanged as they evolve to keep pace with an ever-shifting biotic setting. Hence, the Red Queen's comment about life on the other side of the looking glass: 'Now here, you see, it takes all the running you can do, to keep in the same place.' (Carroll 1872).

Unfortunately, to the extent that mass extinctions exert an anomalous influence on extinction patterns and later recovery, they also make survivorship analysis of extinctions more complex. The great variation in extinction rate through boundaries creates inhomogeneous populations that are difficult to compare through the analysis of simple survivorship curves. The simple exponential survivorship predicted under the Red Queen Hypothesis assumed populations undergoing stochastically similar rates of extinction (Van Valen 1973), an assumption that is not met in the vicinity of most extinction boundaries. More complex techniques of survivorship analysis are thus required to account for the temporal variation caused by perturbations associated with mass extinctions, and time-dependent variation in general (Pearson 1992).

Extinction events may also create even longer-term bias in survivorship analysis. Indeed, the lingering effects of extinction may characterize much of the interval between boundaries. Initially, the intent of this research was to model the survivorship of planktonic foraminifera over the last 145 Ma in order to explore patterns of age-dependence. Our results show that stratigraphic boundaries can play a central role in shaping patterns of macroevolutionary survivorship as well as recovery during the intervals between. We show this by applying the assumptions of the Red Queen Hypothesis across major extinction boundaries.

The data

To test boundary survivorship patterns, we will examine the fossil record of planktonic foraminifera. Planktonic foraminifera have an excellent fossil record, yet were nearly eliminated by the K–T boundary event. This distinctive history gives their recovery pattern particular clarity. Their precisely constrained stratigraphic ranges make them ideal candidates for survivorship analysis. Foraminiferal ranges are known to the level of morphospecies; in addition, much of their phylogeny is known from direct observation of transitions in the fossil record.

Longevity data for the Cenozoic Globigerinida were derived primarily from integration of works by Blow (1979), Kennett & Srinivasan (1983) and Bolli & Saunders (1985). The

Palaeogene foraminiferal history was further refined and developed from the Palaeogene Working Group: Berggren (1977), Boersma & Premoli Silva (1983), Toumarkine & Luterbacher (1985), Fordham (1986), Boersma et al. (1987), Premoli Silva & Boersma (1988), and Olsson et al. (1999). Species origination and extinction times are calibrated to the time scale of Berggren et al. (1995). Cretaceous data are derived from Postuma (1971), Robaszynski et al. (1984), Bolli et al. (1989), Hart (1990), Berggren and Norris (1997), BouDagher-Fadel et al. (1997) and Olsson et al. (1999). The stratigraphic resolution of the Cenozoic provides an excellent background for the study of planktonic foraminiferal survivorship. These data are expanded from the version used by Parker & Arnold (1997). In addition to the longevity data, the data also contain morphological information on all Cenozoic species, including landmark-based distance measures, angles, and parameters derived from measurements (e.g. Raupian parameters, principal component analysis).

The phylogenetic relationships were taken from the literature and are based primarily on the reports of stratigraphically preserved ancestor–descendant transitions and phylogenetic analyses. Because the survivorship study is based on individual species' longevities and is not dependent upon branching topology, phylogenetic relationships will not affect the analyses. However, because branching relationships among Palaeogene foraminifera have been thought to affect species ranges (Pearson 1998b), the authors are also working on a follow-up to this study to account for branching topologies.

Only the planktonic foraminifera currently provide the taxonomic and stratigraphic resolution necessary for a study such as this; nonetheless, some concerns must be addressed. One is that it is possible that specialists have divided lineages into operational taxonomic units that only approximate biological reality (Pearson 1992; Parker & Arnold 1997). This may result from 'pseudoextinction' and 'pseudospeciation' (Pearson 1998a); Pearson discussed this problem at length in the context of survivorship analysis (Pearson 1995, 1996, 1998b; McGowan et al. 1999). Since then, an additional problem has arisen regarding the classification of true biological species (in the sense of Mayr's Biological Species Concept). Classification of two or more true biological species under a single name can be the result of so-called 'cryptic' speciation. Cryptic speciation has become an increasingly common observation for many taxa, including planktonic foraminifera (de Vargas et al. 1999,

2001). Recent studies indicate that pelagic biodiversity in general may be greatly underestimated due to cryptic speciation (Norris 2000). For these reasons, and others, it should be stressed that we define all species in terms of the morphological species concept. These problems do not invalidate survivorship analysis, although some refinement of the analyses and their interpretation may become appropriate as issues such as cryptic speciation and pseudoextinction are clarified over time. This issue is further discussed below.

