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Extinction in the Marine Bivalvia

Paul G. Harnik and Rowan Lockwood

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PART N, REVISED, VOLUME 1, CHAPTER 24: EXTINCTION IN THE MARINE BIVALVIA

Paul G. Harnik and Rowan Lockwood

[Department of Geological and Environmental Sciences, Stanford University, paulharnik@gmail.com; and Department of Geology, The College of William and Mary, rxlock@wm.edu]

Bivalves are diverse and abundant constituents of modern marine faunas, and they have a rich fossil record that spans the Phanerozoic (Hallam & Miller, 1988; McRoberts, 2001; Fraiser & Bottjer, 2007). Due to the high quality of their fossil record, they are well suited for investigating patterns of biodiversity change and the processes that generate these patterns. Extinction and its influence on patterns of diversification in the Bivalvia have figured prominently in a number of previous studies. Did bivalves diversify exponentially over geologic time with little long-term influence of mass extinction events (Stanley, 1975, 1977), or were catastrophic extinction events critical in shaping their dramatic post-Paleozoic radiation (Gould & Calloway, 1980)? Extinction is an important process in the evolutionary history of many clades. Selective or chance survivorship can shape morphological, ecological, and phylogenetic diversity and disparity (Roy & Foote, 1997; Jablonski, 2005; Erwin, 2008). Extinction selectivity can also affect the susceptibility of lineages to later periods of environmental change (Stanley, 1990a; Jackson, 1995; Jablonski, 2001; Roy, Hunt, & Jablonski, 2009). In addition, extinction can open up opportunities for diversification through the removal of incumbent taxa (Walker & Valentine, 1984; Rosenzweig & McCord, 1991; Bambach, Knoll, & Sepkoski, 2002; Jablonski, 2008b). Understanding how and why some organisms, including many bivalves, and not others became extinct in the past may prove useful in predicting the response of modern marine ecosystems to environmental change (Dietl & Flessa, 2009).

Here we briefly review those features of the bivalve fossil record that make it particularly suitable for investigating diversity dynamics over geologic time. We then introduce recently developed analytical methods for estimating rates of extinction and origination from paleontological data that account for temporal variation in the quality of the preserved and sampled fossil record. Applying these methods to data for marine bivalves, we present a new analysis of extinction, origination, and preservation rates for bivalve genera over the Phanerozoic and examine the effect of extinction rate on subsequent origination rate. We review the growing literature on extinction risk in fossil marine bivalves and summarize the roles of several biological factors that have proven important in predicting survivorship over geologic time. Although recent and historical extinction in freshwater mussels has been well studied (Williams & others, 1993; Ricciardi & Rasmussen, 1999; Lydeard & others, 2004; Strayer & others, 2004; Bogan, 2006), we focus on marine bivalves due to the quality of their fossil record over long time scales and the general congruence between phylogenetic hypotheses and morphologic taxonomies (Jablonski & Finarelli, 2009).

MARINE BIVALVES AS A MODEL SYSTEM FOR ECOLOGICAL AND EVOLUTIONARY ANALYSIS

The marine bivalve fossil record has been studied intensively by paleontologists and malacologists for centuries. This body of work has produced a detailed picture of the history of the clade and has advanced our general understanding of the processes that generate and maintain biodiversity in marine systems over time. Data for fossil bivalves

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have been instrumental in informing debates concerning the roles of biological factors in extinction risk (e.g., Stanley, 1986a; Raup & Jablonski, 1993; Jablonski, 2005; Rivadeneira & Marquet, 2007; Crampton & others, 2010), the tempo and mode of evolutionary change (e.g., Kelley, 1983; Geary, 1987; Roopnarine, 1995), the processes underlying geographic gradients in diversity (e.g., Roy & others, 1998; Crame, 2002; Vermeij, 2005; Jablonski, Roy, & Valentine, 2006), and the role of predation in evolutionary trends (e.g., Stanley, 1986b; Kelley, 1989; Dietl & others, 2002). This depth of study is due in part to the high preservation potential of bivalve shells in shallow marine environments.

Marine bivalves are not free from the taphonomic insults experienced by other marine invertebrate taxa, but their fossil record is relatively complete (Valentine, 1989; Foote & Raup, 1996; Harper, 1998; Foote & Sepkoski, 1999; Kidwell, 2005; Valentine & others, 2006), and the taphonomic biases that affect this record are increasingly well understood (Cooper & others, 2006; Valentine & others, 2006). Taxa that have readily soluble shell microstructures, are small-bodied or thin-shelled, geographically restricted, commensal or parasitic, epifaunal, and/or occur in deeper water are less likely to be preserved and sampled (Cooper & others, 2006; Valentine & others, 2006). Yet, the probability of being preserved and sampled is relatively high for bivalves living at shelf to intertidal depths. Approximately 75% of all living genera and subgenera of shallow marine bivalves are also known from the fossil record (Valentine & others, 2006). Although postmortem dissolution of primary shell aragonite has resulted in considerable loss of molluscan skeletal material from the rock record (Cherns & Wright, 2000, 2009), this taphonomic filter does not appear to have biased macroevolutionary patterns inferred from fossil mollusks (Kidwell, 2005).

Recent studies have shown significant agreement between ecological metrics calculated for molluscan death assemblages and the living communities from which they are derived (Kidwell, 2001, 2002, 2005; Lockwood & Chastant, 2006; Valentine & others, 2006). Notably, instances in which the ecological agreement between life and death assemblages is poor tend to be associated with sites affected by recent and pronounced anthropogenic environmental change (e.g., eutrophication and benthic trawling), and not postmortem shell loss (Kidwell, 2007). These taphonomic analyses provide a foundation for examining ecological shifts in the Bivalvia over geologic time as well as the susceptibility of bivalve taxa with particular traits to extinction.

ESTIMATING EXTINCTION AND ORIGINATION FROM INCOMPLETE DATA

Accurately estimating extinction and origination rates is challenging for all taxa, due to incomplete observations. In paleontological studies, the observed stratigraphic distribution of fossil occurrences is affected by preservation and sampling, leading to temporal offsets between a taxon's true time of origination and extinction and its observed first and last occurrences (Signor & Lipps, 1982; Marshall, 1990; Meldahl, 1990; Foote, 2000; Holland & Patzkowsky, 2002; Foote, 2003). Preservation and sampling are biased by a number of factors, including the rarity and body size of taxa, as well as the overall quality and quantity (completeness) of the fossil record. The completeness of the fossil record varies systematically through time with tectonic and/or climatic factors (e.g., Smith, Gale, & Monks, 2001; Crampton, Foote, Beu, Cooper, & others, 2006; S. Peters, 2006). It is also affected by the abundance of unlithified versus lithified sediments (Hendy, 2009; Sessa, Patzkowsky, & Bralower, 2009). Extinctions that occur during intervals of poor preservation and sampling appear to happen earlier in time (back-smearing), whereas originations in those same intervals appear to happen later in time (forward-smearing). This problem is not unique to studies of the fossil record, but rather it presents a general challenge to any attempt to estimate extinction (or origination) from limited observations (SOLOW, 1993, 2005; RIVADENEIRA, HUNT, & ROY, 2009).

The degree of discordance between the timing of true extinction and origination and the observed stratigraphic ranges of taxa depends on temporal variation in preservation and sampling. Accounting for such variation can be critical in reconstructing diversity dynamics over geologic time. Multiple approaches have been developed to account for variable preservation and sampling in paleontological studies. The choice of method depends on the specific question being addressed and the spatiotemporal scale of sampling. For example, at local or regional scales, datasets may be partitioned to examine only samples collected from comparable taphonomic or stratigraphic contexts (e.g., SCARPONI & KOWALEWSKI, 2007; N. HEIM, 2009). At the global scale, two general approaches have been taken to account for temporal variation in the completeness of the known fossil record: occurrence-based approaches that rely on sub- or replicate-sampling methods, such as rarefaction (e.g., ALROY & others, 2001; BUSH, MARKEY, & MARSHALL, 2004; ALROY & others, 2008) and capture-mark-recapture (e.g., CONNOLLY & MILLER, 2002; LIOW & others, 2008), and modeling approaches that estimate rates of extinction, origination, and preservation simultaneously from the observed paleontological data (FOOTE, 2000, 2003, 2005). Preservation rate in this last approach describes jointly the probability of preservation and sampling over time.

