

Non-selectivity in extinction of bivalves in the Late Cretaceous of the Atlantic and Gulf Coastal Plain of North America

M. McClure* and A. J. Bohonak

Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, NY 14853-2701, USA

Key words: Mass extinction; ecology; Tertiary; Maastrichtian; fossil.

Abstract

It has been suggested that the biogeographic and clade-level characteristics of marine invertebrate groups important in survival through mass extinctions are different from those important in survival during normal times. The role played by ecologically important characters in survival across mass extinctions, however, has not been well-studied. We obtained information from the literature about the feeding mode and morphology, burrowing habits, size and depth below sea-level inhabited, temperature range, shell thickness, species richness and abundance of bivalve genera present in the Late Cretaceous of the Atlantic and Gulf Coastal Plain of North America. Non-parametric analysis revealed that there were no significant associations between any of these characteristics and survival across the Cretaceous-Tertiary boundary. This lack of selectivity may be due to varying local conditions, which favor different ecological characteristics in each area and produce no overall pattern of selectivity. It might also be indicative of the severity of this extinction on bivalves – differences in ecological habits may have been virtually irrelevant to survivorship through this event.

Introduction

Considerable attention has recently been focused on the biological implications of mass extinctions (e.g. Kitchell et al., 1986; Jablonski, 1989a; Raup and Jablonski, 1993). In particular, it has been suggested that mass extinctions constitute a “third

* Author for correspondence.

tier" of evolutionary phenomena, operating by different rules than normal (background) extinctions (Gould, 1985) and altering the course of evolution by eliminating taxa well-adapted to periods of background extinction. This elimination of taxa might then allow species not necessarily predictable from normal times to radiate and occupy vacant habitats.

Clade-level traits that affect survivorship and extinction rates during normal times may not affect survivorship through mass extinctions (Valentine and Jablonski, 1986; Jablonski, 1986a, 1986b, 1989a, 1989b). For example, mollusks with lecithotrophic larval development, which may produce a more subdivided population structure than planktotrophic larval development, are more prone to extinction during normal times. Larval development does not appear to affect survivorship through the Cretaceous-Tertiary mass extinction, however. Similarly, the geographic range of individual species and species richness of a genus affect extinction rates of mollusk genera during background times but not during mass extinctions; whereas geographic distribution of the entire genus plays an important role during times of mass extinction, but not normal times (Jablonski, 1989a, 1989b). However, the role of very few ecologically-important characters in the survivorship of groups through mass extinctions has been tested in this manner (but see Kitchell et al., 1986; Sheehan and Hansen, 1986; Johansen, 1989).

Our purpose in this study is to determine whether there are any ecological characteristics of a taxon that might affect its survivorship through a mass extinction. In addition, we assess the distribution of those ecological characteristics before and after the extinction event. Significant differences would suggest that different ecological factors were important during mass extinctions and background times.

Materials and methods

We chose to study marine bivalves at the boundary of the Cretaceous and Tertiary periods in the Gulf and Atlantic Coastal Plains because of the amount of data available for this group at that time. The analysis was conducted at the level of genus because specimens are often identified only to this level in published studies. This approach also reduces the problem of pseudo-extinction of species (the disappearance of a species due to anagenetic change), as well as apparent extinction due to the occasional re-naming of a species at a geologic boundary. A list of 67 bivalve genera found in the Maastrichtian stage of the Cretaceous in the Gulf and Atlantic coastal plains of the Eastern United States was obtained from Jablonski (1979); some ecological data was also obtained from this source. We then used BIOSIS, a computer database of journal articles, to conduct a search for articles published since 1986 concerning bivalves during the Cretaceous and Paleocene. We also conducted searches for articles concerning each genus. We obtained over two-thirds of the ecological data for our analyses from sources located during these searches.

We collected information about the following eight ecological (individual-level) characteristics of each genus (see Tab. 1): 1) *feeding mode* – whether the genus was

Table 1. Categorization of individual and higher-level attributes.

Variable	Categories	Description
<i>Feeding:</i> suspension or deposit feeder, or both	3	predominantly phytoplankton, bacteria and detritus, or species of both types
<i>Siphonate?</i>	2	presence or absence of a siphon
<i>Amount of burrowing:</i> none, shallow, moderate, or deep	4	< 5 cm, 5–50 cm, or > 50 cm
<i>Epifaunal, infaunal, or both</i>	3	living on or in a substrate
<i>Size:</i> small, medium or large	3	categorized as < 15, 15–55, and > 55 mm maximum length
<i>Depth (m):</i> shallow, moderate, deep, or very deep	4	categorized as 0–2, 2–30, 30–100, or > 100 m average depth
<i>Temperature range:</i> cool, variable, or warm	3	temperate and polar, tropical and subtropical, or species of both types
<i>Shell thickness:</i> thin or thick	2	as defined by the collector
<i>Number of pre-KT spp:</i> 1–9, or 11	10	number of species present at the end of the Cretaceous
<i>Abundance:</i> rare, moderate, or common	3	as designated by the collector