Cox survivorship analysis

Survivorship analysis has produced valuable palaeontological insights since the time of Simpson (1944), but has also been the subject of controversy. Application of the Epstein test to planktonic foraminifera indicated that they showed exponential patterns consistent with the Red Queen Hypothesis (Arnold 1982). The Total Life Method of Epstein verified the log linearity of survivorship and therefore lack of age-dependence (Epstein 1960a, b). Pearson (1992, 1995) later observed that temporally heterogeneous extinction rates affected survivorship analysis and ought to be taken into account. Taxa existing at different times could experience vastly different rates of extinction (e.g. those present at the K–T boundary v. an assemblage in the Middle Miocene). Thus, extinction rates in real time, or time-dependency of extinction, had to be separated from the issue of the longevity of the taxon, or age-dependency. Pearson proposed his Corrected Survivorship Score (CSS) to account for this distinction (Pearson 1992, 1995; McGowan et al. 1999). Analysis of survivorship near important geological boundaries is particularly problematic, because it is precisely at these boundaries that temporal variation in extinction becomes most pronounced.

Approaches to survivorship that account for time-dependency can also be found among the models used in failure time analysis (Kalbfleisch & Prentice 1980). Data that have an end point at the time an event occurs are called failure time data. Failure may be broadly defined to include any response pertinent to the field of study in question. Failure time data are distinguished by the presence of censoring; that is, for some individuals we only have partial information about the failure time. The most common type of censoring is right censoring; we know only that the survival time of an individual exceeds some given value, c. This happens in medical situations if a patient drops out of the study

before the event of interest (e.g. death) is observed, or if a patient survives beyond the end of the study period. For the purpose of this analysis, the taxon range is analogous to the survival of a patient, and extant species in the data-set are considered to be censored.

An alternative to the CSS for addressing survivorship across boundaries and eliminating the problem of time-dependence is the use of a proportional hazards model. Regression models of survivorship often assume a proportional hazard function. The non-parametric version of this model is the Cox proportional hazards model (Cox 1972; Lee 1980). The essence of the Cox model consists of a hazard rate calculated as a product of an arbitrary baseline hazard with an exponential function of the covariate. It takes the form:

$$h(t, z) = h_o(t) \ e^{\beta z}$$

where t represents geological time, $h_o(t)$ is the baseline hazard rate, β a regression parameter, and z a covariate of interest; in palaeontological analyses of species, z might be a morphological character (e.g. chamber number). This model might be applied to an entire population – say, all the planktonic foraminifera – with variations in the background extinction rate handled by the function of $h_o(t)$. The model is called a *proportional* hazards model because the ratio of the hazard functions for two individuals with different values, z_1 and z_2, of the covariate, turns out to be:

$$\frac{h(t, z_1)}{h(t, z_2)} = \frac{h_0(t) \ e^{\beta z_1}}{h_0(t) \ e^{\beta z_2}}$$
$$= e^{\beta(z_1 - z_2)}$$

which does not depend on time, that is, the hazard functions are proportional.

In order to examine age-dependence, our model must include species age as a covariate. Since the species age varies with time, we must slightly reformulate the Cox model as follows:

$$h(t, z(t)) = h_o(t) \ e^{\beta z(t)}$$

where t again represents geological time, $z(t)$ the species age at time t; for a species originating at time t_0, we have $z(t) = t - t_0$ for $t < t_0$. The arbitrary baseline hazard rate is again $h_o(t)$. The coefficient is now multiplied by $z(t)$, where species age is a function of time. With this form of the model we may ask questions about temporal variation in survivorship. This alteration of the model preserves and takes into account information about origination and extinction of foraminiferal species at their respective first appearance datums (FADs) and last appearance datums (LADs) within the context of geological time.