MARINE BIVALVE EXTINCTION AND ORIGINATION DYNAMICS THROUGH THE PHANEROZOIC

Here we estimate extinction, origination, and preservation rates simultaneously for marine bivalve genera through the Phanerozoic using a likelihood-based modeling approach developed by FOOTE (2003, 2005). This approach uses numerical optimization to identify the time series of extinction, origination, and preservation rates most likely to have generated the observed data (i.e., the matrices of forward and backward survivorship frequencies calculated from the observed temporal distribution of first and last occurrences of genera) under a given model of evolution and preservation. Our analysis of bivalve diversity dynamics differs from previous studies (e.g., STANLEY, 1977; GOULD & CALLOWAY, 1980; KRUG, JABLONSKI, & VALENTINE, 2009), in that completeness of the preserved and sampled fossil record is explicitly taken into account in estimating evolutionary rates. Our analysis also focuses on rates of extinction and origination rather than diversification rate or standing diversity (cf. STANLEY, 1977; GOULD & CALLOWAY, 1980; MILLER & SEPKOSKI, 1988).

We use a global compilation of observed first and last occurrences of marine bivalve genera for rate estimation (SEPKOSKI, 2002). Data for the 2861 bivalve genera in SEPKOSKI's *Compendium of Fossil Marine Animal Genera* (2002) were compiled primarily from the first *Treatise on Invertebrate Paleontology* devoted to the Bivalvia (COX & others, 1969; STENZEL, 1971); data for the revised *Treatise* are as yet unavailable. The Paleobiology Database (ALROY & others, 2001, 2008)—a global compilation of spatial and temporal occurrences of fossil taxa through the Phanerozoic—is another dataset that could have been used to investigate bivalve evolutionary rates. Although occurrence-based data can also be analyzed in such a way as to account for variable sampling and preservation (see above), we chose to analyze SEPKOSKI's *Compendium* of first and last occurrences to provide a benchmark against which analysis of data from the revised *Treatise* could be compared in the future. While we are eager to see how results differ following the taxonomic revisions anticipated in the revised *Treatise*, we do not expect substantial changes. Studies conducted at comparably broad spatial, temporal, and taxonomic scales have shown that taxonomic errors tend to be randomly distributed and overall macroevolutionary patterns are surprisingly robust (Adrain & Westrop, 2000; Ausich & Peters, 2005; Wagner & others, 2007).

Rates of extinction, origination, and preservation for marine bivalve genera were estimated for 71 time intervals that correspond roughly to geologic stages. Data for some stages were combined to minimize temporal variation in interval duration (median interval duration = 6.4 million years; interquartile range, 4.4 to 10.2 million years). Extinction and origination rates were calculated assuming a pulsed model of taxonomic turnover in which originations cluster at the start of each interval and extinctions at the end of each interval (Foote, 2003, 2005). Under this model, extinction rate equals the number of genera last appearing in an interval divided by the total diversity of the interval; origination rate equals the number of new genera in an interval divided by the number present at the start of the interval; and preservation rate equals the estimated probability of being preserved and sampled per genus per interval; see Foote (2003) for additional methodological details. We have also examined extinction and origination rates generated under an alternative evolutionary model in which taxonomic turnover occurs continuously (Foote, 2003). These models—pulsed versus continuous turnover—both identify peaks in origination and extinction rates for marine bivalves through the Phanerozoic, but the magnitudes and timing of the peaks differ somewhat. We restrict our discussion to the results of the pulsed turnover model, as this model has greater support globally (Foote, 2005) and regionally (Crampton, Foote, Beu, Maxwell, & others, 2006), and also has the advantage of incorporating all genera, including those confined to a single stage, in the estimation of all three rates (Foote, 2003).

Rates of extinction, origination, and preservation estimated for marine bivalve genera through the Phanerozoic are presented in Figure 1. Rates of preservation vary considerably over time, spanning nearly the full range from zero to one, with a median rate equal to 0.33. The median rate of preservation for bivalves in this analysis is lower than previous estimates (Foote & Sepkoski, 1999; Valentine & others, 2006). This moderate rate of preservation overall, combined with its volatility over time, underscores the importance of accounting for temporal variation in the completeness of the fossil record when estimating extinction and origination rates.

In general, bivalves exhibit moderate rates of extinction and origination through the Phanerozoic (median rate of extinction = 0.1; median rate of origination = 0.2), with rare intervals of elevated rates (Fig. 1). Prominent peaks in extinction occurred during the late Cambrian, end-Ordovician, Late Devonian, end-Permian, end-Triassic, and end-Cretaceous, all times of elevated extinction observed at much broader taxonomic scales (Foote, 2003). These extinction peaks have previously been observed in studies of the fossil record that assume perfect preservation, but it is noteworthy that they remain after accounting for the dramatic temporal variation observed in preservation rate.

A secular decline in bivalve extinction and origination rates over the Phanerozoic is observed; the Spearman rank order correlation between extinction and origination rate and time is 0.26 and 0.25, respectively (p-value < 0.05 for both correlation tests). The Phanerozoic-scale decline in rates of extinction and origination has also been observed at broader taxonomic scales (Raup & Sepkoski, 1982; Van Valen, 1984; Foote, 2003) and may result from the loss of extinction-prone lineages over time (Roy, Hunt, & Jablonski, 2009), although other mechanisms have also been proposed (Alroy, 2008 and references therein). Differing taxonomic practice could potentially contribute to the observed temporal variation in bivalve rates of taxonomic extinction and origination.

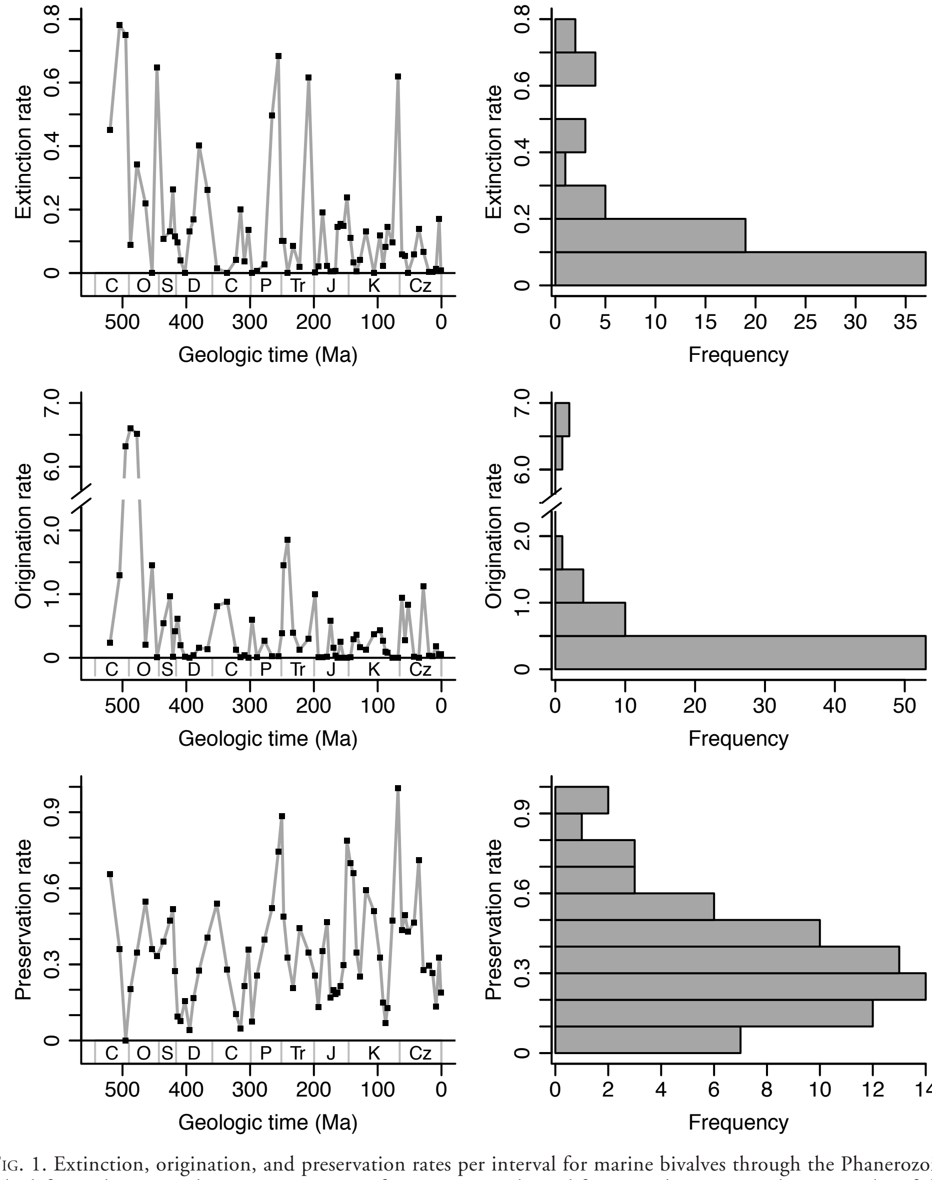

FIG. 1. Extinction, origination, and preservation rates per interval for marine bivalves through the Phanerozoic. The left panel presents the mean time series of rate estimates derived from 100 bootstrap replicate samples of the observed data. The right panel presents the frequency distribution of rate magnitudes. Extinction and origination rates were estimated assuming a pulsed model of taxonomic turnover. Under this model, extinction rate equals the number of genera last appearing in an interval divided by the total diversity of the interval, origination rate equals the number of new genera in an interval divided by the number present at the start of an interval, and preservation rate is the estimated probability of preservation per genus per interval (new).