composed of suspension or deposit feeders, or both; 2) *presence of a siphon* – siphonate or non-siphonate; 3) *burrowing habits* – epifaunal, infaunal, or both; 4) *depth of burrowing* – none, shallow, moderate, or deep. “Shallow” includes those bivalves living just under the substrate surface. Those that burrowed 5 to 50 centimeters were classified as “moderate” burrowers; those that were found below 50 cm were classified as “deep”. When only qualitative information was available, categorization was based on comparative descriptions by the author. 5) *average size (length)* – small (< 15 mm), medium (15–55 mm) or large (> 55 mm). When information was available for more than one species in a genus, an average value was calculated. 6) *depth below sealevel* (depth range below the water surface) – shallow (0–3 m), moderate (3–30 m), deep (30–100 m) or very deep (> 100 m). When only qualitative descriptions were available, intertidal was judged to be “shallow”, upper shoreface as “moderate”, lower shoreface and upper shelf as “deep”, and outer shelf as “very deep”. Again, an average value was calculated when necessary. 7) *temperature range* – warm water (tropical and subtropical), cool water (temperate and polar), or both; and 8) *shell thickness* – thick or thin, as described in the literature (quantitative information was often not available). When

information for any of these characteristics was not available for fossil species, data from extant species in the same genus was used. Data and sources are summarized in Appendices A and B.

In addition, we gathered information concerning two characteristics of the genera not reducible to the individual level: 1) *species richness* – number of species in the Maastrichtian of the Gulf and Atlantic Coastal Plains (from Jablonski, 1979); and 2) *abundance* – rare, moderate or common, as classified by the collector. When the numbers of individuals collected from a locality were available, categorization depended on the total number collected. In general, genera with over 500 collected specimens were “common”, those with 50–500 were “moderate”, and those with under 50 were “rare”.

Intragenetic variation for most of these characters was low. Depth below sea level and size were the most variable, with approximately 15% of the genera incorporating species with dissimilar characteristics. Abundance and temperature range showed less variation, and the remaining characters appeared to be uniform in those genera for which there was information for multiple species.

Genera were judged to have survived the Cretaceous-Tertiary extinction event if any species of the genus was reported from any location in the Paleocene or thereafter. Most of these determinations were made using the list of species in Palmer and Brann (1965), and others were found during the literature search.

We conducted three statistical tests in order to determine if any of these characteristics appeared to influence survivorship of bivalves through the Cretaceous-Tertiary mass extinction. First, Pearson chi-square tests of association were conducted for each pair of ecological and taxon-level traits in order to determine whether significant correlations existed among them. Significantly correlated predictors could cause misleading associations between survival to the Tertiary and the traits examined. In this case, an approach involving multiple univariate tests would be inappropriate. Second, we used chi-square tests to determine whether genera surviving the event were preferentially represented in any ecological categories (e.g. suspension vs. deposit feeding, warm vs. cool water). Finally, chi-square tests were used to determine whether the distribution of species *within* the categories of each of the ten traits was different before and after the extinction event. Exact *p*-values for all statistics were found using SYSTAT's StatXact module. Sample sizes for each of these tests ranged from 21 to 60. However, over 50% of the cells in nearly all of the contingency tables were less than 5.

Results

Associations between ecological variables

Only tendency to burrow (epifaunal/infraunal) and burrowing depth are significantly correlated ($p \leq 0.001$) when a Bonferroni correction for 45 tests is applied (Neter et al., 1990; see Tab. 2). This is not surprising, since all epifaunal species were placed into the non-burrowing category. The use of both characters may be redundant.

Without Bonferroni correction, two more associations become significant (Tab. 2). Size was significantly associated with feeding mode ($p = 0.017$), largely because

Table 2. Pairwise associations between ecological variables, represented as Pearson chi-square probabilities from contingency tables.

	Feeding	Siphon	Burrow	Faunal	Size	Depth	Temper	Shell thickness	# pre-KT	Abundance
Feeding	1.000									
Siphon	0.325	1.000								
Burrow	0.319	0.409	1.000							
Faunal	0.302	0.271	≪ 0.001	1.000						
Size	0.017	0.753	0.852	0.283	1.000					
Depth	0.327	0.397	0.689	0.774	0.776	1.000				
Temperature range	0.918	0.118	0.094	0.810	0.459	0.125	1.000			
Shell thickness	0.217	0.157	0.154	0.485	0.923	0.379	0.027	1.000		
# pre-KT	0.119	0.433	0.836	0.953	0.545	0.539	0.887	0.727	1.000	
Abundance	0.994	0.372	0.853	0.349	0.088	0.281	0.894	0.313	0.024	1.000

all deposit feeders for which we had data were of moderate size. In addition, shell thickness was significantly associated with temperature ($p = 0.024$). In this case, nearly all thick-shelled genera possessed species exploiting both warm and cool water.