For the Cox model, when $z(t)$ is taken to be the species age, a non-zero value of the regression coefficient, β, indicates a relationship between species age and extinction rates. For positive β values, there is an increase in probability of extinction with increasing species range, or 'age'. Negative coefficients show the converse relationship. Naturally, a time-frame must be defined within which to examine survivorship behaviour. Examining short-term variation in survivorship requires that we balance the competing needs for stratigraphic resolution and statistical certainty. For this study, after experimenting with larger and smaller temporal windows, p-values and β coefficients were calculated for 15 Ma windows of time. Shorter and longer time-frames reflect a similar pattern (the authors are pursuing separate work optimizing this balance). The p-value is the probability of obtaining as large or larger a value of $|\hat{\beta}|$, the absolute value of the estimated coefficient, given that the true value β is 0. The β value and p-value plotted for that interval was considered to lie at the midpoint (or 7.5 Ma into the frame; Figs 1 & 2). The window was moved forward in time at 1 Ma intervals and recalculated.

Results

Sequential calculations of age-dependency for species which originate within 15 Ma time frames from the Middle Cretaceous to the present gives a continuously varying pattern punctuated by sudden shifts at critical boundaries. Figure 1 shows a significant shift in β values following the C–T and K–T events. The E–O event does not show the same pattern. Interestingly, p-values for the coefficient are highly significant following both the C–T and K–T events. The age-dependence in extinction lasts approximately 25 Ma after the K–T boundary. Following these extinctions, the β values appear to drop at a nearly constant rate; the drop takes place over a large portion of the Cenozoic, even sometimes dropping into negative values (Fig. 1). Also noticeable are smaller positive shifts in β at about 108, 72 and 27 million years that interrupt the steady declines from earlier high values.

It is known from previous work that age-dependence in planktonic foraminiferal survivorship is statistically significant for the Cen-
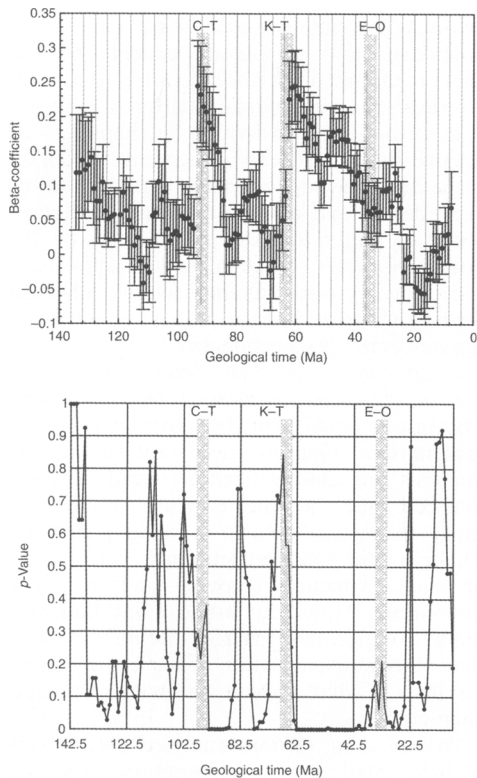
Fig. 1. Beta-coefficient (with standard error bars) and p-values for β by geological time for all species in the data-set. Positive β (top) indicates extinction probability increases as species age increases; negative coefficient indicates the reverse. The p-values (below) show strong significance following the C–T and K–T boundaries, although not the E–O.

Fig. 2. Beta-coefficient (with standard error bars) and p-values for β by geological time for all species in the data-set with ranges greater than 4 Ma. Eliminating shorter-ranged species removes much of the significance of the C–T and K–T events. In both figures, note the somewhat periodic nature of the coefficients and p-values.

ozoic planktonic foraminifera as a whole, and that the elimination of short-ranged species (less than 4 Ma duration) from the analysis causes the survivorship curve to revert to exponential form (Parker & Arnold 1997). Because of this, in Figure 2, only the age-dependence of species lasting 4 Ma or longer was assessed. Removal of the short-ranging species reduced the age-dependence effect following the C–T and K–T boundaries. However, the population immediately following the Jurassic–Cretaceous boundary shows significant age-dependence. The p-values in both analyses appear to exhibit a quasi-periodic spacing.