However, previous studies conducted at comparable scales have generally found taxonomic errors to be randomly distributed (ADRAIN & WESTROP, 2000; WAGNER & others, 2007), and there is little reason to expect rates of pseudoextinction and pseudoorigination to decline toward the present day.

To identify peaks of extinction that stand out substantially above the baseline rate for

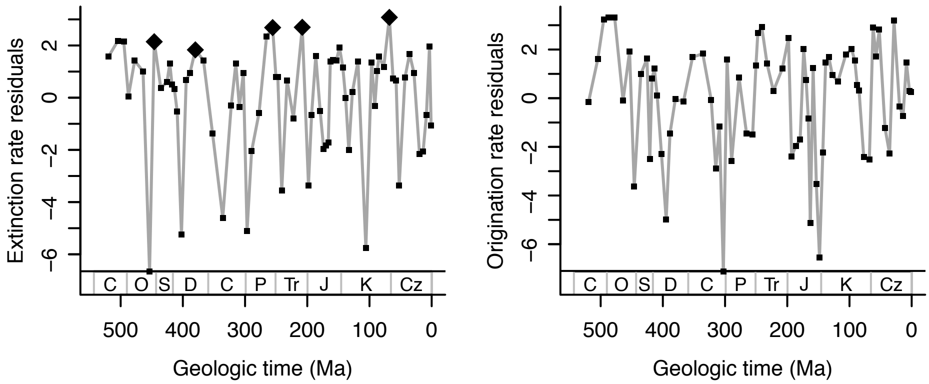

FIG. 2. Residual variation in extinction and origination rates remaining after removing the secular decline in both rates through the Phanerozoic using linear regression. The so-called Big Five mass extinctions recognized in marine invertebrates are denoted with *large black diamonds* (new).

the portion of the Phanerozoic in which they occur, the long-term secular trend in both evolutionary rates was removed by fitting a linear regression to the natural logarithm of evolutionary rate against time (ALROY, 2008). When the residual variation in extinction rate is considered, the late Cambrian, end-Permian, end-Triassic, and end-Cretaceous are times at which extinction was particularly severe for marine bivalves (Fig. 2). Depending on the cut-off value used to define a severe extinction, the Eocene–Oligocene and Plio–Pleistocene are also noteworthy. This is consistent with previous studies that have documented substantial molluscan extinction, at least regionally, during these times (e.g., RAFFI, STANLEY, & MARASTI, 1985; STANLEY, 1986a; ALLMON & others, 1993; PROTHERO, IVANY, & NESBITT, 2002; DOCKERY & LOZOUET, 2003; HANSEN, KELLEY, & HAASL, 2004).

Global patterns such as these emerge as the sum of processes of extinction and origination operating at finer spatial scales. Processes of extinction and recovery are biogeographically complex. There are currently insufficient data to address spatial variation in extinction and recovery in any detail for many events. Intervals in which extinction triggers are both pronounced and widespread should result in greater congruence between patterns of taxonomic turnover at global and regional scales, but such large events are relatively uncommon in the history of life. The end-Cretaceous (K/Pg, formerly K/T) mass extinction and recovery is one example of a large-scale event in which the biogeographic fabric of diversity loss and rebound has received detailed study. At this time, regions differed little in the severity of extinction experienced by marine bivalves, but markedly in the timing and process of recovery (RAUP & JABLONSKI, 1993; JABLONSKI, 1998). Examples of more biogeographically differentiated intervals of extinction and recovery for marine bivalves include the Triassic–Jurassic (e.g., HALLAM, 1981; ABERHAN, 2002) and Plio–Pleistocene (e.g., RAFFI, STANLEY, & MARASTI, 1985; STANLEY, 1986a; ALLMON & others, 1993; TODD & others, 2002), among others.

DIVERSITY-DEPENDENT DYNAMICS IN THE MARINE BIVALVIA THROUGH THE PHANEROZOIC

Over their history, marine bivalves have experienced periods of elevated extinction and origination, as well as periods of relative evolutionary quiescence (Fig. 1). To what extent have the dynamics of extinction and origination been coupled over time? Extinction may facilitate origination through the removal of incumbent taxa and opening up of ecospace. Understanding whether extinction and origination rates operate in a diversity-dependent fashion has important implications for our understanding of the role of biotic interactions in diversification (Sepkoski, 1978; Miller & Sepkoski, 1988; Kirchner & Weil, 2000a, 2000b; Erwin, 2001; Lu, Yogo, & Marshall, 2006; Alroy, 2008; Jablonski, 2008a). If diversity-dependent dynamics have been important for marine bivalves through the Phanerozoic, then times of limited extinction should have been followed by times of limited origination, and times of elevated extinction by times of elevated origination. Whether the response of origination to extinction was immediate or lagged by some period of time depends on the nature of the recovery process. If extinction empties niches, then origination may respond rapidly to new ecological and evolutionary opportunity. However, if niches depend in part upon diversity and need to be reconstructed following major perturbations, then temporal lags between extinction and origination peaks are to be expected.

Pseudoextinction—the apparent evolutionary turnover of taxa resulting from anagenetic morphological evolution and/or variation in taxonomic practice—could also contribute to a positive relationship between extinction and subsequent origination, if rates of pseudoextinction are elevated over some intervals relative to others. If true, this is not necessarily less significant, as pseudoextinction presumably reflects some amount of morphological change. Thus, temporal variation in rates of pseudoextinction could offer insight into the evolutionary response of taxa to changes in the biotic and abiotic environment. In practice, pseudoextinction is probably not a major factor governing the variation we observe in rates of extinction and origination—as well as their association—over the Phanerozoic history of marine bivalves. Previous studies conducted at comparable spatial, temporal, and taxonomic scales that have compared taxonomically standardized data with data aggregated from the literature without taxonomic standardization have generally found taxonomic errors to be randomly distributed (Adrain & Westrop, 2000; Wagner & others, 2007), and rate estimates, as a result, to be affected little by the process of taxonomic standardization (Wagner & others, 2007; but see Ausich & Peters, 2005). Anagenesis within genera cannot be fully accounted for until a comprehensive genus-level phylogenetic framework exists for the Bivalvia.

To determine whether evolutionary rates were diversity-dependent among marine bivalves through the Phanerozoic, we examined the variation in rates of extinction and origination that remains following the removal of the long-term secular decline in rates noted above. The effect of extinction on origination was evaluated using the slope of a linear regression model relating the rate of extinction in an interval (t) to the rate of origination in the next interval (t + 1). We evaluated the support for an effect of extinction on subsequent origination by assessing whether the observed regression slope was significantly greater than zero, and whether it differed from that expected solely by chance via a permutation test. The distribution of null values against which the observed slope was compared was generated by randomly shuffling the detrended rates of extinction and origination and calculating the slope of the extinction versus origination relationship, and repeating this procedure 10,000 times.

A significant positive relationship is observed, such that periods of elevated extinction are followed by elevated origination, and periods of moderate extinction are followed by moderate origination (Fig. 3; Table 1). The results of the permutation test also indicate that the observed relationship between extinction rate and subsequent origination rate among marine bivalves is significantly greater than expected by chance (Fig. 4). There is no indication of a lag in the response of origination to extinction; rather, origination responds immediately in

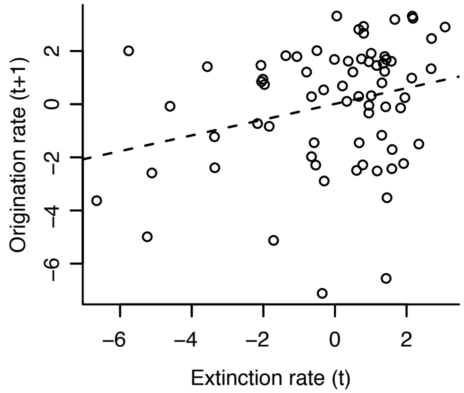

FIG. 3. The effect of extinction on origination for marine bivalve genera through the Phanerozoic. Plotted are the rates of extinction in each interval (t) against origination in the next interval (t + 1). Rates were logarithmically transformed and detrended prior to analysis; details provided in text. The dashed line is a linear regression model fitted to the extinction-origination relationship. A statistically significant positive relationship is observed, indicating that diversity-dependent processes have operated over the evolutionary history of the Bivalvia (new).

