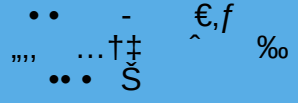
The University of Kansas



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

A . A and A C D

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Bivalves are diverse and abundant constituents of modern marine faunas, and they

have been instrumental in informing debates concerning the roles of biological factors in extinction risk (e.g., A , 1986a; A & AB , 1993; AB , 2005; AD- A & A , 2007; C A & others, 2010), the tempo and mode of evolutionary change (e.g., , 1983; A ,

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 (AD A & , 2000; A C & , 2005; A & 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

However, previous studies conducted at comparable scales have generally found taxonomic errors to be randomly distributed (AD A & , 2000;

nation 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 (, 1978; &

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 (, , & A A , 2006; A , 2008), and corroborate previous work on marine bivalves that documented hyperexponential bursts of diversification following mass extinction events (&

redirect evolutionary or ecological trends by eliminating important innovations (A & A , 1976; C & AB , 1984; AB

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 (B , 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.

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 (AB , 2005), regional patterns from China suggested greater losses of epifaunal than infaunal bivalve genera (& 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 (A A , 1991), but subsequent work found the opposite pattern for bivalve species in Denmark (B , 1999) and the Southern Hemisphere (, 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 , B DA- D , & , 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 (A A , 1975; A , 1986b; B DD & , 1991; AB , 1996b; & , 2006). Among invertebrates, increased body size is often associated with increased fecundity, broader environmental tolerance, and wider geographic range (A , 1986b; C , 1990; , 1995; D , A A , & D D -B , 2007), which suggests that larger taxa should have increased rates of survivorship. Among marine bivalves,

were considered. This emphasizes an underappreciated 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 (, 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 (, , & AB , 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 (& others, 2008;

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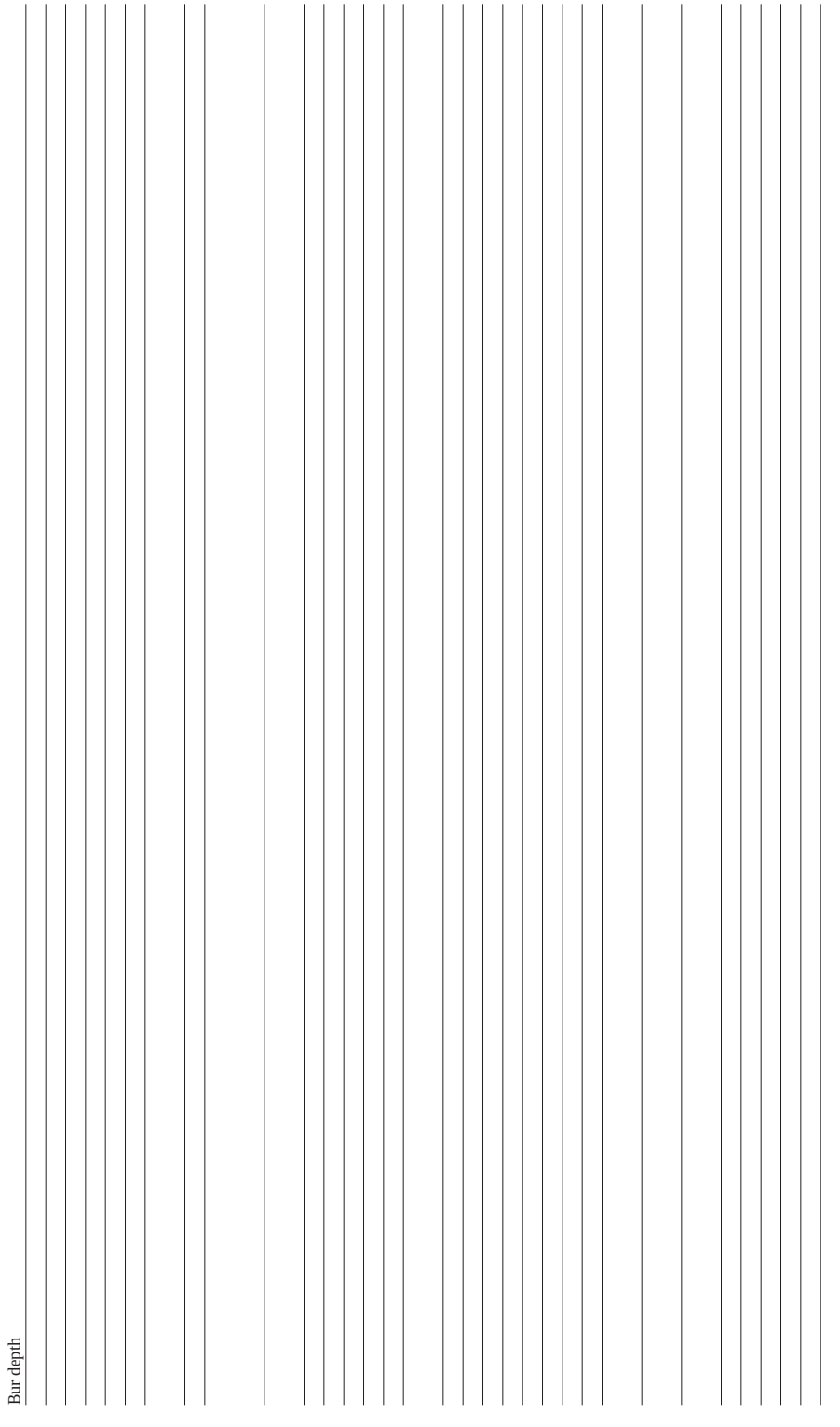
A D . Database of extinction selectivity studies in fossil marine bivalves; please note that the compilation of past work summarized here is ongoing and should not be considered exhaustive (new).

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	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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