Discussion

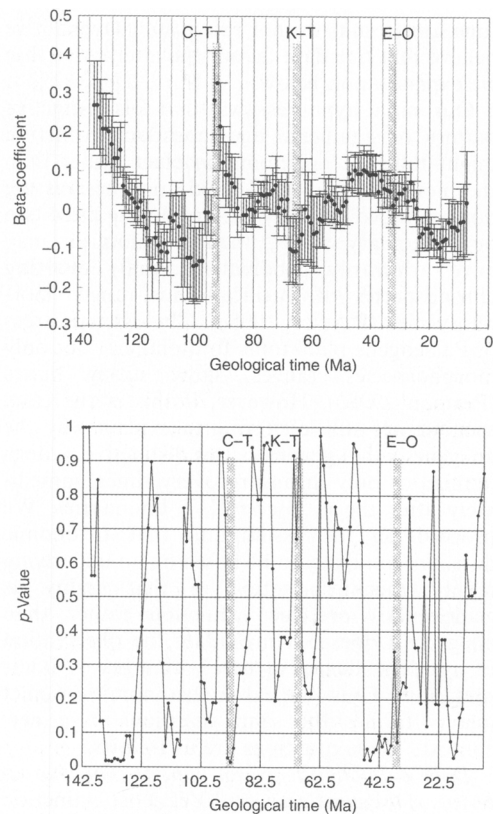Age-dependent extinction is indicated by non-zero β values, and means the probability of extinction increases (or decreases) as a function of species age. Through the Late Mesozoic and Cenozoic, age-dependence of extinction exhibits fluctuations through time; most of this fluctuation is in the direction of positive β indicating that the likelihood of extinction generally tends to increase (rather than decrease) with increasing age; however, we can only speak with confidence about time intervals in which the p-values are significant. The pronounced positive departures immediately following the C–T and K–T events (as demonstrated by simultaneously highly significant p-values and strongly positive β values) suggest that events at these boundaries increase the age-dependence effect. Moreover, the data indicate that short-ranged species are the cause of the age-dependence effect (Fig. 2). Because we cannot test the idea with our data, we have been cautious in giving consideration to the possibility of species senescence; at the same

time, our results do not rule it out. Overall, we believe that our data favour the alternative that we expand upon below.

Our initial hypothesis was that this distinctive pattern of significant age-dependent extinction might reflect a taxonomic artefact rather than the biological reality: if rapid anagenesis is the dominant evolutionary pattern during these two post-boundary times, then taxonomists may have arbitrarily subdivided rapidly evolving chronospecies into artificial short-ranged morphospecies (Pearson 1998*a*). Phylogenetic trees of Palaeogene planktonic foraminifera, not only morphospecies' ranges, show strong biases (Pearson 1998*b*). However, if this is the case, then we are still left trying to explain why the anagenesis that generates this distinctive pattern dominates only during recovery times immediately after the C–T and K–T boundaries. We proceed on the assumption that taxonomic decisions are likely to be based on an underlying reality; misinterpretation of that reality as cladogenesis or true extinction rather than anagenesis does not invalidate the observation of age-dependence, it merely changes its interpretation. Thus, appeal to taxonomic artefact merely frames the same questions in a new context. These questions are as follows.

Does extinction leave an imprint that characterizes subsequent recovery? Yes. Post-extinction age-dependence, now verified by two survivorship models (Parker & Arnold 1997 and herein) and an analysis of mean longevity (Arnold *et al.* 1995*b*) strongly suggest this. The change in species age structure is a signature that lingers for at least 15 Ma after the C–T boundary. Significant age-dependence lingers for about 25 Ma in the case of the K–T. Interestingly, molluscan gamma diversity took 25 Ma before this group showed full recovery after the K–T boundary (Hansen 1988). As with foraminifera, it appears that molluscan faunas spend much, if not most, of their time recovering from extinctions. A contrasting interpretation is that age-dependence is a taxonomic artefact. Pearson removed the age-dependence in post-K–T morphospecies longevities by analysing lineages (Pearson 1996); removal of pseudoextinction and pseudospeciation eliminated the effect. However, we must now ask why age-dependence arises after two extinction boundaries. If it is a result of taxonomic artefact in both instances, then why is this taxonomic artefact concentrated so significantly after extinction events?