Because of these associations, a multivariate statistical approach may be preferable. However, due to the distribution of empty cells in our data set, only univariate tests were used. Since the majority of ecological traits we examined were not correlated, this approach is reasonable.

Associations of traits with survivorship of the Cretaceous mass extinction

None of the traits that we examined was significantly associated with survival of bivalve genera to the Tertiary, with or without a Bonferroni correction for ten tests (see Tab. 3). Probabilities for these tests range from 0.181 to 0.782. In addition, the proportion of genera in each category (of each trait) did not change after the Cretaceous. (For example, the proportion of epifaunal to infaunal genera was the same both before and after the Cretaceous mass extinction event.) Probabilities for these tests ranged from 0.590 to 1.000 (Tab. 3).

Discussion

Survivorship of bivalve genera in the Gulf and Coastal Atlantic plain of North America across the Cretaceous-Tertiary boundary does not appear to be affected by species richness, abundance, size, temperature tolerance, feeding mode, amount of burrowing, shell thickness, depth below sea level at which it was found, or presence

Table 3. Exact Pearson chi-square probabilities from $2 \times n$ contingency tables that 1) survival to the Tertiary was dependent on each trait, and 2) the distribution of the trait differed before and after the event.

Trait	<i>n</i>	df	<i>p</i> -value comparing surviving/extinct genera	<i>p</i> -value comparing total genera before/after
Feeding	49*	2	0.518	0.909
Siphonate?	21*	1	0.505	1.000
Amount of burrowing	48*	3	0.477	0.882
Epi/infaunal, or both	59	2	0.449	0.916
Size	58	2	0.782	0.929
Depth	38*	3	0.734	0.962
Temperature range	28*	2	0.295	1.000
Shell thickness	33	1	0.246	0.590
Number of pre-KT spp	60*	9	0.181	0.981
Abundance	50	2	0.227	0.675

* Denotes contingency tables in which 50% of more of the cells contain less than 5 entries.

of a siphon. In addition, the distribution of these ecological characteristics did not change significantly after that mass extinction.

However, selectivity of mass extinctions on the basis of ecologically relevant characters has been found in previous work on a variety of taxa. For example, species of foraminiferans with a keel, (a correlate with trophic morphology and depth range), were less likely to survive mass extinctions than unkeeled species (Norris, 1991). Trilobites with planktonic larvae were less likely to survive both background and mass extinctions than those with benthic larvae (Chatterton and Speyer, 1989). Selectivity of brachiopod extinction also appears to be affected by ecological characters – reclining and pedically attached species were more strongly affected by the Cretaceous-Tertiary extinction than other ecological groups (Johansen, 1989). In an overview of both marine invertebrates and terrestrial vertebrates, Sheehan and Hansen (1986) found that detritus feeding in both these groups was a “buffer” to extinction at the K-T boundary. Selectivity of extinction in plants has also been seen, as diatoms with resting cysts preferentially survived through the Cretaceous to the Tertiary (Kitchell et al., 1986).

There is a notable difference between most of the characteristics that we examine and many of the ecological characteristics with which survival of mass extinctions has been associated, however. Most of the traits that appear to influence a group’s survival through a mass extinction are likely to have a direct effect on the population structure of a species. In foraminiferans, for example, keeled species (which were more likely to go extinct during mass extinctions) live in deeper water and tend to be more patchily distributed than unkeeled species (Norris, 1991). Species with a patchy distribution, or subdivided population structure, are more likely to be genetically subdivided as well (Hartl and Clark, 1989). A similar effect on population structure is likely to be caused by mode of larval development, which affected trilobite survival during a mass extinction. Marine invertebrates with planktonic larvae tend to have a wider geographic range and more uniform distribution than species with non-planktonic larvae (Jablonski and Lutz, 1983). The presence of a resting phase in diatoms (Kitchell et al., 1986) is unlikely to affect population structure spatially, but does affect it temporally. “Seed banks” of this sort have been seen to preserve genetic variation in phytoplankton (Sandgren, 1988), terrestrial plants (Leck et al., 1989) and animals (Hairston and De Stasio, 1988) by buffering species from the selective consequences of short-term environmental fluctuations. While the effect of mass extinctions clearly vary from group to group, all of these ecological characters, unlike most of the characters that we examined, have direct consequences for the genetic population structure.

An exception to this pattern is the finding that there was a trend (apparently not statistically tested) for detritus (or deposit) feeders to survive the end-Cretaceous mass extinction (Sheehan and Hansen, 1986). However, a detailed examination of a section in Texas revealed that the extinction of mollusks at the K-T boundary took place without regard to feeding mode, killing high percentages of both deposit and suspension feeders (Hansen et al., 1993).