TABLE 1. Effect of extinction on origination for marine bivalve genera through the Phanerozoic. Effect was measured as the slope of the linear regression of extinction rate in an interval (t) on origination rate in the next interval (t + 1). Rates were detrended prior to analysis; details provided in text. A significant positive relationship is observed; intervals of elevated extinction are followed by intervals of elevated origination, and intervals of moderate extinction followed by intervals of moderate origination. This diversity-dependent relationship between extinction and origination is not driven simply by mass extinctions and their associated recovery intervals. Excluding intervals characterized by elevated extinction (e.g., the top 5% of extinctions, top 10%) does not markedly weaken the overall relationship (new).

Data	Effect	p-value
All	0.3	0.02
excluding top 5%	0.25	0.07
excluding top 10%	0.22	0.12
excluding top 20%	0.26	0.09
excluding top 30%	0.33	0.04

the next interval, and this effect subsequently weakens over time. The association between extinction rate in an interval (t) and origination rate in the next interval (t + 1) was approximately double that of extinction rate and origination rate two intervals later (t + 2) (i.e., slopes of 0.30 and 0.16 respectively). These results are consistent with studies of the relationship between extinction and origination for skeletonized marine invertebrates as a whole (LU, YOGO, & MARSHALL, 2006; ALROY, 2008), and corroborate previous work on marine bivalves that documented hyperexponential bursts of diversification following mass extinction events (MILLER & SEPKOSKI, 1988; KRUG, JABLONSKI, & VALENTINE, 2009). It is important to note, however, that the diversity-dependent relationship between rates of extinction and origination for marine bivalves is not limited to mass extinctions and their associated recoveries. While removing the most extreme extinction events from the analysis somewhat weakens the relationship between extinction and subsequent origination, intervals characterized by relatively low extinction rates also exhibit diversity dependence (Table 1). Extinction has been an important evolutionary process throughout the history of marine bivalves, varying considerably in intensity over time, but contributing consistently to bivalve diversification, in part, through its effect on rates of origination.

INFLUENCE OF BIOLOGICAL FACTORS ON EXTINCTION RISK AMONG MARINE BIVALVES

Extinction selectivity, or the selective removal of taxa that possess particular ecological or evolutionary traits, also plays an important role in shaping macroevolutionary and macroecological patterns through time. Extinction selectivity can contribute to ecosystem reorganization by eliminating dominant taxa and allowing subordinate ones to diversify (GOULD & CALLOWAY, 1980; JABLONSKI, 1986, 1989; DROSER, BOTTJER, & SHEEHAN, 1997); it can redirect evolutionary or ecological trends by eliminating important innovations (Pojeta & Palmer, 1976; Fürsich & Jablonski, 1984; Jablonski, 1986); and it can limit the potential evolution of clades by reducing variability (Norris, 1991; Liu & Olsson, 1992). By studying extinction selectivity over long time scales, one can assess not only which taxa went extinct, but potentially how and why they did so. This link between extinction pattern and process can help to bridge the gap between paleontology and conservation biology (see papers in Dietl & Flessa, 2009). If we can determine which traits have influenced susceptibility to extinction during periods of past environmental change, then we may be better able to predict which organisms are most likely to go extinct or persist in the present day.

Extinction selectivity is thought to have significantly influenced the evolutionary trajectory of marine invertebrates and the ecological structure of marine ecosystems through geologic time. Bivalves are no exception; indeed, several classic studies of extinction selectivity have focused on the long and relatively well-preserved fossil record of marine bivalves (e.g., Bretsky, 1973; Kauffman, 1978; Jablonski, 1986; Stanley, 1986a; Jablonski, 2005). This is in part because bivalves display sufficient variation among taxa in traits such as morphology, feeding mode, life habit, larval type, geographic range, and stratigraphic range to allow workers to independently test the extent to which these traits relate to taxon survivorship.

A review of the literature on extinction selectivity in fossil marine bivalves published in 2010 and before (see Appendix, p. 20) demonstrates that selectivity among taxa has been explored with respect to a wide variety of traits, such as abundance, feeding mode, life habit, geographic range, body size, temperature tolerance, species richness, and habitat breadth, among many others (33 traits in total). This review includes 170 tests of extinction selectivity published in 69 studies. The vast majority of selectivity studies have focused on Mesozoic (120 tests) and Cenozoic (114 tests) bivalves, with the Paleozoic receiving considerably less attention (18 tests). The extinctions represented in our database range from the largest and most catastrophic mass extinctions (including all of the so-called Big Five), to six smaller, possibly regional-scale, events (e.g., Eocene/Oligocene and Plio/Pleistocene) and background intervals. Selectivity has been examined at both the species (98 tests) and genus (80 tests) levels. Examining the specific traits tested for selectivity, four traits have received the most attention: geographic range (27 tests), life habit (28 tests), body size (21 tests), and feeding mode (15 tests).

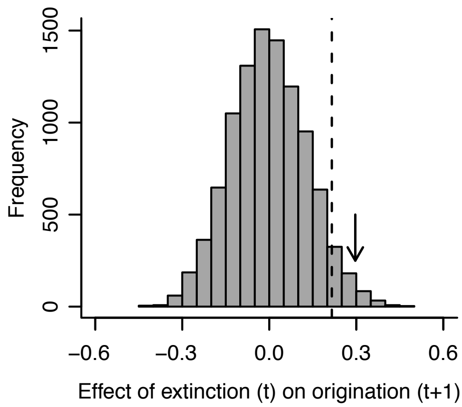

Fig. 4. The effect of extinction on subsequent origination for marine bivalve genera through the Phanerozoic. Effect was measured using the slope of the linear regression of extinction rate in an interval (t) on origination rate in the next interval (t + 1). The gray frequency distribution presents the randomized values, the solid arrow denotes the observed effect, and the dashed line indicates the 95th quantile of randomized values. The observed effect is significantly greater than expected by chance (new).

If extinction is defined as the point in time at which a taxon's geographic range and abundance decrease to zero, taxa with broader geographic ranges should be less prone to extinction. The primary role that geographic distribution plays in determining survivorship has long been recognized for both modern and fossil taxa (see references in Gaston, 1994; Rosenzweig, 1995; Payne & Finnegan, 2007). An early assessment of global survivorship across four mass extinctions—the end-Ordovician, Late Devonian, end-Permian, and end-Triassic events—concluded that geographically widespread bivalve genera were more likely to survive, at least in the initial stages of an extinction event, before drastic deterioration of the physical environment (Bretsky, 1973). The event that has been most thoroughly examined for geographic range selectivity is the K/Pg mass extinction, in conjunction with the interval of background extinction leading up to it. K/Pg survivorship patterns in bivalves and gastropods, along the United States Gulf and Atlantic Coastal Plain and globally, suggest that the only trait reliably associated with genus survivorship is geographic range, whereas several traits are associated with genus- and species-level survivorship during the preceding background interval (Jablonski, 1986, 1987, 1989; Raup & Jablonski, 1993; Jablonski & Raup, 1995; Jablonski, 2005; Jablonski & Hunt, 2006). Data for Southern Hemisphere bivalves across the K/Pg, also compiled at the genus level, support this general pattern (Stilwell, 2003). In contrast, during the end-Triassic extinction, European bivalve species with broader distributions appear no more likely to have survived this event than narrowly distributed taxa (McRoberts & Newton, 1995; McRoberts, Newton, & Allasinaz, 1995). When the spatial scale of analysis is expanded to global coverage, the same nonsignificant species-level pattern is observed for the end-Triassic (Kiessling & Aberhan, 2007).

Taxonomic level and the intensity of extinction complicate the pattern of geographic range selectivity. The data compiled here strongly suggest that widespread bivalve species were significantly more likely to survive background (Jablonski, 1986, 1987; Jablonski & Hunt, 2006; Kiessling & Aberhan, 2007; Crampton & others, 2010; Harnik, 2011), but not mass extinction events (Jablonski, 1986; Hansen & others, 1993; McRoberts & Newton, 1995; McRoberts, Newton, & Allasinaz, 1995; Jablonski, 2005; Kiessling & Aberhan, 2007; for exceptions, see Rode & Lieberman, 2004, for the Late Devonian, and Stilwell, 2003, for the K/Pg). Late Neogene extinctions, intermediate in scale between the Big Five events and background extinction, differ in the effects of geographic range on selectivity among regions. Narrowly distributed species were more likely to become extinct in western South America (Rivadeneira & Marquet, 2007) and tropical America (Roopnarine, 1997), but not in western North America, where there is no evidence of selective extinction (Stanley, 1986b). These complex patterns highlight the importance of assessing selectivity across a range of extinctions that differ in magnitude, as well as across a range of taxonomic levels. It is possible that thresholds exist, such that geographic range no longer ensures the survival of a species, when the scale of environmental perturbation and extinction exceed a critical magnitude. If true, this has enormous implications for assessment of extinction risk and development of effective management strategies in modern ecosystems.