Can mass extinctions be distinguished from background extinction? Our data suggest that some can, again, by their lingering age-dependence signature. The K–T extinction is both a profound extinction and a sharp stratigraphic boundary, and its age-dependent signature lingers for at least 20 Ma after the event. However, the Cenomanian–Turonian extinction is a second-order extinction, perhaps less distinctive than the Eocene–Oligocene (E–O), and yet it carries a post-boundary signature of age-dependence (and equivalent significance levels) for nearly half as long as the K–T, while the E–O boundary shows no age-dependent signal at all. This suggests to us that some feature other than the magnitude of the extinction is responsible for the observed age-dependency.

What can passport characters tell us about macroevolutionary recovery after boundaries? The results lend themselves to two immediate explanations. One is simply that the recovery intervals are characterized by rapid expansion into ecospace; the other is that a more complicated biological scenario is being played out. The first choice is the traditional understanding of mass extinction recovery and cannot be discounted. However, subtle clues indicate a more complicated macroevolutionary picture that reflects juvenilization of surviving lineages, resulting in what we here designate as 'passport characters'.

Arnold *et al.* (1995*a*) analysed the dynamics of how small planktonic foraminifera tend to survive extinction events. Size increase appears to reflect asymmetrical drift from small beginning size with asymmetry being introduced by a biological absorbing boundary at zero or very small size. Arnold *et al.* posit that this is the underlying cause of Cope's Rule. Cope's Rule holds that lineages tend to increase in mean size over time, making the size of the later descendants noticeably greater than that of the earlier species (such as those following mass extinctions). But this proposal simply frames the question in a new perspective: why are post-extinction survivors small? Arnold *et al.* (1995*a*) suggest that it is not because the Early Palaeocene world favours small size, rather because it was small-bodied species that preferentially survived the K–T and Eocene–Oligocene events and necessarily carried that character with them when they began the post-extinction recoveries. The authors suggest that small-bodied species, by virtue of their generally shorter generation times, should have a more rapid evolutionary response to selective pressure than their large-bodied relatives, a factor that not only explains the tendency of small-bodied species to weather mass extinctions, but is a possible explanation for Cope's Rule that is general enough to apply across the full taxonomic and ecological spectrum. They

indirectly supported this hypothesis with the observation that species destined to leave descendants form a significantly greater proportion of the small-bodied foraminiferal biota (as compared with the large-bodied biota) during times of crisis (Fig. 3). After the K–T and E–O extinctions the survivor species, in addition to their smaller mean size, show a globose morphology, an apparent preferential tendency toward pseudoextinction or cladogenesis (rather than true lineage termination) (Arnold *et al.* 1995*a*), and in the case of the post-K–T population, rapid turnover and significantly shorter mean species durations (Arnold *et al.* 1995*b*).

These interrelated features, although characterized as both microevolutionary (small size, globose morphology) and macroevolutionary (rapid turnover, preferential tendency toward cladogenesis/pseudoextinction among small-bodied species, and shorter durations), have one thing in common: the survivors of the K–T and their immediate descendants share them. We hypothesize that the rapid turnover (or the propensity for it) seen during the Early Palaeocene and after the C–T is, like small size at the organism level, a 'passport character' at the macroevolutionary level. That is, it is the continued expression of rapid turnover that one might expect in species that either:

(1) retain the evolutionary responsiveness to evolve through the rapidly changing conditions of a mass extinction; or

(2) share a propensity for such responsiveness (e.g. through paedomorphosis that emerges during extinctions).

The present finding of significant post-boundary age-dependent survivorship is consistent with this hypothesis.