The lack of selectivity relative to ecological characters in our data may be due to the use of information from extant species (see Appendix A); ecological diversifica-

tion since the end-Cretaceous mass extinction may have obscured underlying patterns of survivorship. Alternatively, we may have not chosen the "right" characters for analysis, although we did attempt to choose factors thought to be important in most mass extinction scenarios (e.g. Stanley, 1984; Hallam, 1981), such as temperature tolerance and depth ranges. Finally, selectivity may only be apparent at the species level, due to the inclusion of species with varying ecological characteristics (e.g. both warm and cold tolerant) in one genus.

However, the most economical interpretation of our result is that the lack of association between these ecological characteristics and survival across the K-T boundary is real. One possible explanation for a pattern-less extinction may be that selection pressures varied from locale to locale. Early Paleocene sections on the Brazos River (Texas), for instance, are dominated by deposit-feeders (Hansen et al., 1993), while the early Paleocene sediments of the Braggs section in Alabama, another boundary section, is dominated by suspension feeders (Bryan and Jones 1989). This suggests that different areas at that time may have experienced different selective regimes. Thus, there may be no large-scale pattern, but only local patterns of selectivity.

Another possible explanation for the lack of selectivity seen at the K-T boundary is that the cause and effects of this extinction on bivalves may have been so severe as to make differences in ecology virtually irrelevant. Ecological attributes that make organisms good survivors in normal times appear to have no effect during times of mass extinction. Hansen et al.'s (1993) analysis of the Brazos River section supports this notion. Suspension feeders dominated the Cretaceous fauna, but did not survive the mass extinction in greater proportions than deposit feeders. They did, however, become a substantial part of the fauna later in the Paleocene (Hansen et al., 1993), suggesting that suspension feeding is advantageous during normal times. "Different rules" (Gould, 1985) have been shown to operate during mass extinctions and normal times, for both biogeographic and clade-level characteristics (Jablonski, 1989a). While this study does not prove that such different rules operate for ecologically relevant traits as well, it does show that a variety of these traits have no effect on survivorship through end-Cretaceous mass extinction.

Note added in proof. The selectivity of the end-Cretaceous mass extinction on bivalve genera with regards to three of the variables we analyzed (epifaunal/infaunal, size and depth), as well as depth range has recently been assessed at a global level by Jablonski and Raup (1995). They found that there was no association between these characteristics and survival across the Cretaceous-Tertiary boundary, even at this larger scale.

Jablonski, D. and D. M. Raup. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. *Science* 268: 389–391.

Acknowledgements

We thank A. R. McCune, W. Allmon, and N. G. Hairston, Jr. for critical reading and thoughtful discussions of this work, as well as for much encouragement in pursuing it. An anonymous reviewer provided helpful suggestions. This work was supported by grants from the National Science Foundation and Hatch project funds to Amy R. McCune.

References

- Bryan, J. R. and D. S. Jones. 1989. Fabric of the Cretaceous-Tertiary marine macrofaunal transition at Braggs, Alabama. *Palaeogeography, Palaeoclimatology and Palaeoecology* 69: 279–301.
- Chatterton, B. D. E. and S. E. Speyer. 1989. Larval ecology, life history strategies and patterns of extinction and survivorship among Ordovician trilobites. *Paleobiology* 15: 118–132.
- Gould, S. J. 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11: 2–12.
- Hairston, N. G., Jr. and B. T. De Stasio, Jr. 1988. Rate of evolution slowed by a dormant propagule pool. *Nature* 336: 239–242.
- Hallam, A. 1981. *Facies interpretation and the stratigraphic record*. W. H. Freeman and Co., 291 p.
- Hansen, T. A., B. Upshaw, E. G. Kauffman and W. Gose. 1993. Patterns of molluscan extinction and recovery across the Cretaceous-Tertiary boundary in east Texas; report on new outcrops. *Cretaceous Research* 14: 685–706.
- Hartl, D. L. and A. G. Clark. 1989. *Principles of population genetics*. 2nd ed. Sinauer Associates, Sunderland, Mass.
- Johansen, M. B. 1989. Adaptive radiation, survival and extinction of brachiopods in the Northwestern European Upper Cretaceous-Lower Palaeocene chalk. *Palaeogeography, Palaeoclimatology and Palaeoecology* 74 (3–4): 147–204.
- Jablonski, D. 1979. *Paleoecology, paleobiogeography and evolutionary patterns of Late Cretaceous Gulf and Atlantic Coastal Plain Mollusks*. PhD Dissertation, Yale University.
- Jablonski, D. 1986a. Larval ecology and macroevolution in marine invertebrates. *Bulletin of Marine Science* 39: 565–587.
- Jablonski, D. 1986b. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* 231: 129–133.
- Jablonski, D. 1989a. The biology of mass extinction: a palaeontological view. *Philosophical Transactions of the Royal Society of London. Series B*. 325: 357–368.
- Jablonski, D. 1989b. K-T bivalves of Europe and North America: comparison of patterns of extinction and rebound. *Geological Society of America Abstracts* 21: A208.
- Jablonski, D. and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58: 21–89.
- Kitchell, J. A., D. L. Clark and A. M. Gombros, Jr. 1986. Biological selectivity of extinction: a link between background and mass extinction. *Palaos* 1: 504–511.
- Leck, M. A., V. T. Parker and R. L. Simpson, eds. 1989. *Ecology of soil seed banks*. Academic Press, New York.
- Neter, J., W., Wasserman and Kutner, M. H. 1990. *Applied linear statistical models*. 3rd ed. Irwin, Boston.
- Norris, R. D. 1991. Biased extinction and evolutionary trends. *Paleobiology* 17: 388–399.
- Palmer, K. V. W. and D. C. Brann. 1965. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. *Bulletins of American Paleontology* 48: 1–1057.
- Raup, D. M. and D. Jablonski. 1993. Geography of end-Cretaceous marine bivalve extinctions. *Science* 260: 971–973.
- Sandgren, C. D. 1988. *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge University Press, New York.
- Sheehan, P. M. and T. A. Hansen. 1986. Detritus feeding as a buffer to extinction at the end of the Cretaceous. *Geology* 14: 868–870.
- Stanley, S. M. 1984. Temperature and biotic crises in the marine realm. *Geology* 12: 205–208.
- Valentine, J. W. and D. Jablonski. 1986. Mass extinctions – sensitivity of marine larval types. *Proceedings of the National Academy of Sciences, U.S.A.* 83: 6912–6914.