Bivalve life habit, specifically the sites the animals occupy relative to the sediment-water interface, is another ecological trait that is thought to affect survivorship. Which life habit favors survival probably depends on the mechanism of extinction. For example, epifaunal taxa are thought to be more vulnerable to predation pressure (Stanley, 1977, 1982, 1986b; Vermeij, 1987), which could lead to decreased population size and an increase in extinction risk. In contrast, an epifaunal life habit may be advantageous in escaping sudden changes in bottom water chemistry and/or oxygenation. Of the studies compiled here, 14 suggested that epifaunal taxa were more likely to become extinct than infaunal, 5 suggested the opposite, and 8 found no evidence of selectivity either way. When these results are parsed according to the size of the extinction event, an interesting pattern emerges. The majority of background intervals studied (8 out of 10) suggest that infaunal bivalves were less likely to go extinct, while mass extinctions yield contradictory results (4 negative, 5 positive, 6 nonsignificant). When the mass extinction events are broken down by specific event, the results remain mixed. For example, while bivalve genera globally did not exhibit differential survival with respect to life habit across the end-Permian mass extinction (JABLONSKI, 2005), regional patterns from China suggested greater losses of epifaunal than infaunal bivalve genera (KNOLL & others, 2007). Perhaps these differences reflect the extent to which different geographic regions were affected by environmental deterioration. In another example, preferential extinction of infaunal bivalve species was documented across the K/Pg boundary in New Jersey and the Delmarva Peninsula of the United States (GALLAGHER, 1991), but subsequent work found the opposite pattern for bivalve species in Denmark (HEINBERG, 1999) and the Southern Hemisphere (STILWELL, 2003).

Although global analyses of selectivity can be very useful in seeking possible causes of extinction, they can obscure regional patterns that may be less predictable and yet likely to provide more information about the interacting effects of biotic and abiotic factors on survivorship. Spatial variation in environmental change, coupled with spatial heterogeneity in the distributions of taxa and associated biological traits, effectively ensure that patterns of selectivity will vary regionally (see FRITZ, BININDA-EMONDS, & PURVIS, 2009, for an example of geographic variation in extinction risk among extant mammals). Spatial variation may provide useful information about gradients of environmental change and the existence of environmental thresholds affecting taxon survivorship. Despite the clear importance of regional-scale studies in modern conservation biology, paleontological examples are few and far between.

Although large body size is widely thought to increase extinction risk in vertebrates, the link between size and extinction risk in marine invertebrates is considerably more ambiguous (HALLAM, 1975; STANLEY, 1986b; BUDD & JOHNSON, 1991; JABLONSKI, 1996b; SMITH & ROY, 2006). Among invertebrates, increased body size is often associated with increased fecundity, broader environmental tolerance, and wider geographic range (STANLEY, 1986b; MCKINNEY, 1990; ROSENZWEIG, 1995; HILDREW, RAFFAELLI, & EDMONDS-BROWN, 2007), which suggests that larger taxa should have increased rates of survivorship. Among marine bivalves, however, large body size is not generally associated with either extinction risk or survivorship. Body size and extinction are positively linked in only 7 and negatively linked in only 2 (out of a total of 21) studies. Four of the 7 studies that documented selective extinction of large taxa focused on regional patterns during intervals characterized by background rates of extinction; these include the Jurassic (HALLAM, 1975), Miocene (ANDERSON & ROOPNARINE, 2003, for the Western Atlantic and Caribbean, but not the Eastern Pacific), and Pleistocene (STANLEY, 1986a, 1990b). Interestingly, not a single one of the 10 studies that considered size across a mass extinction event found a strong, conclusive link between body size and extinction, although the only 2 events investigated thus far are the end-Triassic (MCROBERTS & NEWTON, 1995; MCROBERTS, NEWTON, & ALLASINAZ, 1995; MCROBERTS, KRYSTYN, & SHEA, 2008) and K/Pg (HANSEN & others, 1987; RAUP & JABLONSKI, 1993; JABLONSKI & RAUP, 1995; MCCLURE & BOHONAK, 1995; JABLONSKI, 1996a; LOCKWOOD, 2005; ABERHAN & others, 2007) events. Three of these 10 studies documented a decrease in bivalve size across a mass extinction boundary (Norian–Rhaetian: MCROBERTS, KRYSTYN, & SHEA, 2008; K/Pg: HANSEN & others, 1987; ABERHAN & others, 2007), but it is unclear in each case whether these patterns were driven by extinction selectivity, within lineage size change, or size-biased origination.

One of the few instances in which a connection between large body size and survivorship has been documented convincingly focused on scallops across the Plio–Pleistocene extinction in California (SMITH & ROY, 2006). This positive relationship was not apparent until phylogenetic relationships were considered. This emphasizes an under-appreciated problem that may affect many selectivity studies. Patterns of selectivity can sometimes be masked or artificially exaggerated when phylogenetic relationships are not taken into account (Purvis, 2008). Taxa may share a particular trait and similar pattern of survivorship because they are related to each other and not necessarily because the trait under consideration, by itself, confers survivorship. A recent analysis (Roy, Hunt, & Jablonski, 2009) of Jurassic to Recent bivalves demonstrated conclusively that phylogenetic clustering of extinction occurs. Phylogenetic relationships do not always affect patterns of selectivity, however; for example, patterns of selectivity among Cenozoic mollusks from New Zealand did not change appreciably after accounting for phylogeny (Foote & others, 2008; Crampton & others, 2010). The fact that taxa in some clades are significantly more extinction-prone than others does strongly suggest that future paleontological studies of selectivity should explicitly account for phylogenetic effects.

In general, deposit feeding is thought to represent a more generalized dietary mode than suspension feeding and could promote survivorship, especially across events that involve a collapse in primary productivity. Levinton's (1974) observation that genera of deposit-feeding bivalves were geologically longer-lived than suspension-feeders, has inspired an ongoing debate over whether bivalves with different feeding modes experience different extinction trajectories. Building on this work, a qualitative examination of background extinction in Cretaceous bivalve species documented particularly slow rates of evolution and long stratigraphic durations in deposit-feeders relative to suspension-feeders (Kauffman, 1978). The majority of studies that have explicitly tested for extinction selectivity according to feeding mode have focused on the K/Pg event, with mixed results. Seven out of 11 studies have reported selective extinction of suspension-feeding genera (e.g., Sheehan & Hansen, 1986; Rhodes & Thayer, 1991; Raup & Jablonski, 1993; Jablonski & Raup, 1995; Jablonski, 1996a; Stilwell, 2003; Aberhan & others, 2007). There is preliminary evidence to suggest that the strength of the selectivity may have increased with distance away from the United States Gulf Coastal Plain, which raises the question as to whether proximity to the killing agent, in this case the K/Pg bolide impact that occurred in the Yucatan, has an effect on selectivity patterns. Studies limited to eastern Texas (Hansen & others, 1987; Hansen, Farrell, & Upshaw, 1993; Hansen & others, 1993, for exception see Sheehan & Hansen, 1986) or the United States Gulf and Atlantic Coastal Plain (McClure & Bohonak, 1995), have yielded either weak or no evidence for selectivity. On the other hand, regional studies in the Southern Hemisphere (e.g., Stilwell, 2003) and Argentina (Aberhan & others, 2007) have suggested that proximity matters, as they have shown strong evidence for selectivity. Although Jablonski's work (Raup & Jablonski, 1993; Jablonski & Raup, 1995; Jablonski, 1996a) clearly supports a global pattern of selective extinction of suspension-feeding bivalves at the K/Pg, he has argued that this was driven by taxonomic factors, rather than selectivity according to feeding mode. He and his colleagues pointed to anomalously low rates of extinction in the two bivalve orders Nuculoida and Lucinoida and argued that other attributes of these two clades helped to promote their survivorship. Sheehan and Hansen (1986), Hansen and others (1987, 1993), and Hansen, Farrell, and Upshaw (1993) emphasized the shift from molluscan communities dominated by suspension-feeders to those dominated by deposit-feeders across the K/Pg boundary, a pattern that could have been caused by selective extinction against suspension-feeders, preferential recovery of deposit-feeders, or some combination of the two. Explicit evaluation of this possibility, in addition to detailed tracking of feeding mode across the recovery interval, is still lacking. Although early studies heralded the usefulness of patterns of extinction selectivity based on feeding habits in differentiating among possible extinction mechanisms, this potential has seldom been realized (but see Knoll & others, 1996, 2007, for exceptions). As our understanding of changes in primary productivity associated with mass extinctions deepens, aided by geochemical proxies, it should be possible to further refine and test hypotheses bearing on the relationship between feeding mode and extinction risk across an array of marine environments.