A second insight that can be gained is in regard to the organismal and ecological characters that might drive rapid post-boundary turnover. Throughout most of the time that we cover, age-dependency is usually asymmetrical in the positive direction; that is, with increasing age species tend to show increasing probability of extinction rather than increasing immunity to extinction. Further, it is the short-lived species that explain (in a statistical, rather than a causal, sense) the age-dependency, and it is therefore these species that bear closer examination. Indeed, as noted by Arnold *et al.* (1995*b*; fig. 4) and in temporally expanded form in Figure 4 (herein), there are quasi-periodic windows during which short-lived species (those less than 4 Ma duration) apparently do not originate. Cox & Weibull's (Parker & Arnold 1997) model allows for removal of short-duration cases from the statistical population without compromising the results. When this is done, no age-dependent effect is observed in either Cox or Weibull analysis. Since trophic ecology and population structure have been strongly related to longevity for Palaeogene species (Norris 1992), its influence on speciation rates may point to the causal underpinnings of the post-boundary rapid turn-
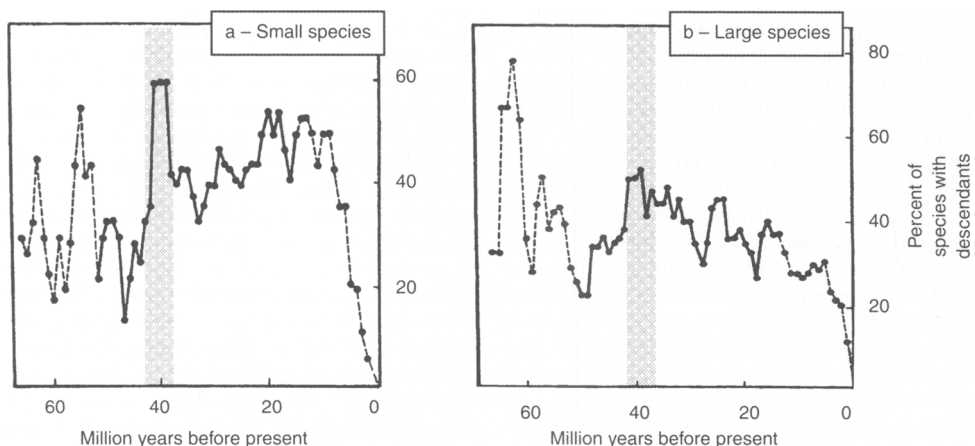