Received 7 June 1994;

accepted 13 July 1994.

Corresponding Editor: M. J. Benton

Appendix A.

Ecological data for 67 bivalve genera. Italicized references contain information from extant species. Codings are as follows: KT survival (0 = not found after the Late Cretaceous, 1 = appears after the KT boundary), Pre-KT species (number of species in the Late Cretaceous), Feeding (0 = suspension, 1 = deposit, 2 = both types present in the genus), Siphonate (0 = nonsiphonate, 1 = siphonate), Amount of burrowing (1 = none, 2 = shallow, 3 = moderate, 4 = deep), Epi/infraunal (0 = epifaunal, 1 = infraunal, 2 = both), Size (1 = < 15 mm, 2 = 15–55 mm, 3 = > 55 mm), Depth (1 = 0–2 m, 2 = 2–30 m, 3 = 30–100 m, 4 = 100+ m), Abundance (1 = rare, 2 = common, 3 = widespread), Temperature range (1 = warm, 2 = variable, 3 = cool), and Shell thickness (0 = thin, 1 = thick). See text for more information on categorization of traits.

Genus	KT survival	Pre-KT species	Feeding	Siphonate?	Amount of burrow	Epi/infraunal	Size	Depth	Abundance	Temp range	Shell thickness	References
Aenona	0	4	2	–	3	1	–	–	1	–	0	7, 35, 65
Amusium	1	1	0	–	1	0	3	2	–	3	–	17, 30, 49
Anomia	1	5	0	–	1	0	1	3	2	3	0	7, 12, 20, 39, 49, 58, 65, 70, 71
Aphrodina	0	1	0	–	3	1	3	3	2	–	–	35, 65
Arca	1	1	0	–	3	2	1	2	1	–	–	29, 35, 49, 58, 67
Bathytormus	1	1	0	–	2	1	2	–	1	–	–	12, 26, 35, 49, 65
Brachidontes	0	2	0	–	1	0	2	–	3	–	–	20, 35, 49
Caesticorbula	0	3	0	–	2	1	1	2	3	–	–	35
Camponectes	0	4	1	–	1	0	2	–	2	–	–	31, 35, 41, 65
Cardium	1	–	–	1	2	1	3	–	3	3	1	7, 49, 58, 65
Caryocorbula	1	1	0	1	2	1	2	3	2	–	–	12, 18, 20, 35, 49
Chlamys	1	1	0	–	1	0	3	4	2	2	0	8, 22, 24, 28, 39, 42, 44, 49, 65, 70
Corbula	1	4	0	1	2	1	1	1	2	3	1	7, 8, 18, 30, 36, 40, 49
Crassatella	1	5	0	0	3	1	2	2	2	3	1	30, 35, 49
Crassostrea	1	4	0	–	1	0	3	1	3	–	–	20, 22, 34, 35
Crenella	1	2	0	–	1	0	1	2	3	–	–	7, 35, 39, 65
Cucullaea	1	6	0	0	2	1	3	3	2	3	1	7, 30, 35, 49, 71