Most of the studies outlined above focus on the selectivity of single traits and do not consider the potential interactions among multiple traits. We have every reason to believe, based on ecological studies of extant bivalves and many other clades, that several of these traits, for example, body size and geographic range (Jablonski & Roy, 2003; Crampton & others, 2010; Harnik, 2011), are linked to one another. This raises the question—to what extent do these interactions influence patterns of selectivity? A handful of recent studies have tackled this question for marine bivalves (Jablonski & Hunt, 2006; Rivadeneira & Marquet, 2007; Jablonski, 2008a; Crampton & others, 2010; Harnik, 2011). Almost all of them have found that geographic range played a more important role in survivorship than any other ecological trait. For example, in a genus-level analysis of selectivity across the K/Pg mass extinction, Jablonski (2008a) independently tested the effects of body size, geographic range, and species richness, and found that the last two traits were both statistically significantly correlated with survivorship. However, once the covariation among these three traits was controlled for, geographic range yielded the only significant evidence for selectivity. In what is perhaps the most extensive multivariate selectivity study to date, Crampton and others (2010) assessed the relative importance of several traits, including geographic range, body size, feeding mode, life habit, and larval type, in promoting survivorship among Cenozoic bivalve species from New Zealand. Once again, in a multivariate framework, the only trait to show demonstrable selectivity was geographic range. Such multivariate approaches are crucial to studies of selectivity, offering considerable insight into the direct and indirect effects of extinction on the evolution of correlated traits. A clear understanding as to how traits interact, influencing extinction risk across a range of past events, is needed, if bivalve workers are to make such patterns relevant to managers predicting biotic response to current extinction pressures.

CONCLUSIONS

One of the major insights of paleontology is the importance of extinction in shaping the diversity of life through time. The effects of extinction on diversity dynamics have been intensively studied in the marine Bivalvia because of their relatively complete fossil record, the considerable biological variation that exists among taxa, and their diversity and abundance in shallow marine environments today and in the past. In this contribution, we provide new estimates of global extinction and origination rates for marine bivalve genera through the Phanerozoic that explicitly account for temporal variation in preservation. These analyses, using data compiled primarily from the first *Treatise on Invertebrate Paleontology* (Part N: Cox & others, 1969; Stenzel, 1971), underscore the important contributions of the *Treatise* to our understanding of bivalve macroevolutionary history. While rates of extinction and origination are moderate for marine bivalves overall, times of severe extinction and times of general quiescence are observed through the Phanerozoic. Intervals of elevated global extinction for marine bivalves correspond to intervals of elevated extinction for marine invertebrates more broadly, and bivalves exhibit secular declines in rates of extinction and origination over the Phanerozoic that are also observed at much broader taxonomic scales. Throughout their history, marine bivalves exhibited coupled dynamics of extinction and origination, with periods of elevated extinction followed by periods of elevated origination, and moderate extinction by moderate origination. This diversity-dependent process is most pronounced following mass extinctions, but operated consistently throughout the history of the clade. Studies of marine bivalves have yielded important insights into extinction selectivity, and specifically, the effects of biological traits on survivorship. We review this literature, focusing on four traits that have received the most attention. Geographic range size is the most consistent predictor of bivalve survivorship considered to date. Traits like feeding mode and life habit may also be important, but these are probably more dependent on the particular context of environmental change. Body size is largely decoupled from extinction risk despite reasons to expect otherwise. The growing paleontological literature on selectivity underscores the major contribution of fossil bivalves to our understanding of the factors that influence extinction risk. It highlights a fruitful area for collaboration between researchers studying the effects of extinction on marine systems today and in the past.

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APPENDIX. Database of extinction selectivity studies in fossil marine bivalves; please note that the compilation of past work summarized here is ongoing and should not be considered exhaustive (new).

Trait	Reference	Pattern	Taxon	Taxon level	Age	Location	Notes
Abundance	Harnik, 2011	NS	3 superfm	sp	Eo	US Gulf CP	
Abundance	Kiessling & Aberhan, 2007	NS	biv	sp	T/J	Global	
Abundance	Kiessling & Aberhan, 2007	Neg	biv	sp	Tri-Jur	Global	Geo range more important than abundance in determining extinction risk.
Abundance	Lockwood, 2003	NS	biv	gen	K/Pg	US CP	
Abundance	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Abundance	Simpson & Harnik, 2009	Nonlinear	biv	gen	post Pz	Global	Rare and abundant genera exhibit elevated extinction rates.
Active locom	Aberhan & others, 2007	Pos?	moll dom	sp	K/Pg	Argentina	Decline of individuals with active lifestyles across boundary, excluding nuculoids and lucinids. May or may not be due to extinction selectivity.
Active locom	Rhodes & Thayer, 1991	Pos	biv	gen	K/Pg	Global	
Aragonite	Hautmann & others, 2008	Pos	biv dom	sp	T/J	Tibet	
Bathy range	Jablonski & Raup, 1995	NS	biv	gen	K/Pg	US CP	
Bathy range	Jablonski, 1996a	NS	biv, gast	gen	K/Pg	Global	
Bathy range	Raup & Jablonski, 1993	NS	biv	gen	K/Pg	Global	
Body size	Aberhan & others, 2007	Pos?	moll dom	sp	K/Pg	Argentina	Size decrease may or may not be due to extinction selectivity.
Body size	Anderson & Roopnarine, 2003	Pos	corbulids	gen	Mio	Carib/W Atl	
Body size	Anderson & Roopnarine, 2003	NS	corbulids	gen	Mio	E Pacific	
Body size	Crampton & others, 2010	NS	biv	sp	Cz	NZ	
Body size	Hallam, 1975	Pos	biv, ammon	gen, sp	Jur	W Euro	
Body size	Hansen & others, 1987	Pos?	biv	sp	K/Pg	E Texas	Shift to smaller bivalves. May or may not be extinction selectivity.
Body size	Harnik, 2011	Varies	3 superfm	sp	Eo	US Gulf CP	Correlation between size and duration positive in veneroids, negative in pectinoids, not significant in carditoids
Body size	Jablonski & Raup, 1995	NS	biv	gen	K/Pg	Global	
Body size	Jablonski, 1996a	NS	biv	gen	K/Pg	Global	
Body size	Jablonski, 1996b	NS	biv, gast	sp	Late Cret	US CP	
Body size	Lockwood, 2005	NS	3 groups	gen	E/O	N Am, Euro	Large taxa radiate after extinction. Groups include veneroids, arcticoids, and glossoids.
Body size	Lockwood, 2005	NS	3 groups	gen	K/Pg	N Am, Euro	Small taxa radiate after extinction. Groups include veneroids, arcticoids, and glossoids.
Body size	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Body size	McRoberts & Newton, 1995	NS	biv	sp	T/J	Euro	
Body size	McRoberts, Newton, & Allasinaz, 1995	NS	biv	sp	T/J	Euro	
Body size	McRoberts, Krystyn, & Shea, 2008	Pos?	*Monotis*	sp	Nor/Rhaet	Austria	Size decrease may or may not be due to extinction selectivity.
Body size	Raup & Jablonski, 1993	NS	biv	gen	K/Pg	Global	
Body size	Smith & Roy, 2006	Neg	scallops	gen	Plio/Pleist	California	Pattern significant only when adjusted for phylogenetic bias.
Body size	Stanley, 1986a	Neg	biv	sp	Plio/Pleist	SE US	Siphonate bivalves only.
Body size	Stanley, 1986a	Pos	biv	sp	Pleist-Rec	W N Am, Japan	Siphonate bivalves only.
Body size	Stanley, 1990b	Pos	biv	sp	Pleist-Rec	W N Am, Japan	
Bur depth	Kauffman, 1978	Neg	biv	sp	Cret	N Amer	Suspension feeders only.
Bur depth	Lockwood, 2004	NS	3 groups	gen	K/Pg	N Am, Euro	Deeper burrowing taxa radiate during recovery.