Fig. 3. Differential macroevolutionary characteristics of small ($< 300 \, \mu m$) versus large-bodied species during the E–O event. At the 38 Ma peak, note the significantly greater proportion of small species that leave descendants, as compared with that of large-bodied species. Dashed lines indicate where data are untrustworthy due to edge effects. Reproduced with permission of the *Journal of Paleontology*.
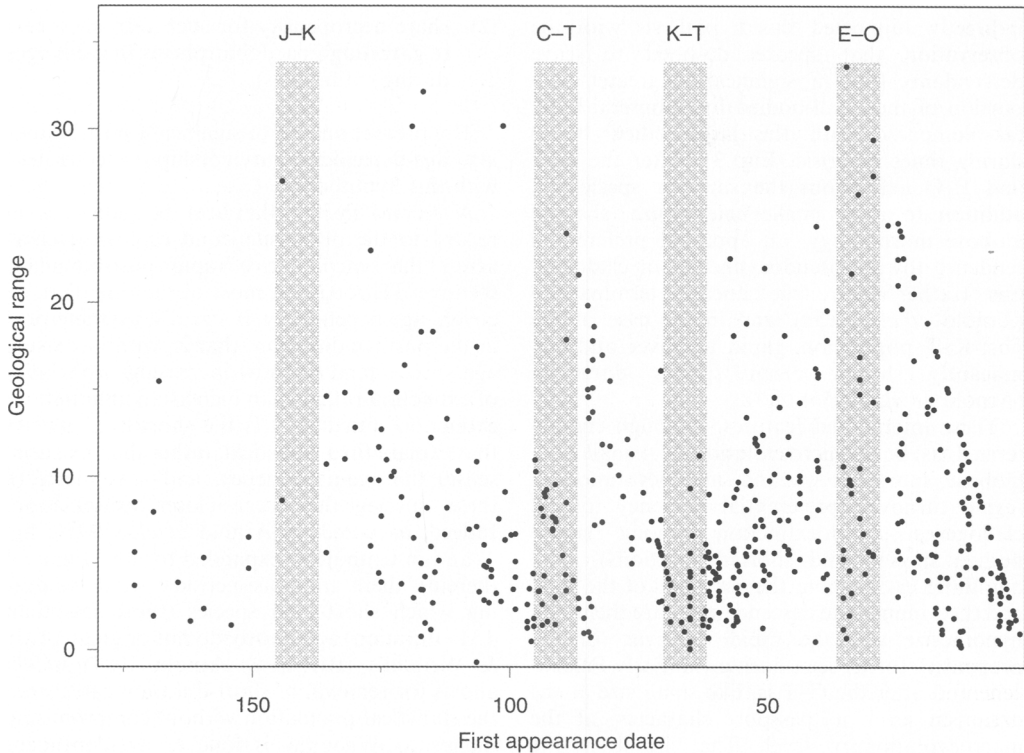
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Fig. 4. Comparison of times of origination versus species longevity. Absence of data in upper right part of the graph is an artefact of censorship at the recent (a similar effect is seen at the K–T). 'Gaps' in the origination distribution of short-ranged species (e.g. 18–36 and 45–52 Ma) indicate variations in age-dependent extinction. Cenozoic and Cretaceous short-ranged foraminifera species have had quasi-periodic absences. Note the absence of short-ranged species immediately prior to the K–T boundary and the large number immediately following. The major extinction boundaries, including the Jurassic–Cretaceous boundary (J–K), are marked in grey.

over and age-dependence. Shorter-ranged populations also display a number of morphological differences from their longer-ranged counterparts. The explanatory role of these characters is the subject of ongoing investigation by the present authors.

What does age-dependency imply with respect to the Red Queen Hypothesis? The Red Queen was initially invoked to explain the surprising failure of taxonomic survivorship curves to deviate from exponentiality in the negative direction, as would be predicted if long-lived species tended to develop extinction immunity by adaptation over their durations. The Red Queen Hypothesis holds that species are, in effect, constantly evolving to keep up with adaptive peaks that shift at random with respect to their ability to adapt.

Due to the changing hazard rates experienced by any taxon during its existence, a few preconditions should be added to the application of the Red Queen Hypothesis. These

preconditions must address whether hazard rates show significant temporal variation for the population in question. The original Red Queen concept assumed a stochastically constant underlying hazard rate; this assumption may be valid over shorter time-scales, with species populations experiencing identical extinction rates. However, over longer time-scales – with strongly variable extinction rates – background hazard rates must be taken into account (McGowan *et al.* 1999). Unfortunately, the Red Queen Hypothesis is usually envisioned in relation to an exponential survivorship curve. For periods that comprise homogeneous populations (with regard to extinction rates) this is appropriate. Therefore, with constant background hazard rates, the exponential model applies. But when discussing survivorship in the context of fluctuating background hazards, a more complex model needs to be employed, because species undergoing varying extinction rates would not yield a straightforward survivor-

ship curve. For this reason, in the context of changing background rates, it is better to think of the Red Queen Hypothesis as the *absence* of age-dependence in extinction, and the macro-evolutionary consequences devolving therefrom. This absence of age-dependence must be measured in the context of a survivorship model that accounts for temporal inhomogeneities of extinction.

The early expectation of the Red Queen Hypothesis was that extinction probability would decrease with increasing species age. This study shows that planktonic foraminifera, in fact, show preferential deviation in the opposite direction, primarily after mass extinction boundaries, followed by a gradational return to age independence consistent with the Red Queen Hypothesis. In a sense, one might suggest that immediately after the K–T the survivor species are still 'running' – not because they have momentum, but because it was the 'runners' that got through the K–T event. Their ability to speciate rapidly (or their anagenetic responsiveness) explains the post-event pattern of rapid turnover, shortened durations, and age-dependency, and is consistent with their small size.