Cuspidaria	1	5	2	1	-	1	1	4	2	2	0	7, 29, 30, 35, 39, 65
Cymbophora	0	6	0	1	2	1	1	2	1	-	-	29, 35, 41
Cyprimeria	0	3	-	-	2	1	3	2	3	-	1	7, 35, 65
Exogyra	0	2	0	-	1	0	2	-	1	-	-	8, 35, 41
Flemingostrea	0	1	0	-	1	0	-	-	2	-	-	35
Gastrochaena	1	1	0	-	1	0	2	-	-	-	-	49, 52
Glycymeris	1	4	-	0	-	1	2	3	2	3	1	7, 22, 39, 44, 48, 49, 65, 71
Gryphae	1	1	-	-	-	-	2	-	-	-	0	7, 8, 49
Inoceramus	0	11	0	-	1	0	3	3	2	3	1	5, 7, 9, 13, 19, 29, 35, 41, 43, 47, 51, 59
Isoognomon	1	1	0	-	1	0	3	3	-	3	1	9, 18, 49
Laternula	0	1	0	-	3	1	3	2	2	1	-	1, 4, 18, 20, 35, 57
Legumen	0	2	0	-	3	1	-	-	2	-	0	7, 35, 65
Leptosolen	0	3	-	-	-	-	2	-	-	-	0	7, 12, 35
Lima	0	9	0	-	1	0	3	4	1	2	0	7, 8, 18, 29, 35, 39, 44, 50, 61, 65
Limatula	0	1	-	-	1	0	1	1	-	3	-	6, 35, 38, 65
Limopsis	1	-	2	0	2	2	1	3	2	3	-	18, 30, 38, 39, 41, 49, 64
Linearra	0	4	-	-	2	1	1	3	-	-	-	7, 35, 65
Liopistha	0	2	1	-	-	1	2	-	1	-	0	16, 35, 46
Lithophaga	1	6	-	-	1	0	3	2	3	-	0	2, 7, 35, 39, 44, 49, 52, 61, 62
Lucina	1	1	0	1	4	1	2	-	1	3	-	19, 29, 30, 40, 45, 49, 54
Martesia	1	1	0	-	1	0	2	-	1	-	-	10, 30, 39, 44, 49
Modiolus	1	3	0	-	1	2	3	2	-	2	0	7, 24, 39, 49, 56, 58, 63, 65
Nemodon	1	2	0	0	1	2	1	-	1	-	-	7, 29, 30, 35, 41, 65
Nucula	1	8	1	1	1	1	2	4	2	-	1	3, 7, 18, 20, 22, 29, 30, 35, 39, 45, 49
Nuculana	1	-	1	1	-	1	-	3	3	-	-	29
Opertochasna	0	1	-	-	1	0	1	-	-	-	-	10, 35
Ostrea	1	1	0	-	1	0	3	-	2	2	0	7, 11, 30, 33, 34, 39, 44, 45, 49, 65, 70
Panopea	1	1	0	1	4	1	3	3	3	2	1	18, 24, 27, 30, 49, 66, 70
Periploma	1	1	0	1	-	1	3	2	2	2	0	7, 28, 30, 39, 48, 49, 65
Phacoides	1	1	0	1	-	2	2	-	1	3	1	7, 30, 44, 49, 53
Pholadomya	1	4	-	-	-	-	3	4	2	-	0	7, 49
Pinna	0	1	-	-	2	2	2	-	-	3	0	7, 35
Pleurocardia	0	4	0	-	2	1	-	2	-	-	-	24, 35
Plicatula	1	3	-	-	1	0	2	-	-	-	-	8, 35, 49
Postigata	0	2	0	-	2	1	1	1	1	-	-	12, 35
Protocardia	0	3	-	-	-	-	2	-	3	-	-	8, 35, 60

Genus	KT survival	Pre-KT species	Feeding	Siphonate?	Amount of burrow	Epi/Infanal	Size	Depth	Abundance	Temp range	Shell thickness	References
<i>Pseudolimea</i>	0	1	-	-	-	-	1	3	1	2	-	15, 35
<i>Pterotrigonia</i>	0	7	-	-	-	-	3	-	1	-	-	21, 35
<i>Pulvinites</i>	1	1	-	-	-	-	2	1	1	-	0	35, 69
<i>Pycnodonte</i>	1	3	0	-	1	0	3	-	3	3	0	19, 28, 30, 32, 35, 54, 64
<i>Solyma</i>	0	2	1	1	1	1	2	-	1	-	0	3, 7, 29, 35, 41
<i>Spondylus</i>	0	2	0	-	1	0	3	2	1	3	-	35, 64, 68, 72
<i>Striaria</i>	1	3	0	0	2	1	3	3	3	-	-	12, 29, 30, 35, 49
<i>Synyclonema</i>	1	3	0	-	1	0	-	-	2	2	-	12, 14, 29, 30, 35, 65, 67
<i>Tellina</i>	1	2	2	1	3	1	3	3	3	3	0	7, 11, 18, 22, 23, 30, 35, 37, 39, 49, 65, 70
<i>Tenea</i>	0	1	-	-	-	-	-	-	-	-	0	7, 35
<i>Teredo</i>	1	-	-	-	1	2	1	-	-	-	-	39, 49, 58
<i>Venericardia</i>	1	-	0	0	-	1	3	-	-	3	-	28, 29, 30, 38, 49, 65
<i>Vetericardiella</i>	1	-	0	0	-	1	-	3	2	-	-	29
<i>Ventiella</i>	1	1	0	-	-	1	2	-	-	-	1	7, 35, 49

Appendix B:

Sources used in construction of data table (see Appendix A).