APPENDIX *(Continued).*

Bur depth	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Bur depth	Stanley, 1990b	Neg	biv	sp	Pleist-Rec	W N Am, Japan	
Endemicity	Aberhan & Fürsich, 1997	Pos	biv	sp	Pliens-Toar	Andean basin	
Endemicity	Aberhan & Fürsich, 2000	Pos	biv	sp	Pliens-Toar	Andean basin	
Endemicity	Hallam, 1981	Neg	biv	gen	T/J	Global	
Endemicity	Stanley, 1986a	Pos	biv	sp	Plio/Pleist	SE US	
Endemicity	Vermeij, 1986	Pos	moll	sp	Plio	N Atl	
Environment	Rode & Lieberman, 2004	See notes	biv, brach	sp	F/F	N Amer	Increased survival for taxa inhabiting middle-outer platform environments, but not taxa inhabiting open shelf.
Epifaunal	Aberhan & Baumiller, 2003	Neg	biv	sp	early Jur	NW Euro, Andes	
Epifaunal	Aberhan & Fürsich, 1997	Pos?	biv	sp	Pliens-Toar	Andean basin	Long-term increase in infaunal suspension feeders may be due to extinction selectivity or environmental change. Both infaunal and epifaunal suspension-feeders decrease across boundary.
Epifaunal	Clapham & Bottjer, 2007	Pos?	biv, gast	gen	Perm	Global	Increase in abundance of infaunal bivalves may or may not be due to extinction selectivity.
Epifaunal	Cope, 2002	Pos	biv	gen	O/S	Global	
Epifaunal	Crame, 2002	Pos	biv	gen, sp	Cret	Global	In higher latitudes.
Epifaunal	Crampton & others, 2010	NS	biv	sp	Cz	NZ	
Epifaunal	Gallagher, 1991	Neg	moll	sp	K/Pg	US Atl CP	
Epifaunal	Hautmann & others, 2008	Neg	biv dom	sp	T/J	Tibet	
Epifaunal	Heinberg, 1999	Pos?	biv	sp	K/Pg	Denmark	Within habitat comparison shows increase in infaunal species across boundary, may or may not be due to extinction selectivity.
Epifaunal	Jablonski & Raup, 1995	NS	biv	gen	K/Pg	Global	Excluding rudists.
Epifaunal	Jablonski, 1996a	NS	biv	gen	K/Pg	Global	Excluding rudists.
Epifaunal	Jablonski, 2005	NS	biv	gen	K/Pg	Global	
Epifaunal	Jablonski, 2005	NS	biv	gen	P/T	Global	
Epifaunal	Jablonski, 2005	Pos	biv	gen	T/J-K/Pg	Global	
Epifaunal	Kauffman, 1977	Pos	biv	sp	Cret	W Interior	
Epifaunal	Kauffman, 1978	Pos	biv	sp	Cret	N Amer	
Epifaunal	Knoll & others, 2007	Pos	biv	gen	P/T	China	
Epifaunal	Levinton, 1973	Pos	6 species	sp	Rec	New York	Slower evolutionary rates among infaunal and deep water epifaunal, relative to shallow water epifaunal taxa.
Epifaunal	Levinton, 1974	Pos	4 groups	gen	Phan	Global	Comparison of mortality rates between selective suspension-feeders (Pectinacea, Pteriacea, Veneracea) and detritus feeders (Nuculoida).
Epifaunal	Mander & Twitchett, 2008	-	biv	gen	T/J	NW Euro	Poor preservation of early Jurassic infaunal taxa indicates that selectivity may be artifactual.
Epifaunal	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Epifaunal	McRoberts & Newton, 1995	Neg	biv	sp	T/J	Euro	
Epifaunal	McRoberts, 2001	Pos	biv	gen	T/J	Global	
Epifaunal	McRoberts, Newton, & Allasinaz, 1995	Neg	biv	sp	T/J	Euro	
Epifaunal	Raup & Jablonski, 1993	NS	biv	gen	K/Pg	Global	
Epifaunal	Rivadeneira & Marquet, 2007	Pos	biv	sp	Late Ng	W S Amer	

APPENDIX *(Continued)*.

Trait	Reference	Pattern	Taxon	Taxon level	Age	Location	Notes
Epifaunal	Stanley, 1986a	NS	biv	sp	Plio/Pleist	SE US	
Epifaunal	Stilwell, 2003	Pos	moll	gen, sp	K/Pg	S hemis	
Escalation	Hansen & others, 1999	NS	biv, gast	sp	E/O	US CP	Used morphology as proxy for escalation.
Escalation	Hansen & others, 1999	NS	biv, gast	sp	K/Pg	US CP	Used morphology as proxy for escalation.
Escalation	Hansen & others, 1999	NS	biv, gast	sp	Mio	US CP	Used morphology as proxy for escalation.
Escalation	Hansen & others, 1999	Pos	biv, gast	sp	Plio/Pleist	US CP	Used morphology as proxy for escalation.
Escalation	Reinhold & Kelley, 2005	NS	biv, gast	gen, sp	K/Pg	Mississippi	Used morphology as proxy for escalation, only one trait (crenulate margins) associated with higher extinction risk in bivalves.
Geo range	Bretsky, 1973	Neg	biv	gen	F/F	Global	
Geo range	Bretsky, 1973	Neg	biv	gen	O/S	Global	
Geo range	Bretsky, 1973	Neg	biv	gen	P/T	Global	
Geo range	Bretsky, 1973	Neg	biv	gen	T/J	Global	
Geo range	Crampton & others, 2010	Neg	biv	sp	Cz	NZ	
Geo range	Hallam & Wignall, 1997	Neg	biv	gen	T/J	Global	
Geo range	Hansen & others, 1993	NS	moll	sp	K/Pg	E Texas	
Geo range	Harnik, 2011	Neg	3 superfm	sp	Eo	US Gulf CP	
Geo range	Jablonski & Hunt, 2006	Neg	moll	sp	Cret-Cz	US CP	Geo range is more important than larval mode in predicting extinction risk.
Geo range	Jablonski & Raup, 1995	Neg	biv	gen	K/Pg	Global	
Geo range	Jablonski, 1986	NS	biv, gast	gen	K/Pg	US CP	
Geo range	Jablonski, 1986	NS	biv, gast	sp w/in gen	K/Pg	US CP	
Geo range	Jablonski, 1986	Neg	biv, gast	sp w/in gen	Late Cret	US CP	
Geo range	Jablonski, 1987	Neg	biv, gast	sp	Cret	US CP	
Geo range	Jablonski, 1989	Neg	biv, gast	gen	K/Pg	N Am	
Geo range	Jablonski, 2005	NS	biv, gast	sp w/in gen	K/Pg	US CP	
Geo range	Jablonski, 2005	Neg	biv, gast	sp w/in gen	Late Cret	US CP	Genera containing widespread species more extinction resistant.
Geo range	Kiessling & Aberhan, 2007	NS	biv	sp	T/J	Global	
Geo range	Kiessling & Aberhan, 2007	Neg	biv	sp	Tri-Jur	Global	Geo range more important than abundance in determining extinction risk.
Geo range	McRoberts & Newton, 1995	NS	biv	sp	T/J	Euro	
Geo range	McRoberts, Newton, & Allasinaz, 1995	NS	biv	sp	T/J	Euro	
Geo range	Raup & Jablonski, 1993	Neg	biv	gen	K/Pg	Global	
Geo range	Rivadeneira & Marquet, 2007	Neg	biv	sp	Late Ng	W S Amer	
Geo range	Rode & Lieberman, 2004	Neg	biv, brach	sp	F/F	N Amer	
Geo range	Roopnarine, 1997	Neg	chionines	sp	Late Ng	trop Amer	Regions with higher degrees of endemism affected more severely.
Geo range	Stanley, 1986b	NS	biv	sp	Late Ng	W N Amer	
Geo range	Stilwell, 2003	Neg	moll	gen, sp	K/Pg	S hemis	
Hypercapnia	Bottjer & others, 2008	Pos?	biv	gen	P/T	Global	4 cosmopolitan bivalve genera flourish after P/T, probably tolerant of H_2S and CO_2, may or may not be due to extinction selectivity.
Hypercapnia	Knoll & others, 1996	Pos	biv	gen	P/T	China	
Hypercapnia	Knoll & others, 1996	Pos	biv	gen	P/T	China	
Invaders	Rode & Lieberman, 2004	Neg	biv, brach	sp	F/F	N Amer	