'Step' v. 'spike' perturbations and extinction

We might envision the abiotic environmental changes that drive extinction as varying from 'spike perturbation' (in which abiotic conditions return to the pre-extinction state after the event) to 'step perturbation' (in which conditions remain changed; steps might vary in height and abruptness. The concept of step perturbation should be distinguished from that of stepwise extinction, which describes multiple steps in extinction response). There is evidence that the K–T extinctions were caused by an impact event (Alvarez *et al.* 1980 *inter alia*); this would be an excellent example of a spike perturbation in which conditions were altered dramatically for a short period, and then recovered. The C–T event was of a lower magnitude than the K–T, with only 27% of marine genera disappearing. Since deep-water foraminifera disappear first, an ocean anoxic event (OAE) has been a strong candidate for the extinction (Jarvis *et al.* 1988; Tur 1996). Interestingly, fluctuations in β values are reminiscent of Raup–Sepkoski periodicities recently affirmed in planktonic foraminifera through time-series analysis (Prokoph *et al.* 2000). In either scenario – an impact or a transient OAE – these extinctions might be characterized as 'spike' perturbations. We stress that although the mechanics of these extinctions

may have been vastly different, the recoveries appear similar and are the basis of our distinction.

In contrast to the K–T and C–T, the most generally accepted explanations for the E–O extinctions are related to the (step) development of the modern mode of thermohaline circulation, driven primarily by colder bottom-water masses. Of course there is a body of evidence suggesting that other factors might have influenced these events. The E–O boundary has a variety of additional scenarios, including several micro-tektite horizons, global deepening of the calcium carbonate compensation depth (CCD), and volcanism, in addition to long-term climatic changes (Kennett *et al.* 1985; Keller 1986*b*). It would be premature to suggest that the step/spike distinction explains our observed differing patterns in age-dependency, but its consistency leads us to draw attention to the possibility.

Conclusion

Cox survivorship analysis of the planktonic foraminifera indicates that events at the C–T and K–T boundaries caused significant age-dependent effects. This is in contrast to the expectations of the Red Queen Hypothesis, where extinction is postulated to occur randomly with respect to species age. Boundaries may therefore complicate our expectations under the Red Queen Hypothesis. Post-boundary populations show an increased probability of extinction with age, and this deviation remains significant for nearly 25 Ma in the case of the K–T boundary, and nearly half that time in the case of the C–T. During the post-boundary period of significant age-dependence, there appears to be a pattern of gradational return toward Red Queen survivorship behaviour (i.e. absence of age-dependence). Ironically, our results, in demonstrating significant but transient deviation from Red Queen behaviour, lend support to the Red Queen Hypothesis, because they suggest that Red Queen behaviour may express the 'normal' conditions to which the biota return after the perturbation of an extinction event. Coefficient values even appear to trend toward negative values – indicating greater resistance to extinction with increasing age. Interestingly, this perturbation and gradational return is not seen after the E–O extinction events.

These results imply that some mass extinctions may exhibit an age-dependency signature that distinguishes them from background diversity fluctuation. It has been unclear whether mass extinctions and background extinctions are end members of a continuous distribution of

extinction intensities. According to the Cox model, age-dependency fluctuates through time but appears strongly altered at some boundaries; it may be that post-extinction recovery behaviour provides an important, yet overlooked, signature that distinguishes mass from background extinction.

Since the Red Queen Hypothesis implies that on balance, biotic interaction dominates over abiotic factors in controlling species survivorship, it may follow that the extinction-driven departures from exponential Red Queen behaviour reported herein may signal a shift in the balance from biotic interaction to transient abiotic control of survivorship patterns immediately after some extinctions.

Our results further suggest that Jablonski (1986) may be right in his suggestion that extinction is the most important factor in evolution. The planktonic foraminifera appear to have spent a significant part of their history recovering from the effects of extinction, and much of their macroevolutionary behaviour during recovery seems to be influenced as much by the characteristics that survivors carry through extinction events as by the environments that they encounter during post-extinction times.

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