1. Ahn, I. Y. 1993. Enhanced particle flux through the biodeposition by the Antarctic suspension feeding bivalve *Laternula elliptica* in Marian Cove, King George Island. *Journal of Experimental Marine Biology and Ecology* 171: 75–90.
2. Akpan, E. B. 1991. Palaeoecological significance of *Lithophaga* borings in Albian stromatolites, southeast Nigeria. *Paleogeography, Paleoclimatology, Paleoecology* 88: 185–192.
3. Arva, I. and M. Hoque. 1989. Predatory gastropod assemblages in an Eocene molluscan assemblage from Nigeria. *Lethaia* 22: 49–59.
4. Berkman, P. A., T. R. Waller and S. P. Alexander. 1991. Unprotected larval development in the Antarctic scallop, *Adamussiu colbecki* (Mollusca, Bivalvia, Pectinidae). *Antarctic Science* 3: 154–158.
5. Buck, S. P. and D. J. Bottjer. 1985. Continental slope deposits from a Late Cretaceous, tectonically active margin, S. California. *Journal of Sedimentary Petrology* 55: 843–855.
6. Caldara, M., A. D'Alessandro and I. Di Geronimo. 1990. A new species of bivalve, *Limatula gravinae* (Pleistocene, Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 95: 441–448.
7. Clark, W. B. C. 1916. Upper Cretaceous, text. Maryland Geological Survey. John Hopkins, Baltimore.
8. Cox, L. R. 1935. The Triassic, Jurassic, and Cretaceous Gastropoda and Lamellibranchia of the Attock District. *Memoirs of the Geological Survey of India: Palaeontologia Indica*. Vol. 20 (5).
9. Crampton, J. S. 1988. Comparative taxonomy of the bivalve families Isognomonidae, Inoceramidae, and Retroceramidae. *Paleontology* 31: 965–996.
10. Crampton, J. S. 1990. A new species of Lower Cretaceous wood-boring bivalve from New Zealand. *Paleontology* 33: 981–992.
11. Creutzberg, F. 1986. Distributional patterns of 2 bivalve species (*Nucula turgida*, *Tellina fabula*) along a frontal system in the southern North Sea. *Netherlands Journal of Sea Research* 20: 305–311.
12. De Cauwer, G. 1987. Additional notes on the Cretaceous bivalve genus *Postligata* Gardner. *Annales de la Société Royale Zoologique de Belgique* 117: 139–145.
13. Dhondt, A. V. 1983. An inoceramid-like limid of Late Maastrichtian Age from Maastricht. *Bulletin de l'institut Royal des Sciences Naturelles Belgique. Sci. de la Terre* 55: 1–10.
14. Dhondt, A. V. 1985. Late Cretaceous bivalves from the AIO Exposures in northern Aquitaine. *Cretaceous Research* 6: 33–74.
15. Dhondt, A. V. 1989. Late Cretaceous *Limea* (*Pseudolimea*) species of Europe. *Bulletin de l'institut Royal des Sciences Naturelles Belgium Sci. de la Terre* 59: 105–125.
16. Dhondt, A. V. and J. W. M. Jagt. 1988. Upper Cretaceous *Liopistha* species of Europe. *Bulletin de l'institut Royal des Sciences Naturelles Belgium Sci. de la Terre* 58: 187–197.
17. Dredge, M. C. L. 1985. Estimates of natural mortality and yield-per-recruit for *Amusium japonicum balloti* Bernardi (Pectinidae) based on tag recoveries. *Journal of Shellfish Research* 5: 103–109.
18. Eagle, M. and B. W. Hayward. 1992. Paleontology and paleoecology of Early Miocene sequences in Hays and Tipakuri Streams, northern Hunua Ranges, Auckland. *Records of the Auckland Institute and Museum* 29: 113–133.
19. Elder, W. P. 1989. Molluscan extinction patterns across the Cenomanian-Turonian Stage boundary in the western interior of the United States. *Paleobiology* 15: 299–320.
20. Farsich, F. T. and J. I. Kirkland. 1986. Biostratigraphy and paleoecology of a Cretaceous brackish lagoon. *Palaios* 1: 543–560.
21. Fleming, C. A. 1987. New Zealand Mesozoic bivalves of the superfamily Trigoniacea. *New Zealand Geological Survey Paleontological Bulletin*, number 53.
22. Foster, N. R. 1991. Intertidal bivalves: a guide to the common marine bivalves of Alaska. n.c: University of Alaska Press.