APPENDIX *(Continued).*

Latitude	Crame, 2002	Pos	biv	gen, sp	Cret	Global	Epifaunal taxa only.
Meta rate	Knoll & others, 2007	Neg	biv	gen	P/T	China	
Morph com	Kauffman, 1978	NS	biv	sp	Cret	N Amer	
Morph var	Kolbe, Lockwood, & Hunt, 2011	Neg	veneroids	sp	Late Ng	Florida	
Multivariate	Crampton & others, 2010	See notes	biv	sp	Cz	NZ	Geographic range significant. Epifaunal, suspension-feeder, body size, and planktonic larva not significant.
Multivariate	Harnik, 2011	See notes	3 superfm	sp	Eo	US Gulf CP	Geographic range strong. Abundance weak. Body size weak overall but can be as strong as geographic range in specific superfamilies.
Multivariate	Jablonski & Hunt, 2006	See notes	moll	sp	Cret-Cz	US CP	Geographic range more important than larval type.
Multivariate	Jablonski, 2008a	See notes	biv	gen	K/Pg	Global	Geographic range significant. Body size and species richness nonsignificant.
Multivariate	Rivadeneira & Marquet, 2007	See notes	biv	sp	Late Ng	W S Amer	Epifaunal, geographic range, body size significant.
Occupancy	Foote & others, 2007	Neg	moll	sp	Cz	NZ	Species at greatest risk are those that have already been in decline for a substantial period of time.
Pachyodont	Jablonski, 2008a	Pos	rudists	gen	K/Pg	Global	May be example of trait hitch-hiking. Geographic range is more important in determining risk.
Phylogenetic	Roy, Hunt, & Jablonski, 2009	Pos	biv	fam, gen	Jur-Rec	Global	
Plank larva	Crampton & others, 2010	NS	biv	sp	Cz	NZ	
Plank larva	Gallagher, 1991	Pos	moll	sp	K/Pg	US Atl CP	
Plank larva	Jablonski & Hunt, 2006	NS	moll	sp	Cret-Cz	US CP	
Plank larva	Jablonski, 1987	NS	biv, gast	sp	Cret	US CP	
Plank larva	Stanley, 1986b	NS	biv	sp	Late Ng	W N Amer	
Plank larva	Valentine & Jablonski, 1986	NS	biv, gast	gen	K/Pg	US CP	
Schizodont	Jablonski, 2008a	Pos	biv	gen	K/Pg	Global	May be example of trait hitch-hiking. Geographic range is more important in determining risk.
Shell thick	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Sp richness	Hoffman, 1986	NS	biv	gen	K/Pg	Euro	
Sp richness	Jablonski, 1986	NS	biv, gast	sp	K/Pg	US CP	
Sp richness	Jablonski, 1986	Neg	biv, gast	sp	Late Cret	US CP	
Sp richness	Jablonski, 1989	NS	biv, gast	gen	K/Pg	N Am, Euro	
Sp richness	Jablonski, 2005	NS	biv, gast	gen	K/Pg	US CP	
Sp richness	Jablonski, 2005	Neg	biv, gast	gen	Late Cret	US CP	
Sp richness	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Sp richness	Smith & Roy, 2006	Neg	scallops	gen	Plio/Pleist	California	
Sp richness	Vermeij, 1986	NS	moll	sp	Plio	N Atl	
Stenohaline	Hallam, 1981	Pos	biv	gen	T/J	Global	
Stenotherm	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Stenotherm	Stanley, 1986a	Pos	biv	sp	Plio/Pleist	SE US	
Stenotherm	Stanley, 1990a	Pos	biv	sp	Late Ng	W Atl	
Stenotopic	Anderson & Roopnarine, 2003	NS	corbulids	gen	Mio	E Pacific	Examined within phylogenetic framework.
Stenotopic	Hansen & others, 1993	NS	moll	sp	K/Pg	E Texas	Used lithofacies tolerance as proxy for stenotopy.
Stenotopic	Kauffman, 1977	Pos	biv	sp	Cret	W Interior	
Stenotopic	Kauffman, 1978	Mixed	biv	sp	Cret	N Amer	
Stenotopic	Levinton, 1974	Pos	4 groups	gen	Phan	Global	Comparison of mortality rates between selective suspension-feeders (Pectinacea, Pteriacea, Veneracea) and detritus feeders (Nuculoida).

APPENDIX *(Continued).*

Trait	Reference	Pattern	Taxon	Taxon level	Age	Location	Notes
Stenotopic	Posenato, 2009	Varies	biv, brach	gen	Perm	W Tethys	Selectivity varies according to site.
Strat range	Stilwell, 2003	Neg	moll	gen, sp	K/Pg	S hemis	
Susp feeding	Aberhan & others, 2007	Pos	moll dom	sp	K/Pg	Argentina	
Susp feeding	Crampton & others, 2010	NS	biv	sp	Cz	NZ	
Susp feeding	Hansen & others, 1987	Pos?	biv	sp	K/Pg	E Texas	Shift from susp to dep feeders. May or may not be extinction selectivity.
Susp feeding	Hansen, Farrell, & Upshaw, 1993	Pos?	moll	sp	K/Pg	E Texas	Shift from susp to dep feeders at one site. May or may not be extinction selectivity.
Susp feeding	Hansen & others, 1993	NS	moll	sp	K/Pg	E Texas	Long-term shift from susp to dep feeders. Both go extinct at boundary.
Susp feeding	Hautmann & others, 2008	Pos	biv dom	sp	T/J	Tibet	
Susp feeding	Jablonski & Raup, 1995	Pos	biv	gen	K/Pg	Global	Selectivity due to low extinction in Nuculoida and Lucinoida.
Susp feeding	Jablonski, 1996a	Pos	biv	gen	K/Pg	Global	Argues that this is a taxonomic pattern.
Susp feeding	Kauffman, 1978	Pos	biv	sp	Cret	N Am	
Susp feeding	Levinton, 1974	Pos	4 groups	gen	Phan	Global	Comparison of mortality rates between selective suspension-feeders (Pectinacea, Pteriacea, Veneracea) and detritus feeders (Nuculoida).
Susp feeding	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Susp feeding	Raup & Jablonski, 1993	Pos	biv	gen	K/Pg	Global	Pattern due to low extinction in Nuculoida and Lucinoida.
Susp feeding	Rhodes & Thayer, 1991	Pos	biv	gen	K/Pg	Global	
Susp feeding	Sheehan & Hansen, 1986	Pos	moll	sp	K/Pg	E Texas	
Susp feeding	Stilwell, 2003	Pos	moll	gen, sp	K/Pg	S hemis	
Tax structure	Rivadeneira & Marquet, 2007	NS	biv	sp	Late Ng	W S Amer	
Tropical	Stanley, 1986a	Pos	biv	sp	Plio/Pleist	SE US	
Water depth	Jablonski & Raup, 1995	NS	biv	gen	K/Pg	US CP	
Water depth	Jablonski, 1996a	NS	biv, gast	gen	K/Pg	Global	
Water depth	Levinton, 1973	Pos	6 species	sp	Rec	New York	Epifaunal taxa only.
Water depth	McClure & Bohonak, 1995	NS	biv	gen	K/Pg	US CP	
Water depth	Raup & Jablonski, 1993	NS	biv	gen	K/Pg	Global	
Water depth	Valentine & Jablonski, 1993	Pos	moll	sp	Pleist	California	

Key:

Traits: Active locom = active locomotion; Aragonite = aragonitic shell composition; Bathy range = bathymetric range; Bur depth = burrowing depth; Escalation = escalated traits; Geo range = geographic range; Hypercapnia = sensitivity to hypercapnia; Meta rate = metabolic rate; Morph com = morphological complexity; Morph var = morphological variation; Multivariate = multivariate approaches; Plank larva = planktonic larva; Shell thick = shell thickness; Sp richness = species richness; Stenotherm = Stenothermal; Strat range = stratigraphic range; Susp feeding = suspension feeding; Tax structure = taxonomic structure.

Pattern: Neg = negative selectivity (i.e., these taxa or taxa with higher levels of these traits are less likely to go extinct); NS = not significant; Pos = positive selectivity (i.e., these taxa or taxa with higher levels of these traits are more likely to go extinct); ? = unclear whether this pattern is due to extinction selectivity.

Taxon: ammon = ammonites; biv = bivalve; brach = brachiopods; dom = dominated; gast = gastropods; moll = mollusks; superfm = superfamilies.

Taxon level: fam = families; gen = genera; sp = species.

Age: Cret = Cretaceous; Cz = Cenozoic; Eo = Eocene; E/O = end-Eocene extinction; F/F = late Devonian extinction; Jur = Jurassic; K/Pg = end-Cretaceous extinction; Mio = Miocene; Ng = Neogene; Nor = Norian; O/S = end-Ordovician; Perm = Permian; P/T = end-Permian extinction; Phan = Phanerozoic; Pleist = Pleistocene; Pliens = Pliensbachian; Plio = Pliocene; Pz = Paleozoic; Rec = Recent; Rhaet = Rhaetian; T/J = end-Triassic extinction; Toar = Toarcian; Tri = Triassic.

Location: Am = America; Atl = Atlantic; Carib = Caribbean; CP = Coastal Plain; E = East; Euro = Europe; hemis = hemisphere; N = North; NZ = New Zealand; S = South; trop = tropical; W = West.

Notes: dep = deposit; susp = suspension.