23. Freneix, S., J. P. St. Martin and P. Moissette. 1987. Heterodont bivalves from the Messinian of Oranie (western Algeria). *Bulletin du Museum National d'Histoire Naturelle, Section C9*: 415–454.
24. Funder, S. and A. Weidick. 1991. Holocene boreal molluscs in Greenland – Paleoceanographic implications. *Paleogeography, Paleoclimatology, Paleococology* 85: 123–135.
25. Geary, D. H. 1987. Evolutionary tempo and mode in a sequence of the Upper Cretaceous bivalve *Pleurocardia*. *Paleobiology* 13: 140–151.
26. Glibert, M. 1985. Les bivalves et gasterpodes du Bruxellien inferieur de la Belgique. *Annales de la Societ  Royale Zoologique de Belgique* 115: 261–368.
27. Goodwin, C. L. and B. C. Pease. 1991. Geoduck, *Panopea abrupta* (Conrad, 1849) size, density and quality as related to various environmental parameters in Puget Sound, WA. *Journal of Shellfish Research* 10: 65–77.
28. Griffin, M. 1991. Eocene bivalves from the Rio Turbio Formation, southwest Patagonia (Argentina). *Journal of Paleontology* 65: 119–146.
29. Hansen, T., R. B. Farrand, II. A. Montgomery, H. G. Billman and G. Blechschmidt. 1987. Sedimentology and extinction patterns across the Cretaceous-Tertiary boundary interval in East Texas. *Cretaceous Research* 8: 229–252.
30. Hansen, T. A., B. R. Farrell and B. Upshaw III. 1993. The first 2 million years after the Cretaceous-Tertiary boundary in East Texas: rate and paleocology of the molluscan recovery. *Paleobiology* 19: 251–265.
31. Hayami, I. 1991. Living and fossil scallop shells as airfoils: an experimental study. *Paleobiology* 17: 1–18.
32. Hayami, I. and T. Kase. 1992. A new cryptic species of *Pycnodonte* from Ryuku Islands: a living fossil. *Transactions and Proceedings of the Paleontological Society of Japan New Series* 1992: 1070–1089.
33. Honda, Y. 1989. Paleogene molluscan faunas from the Kushiro Coal Field, Eastern Hokkaido, Japan. *Tohoku University Scientific Report, 2nd Series, number* 60.
34. Hu, Y. P., S. C. Fuller, M. Castagna, R. C. Vrijenhoek and R. A. Lutz. 1993. Shell morphology and identification of early life history stages of congeneric species of *Crassostrea* and *Ostrea*. *Journal of the Marine Biological Association of the United Kingdom* 73: 471–496.
35. Jablonski, D. 1979. Paleocology, paleobiogeography and evolutionary patterns of Late Cretaceous Gulf and Atlantic Coastal Plain Mollusks. PhD Dissertation, Yale University.
36. Jensen, J. 1990. Increased abundance and growth of the suspension-feeding bivalve *Corbula gibba* in a shallow part of the eutrophic limfjord, Denmark. *Netherlands Journal of Sea Research* 27: 101–108.
37. Jones, G. P., D. J. Ferrel and P. F. Sale. 1990. Spatial pattern in the abundance and structure of mollusc palps in the soft sediments of a coral reef lagoon. *Marine Ecology Progress Series* 62: 109–120.
38. Kanazawa, K. 1990. Early Pleistocene glacio-eustatic sea-level fluctuations as deduced from periodic changes in cold and warm-water molluscan associations in the Shimokita Peninsula, northeast Japan. *Paleogeography, Paleoclimatology, Paleocology* 79: 263–273.
39. Keen, A. M. and D. L. Frizzel. 1939. *Illustrated key to west North American Pelecypod genera*. Stanford: Stanford University Press.
40. Kelley, P. H. 1988. Predation by Miocene gastropods of the Chesapeake Group: stereotyped and predictable. *Palaios* 3: 436–448.
41. Koch, C. F. 1980. Bivalve species duration, areal extent and population size in a Cretaceous sea. *Paleobiology* 6: 184–192.
42. Legault, C. and J. H. Himmelman. 1993. Relation between escape behaviour of benthic marine invertebrates and the risk of predation. *Journal of Experimental Marine Biology and Ecology* 170: 55–74.
43. Macleod, K. G., and W. N. Orr. 1993. The taphonomy of Maastrichtian Inoceramids in the Basque region of France and Spain and the pattern of their decline and disappearance. *Paleobiology* 19: 235–250.

44. Manker, J. P. and B. D. Carter. 1987. Paleocology and paleogeography of an extensive rhodolith facies from the lower Oligocene of south Georgia and north Florida. *Palaios* 2: 181–188.
45. Miller, W. III and J. R. DuBar. 1988. Community replacement of a Pleistocene *Crepidula* biostrome. *Lethaia* 21: 67–78.
46. Mokady, O., D. B. Bonar, G. Arazi and Y. Loya. 1993. Spawning and development of three coral-associated *Lithophaga* species in the Red Sea. *Marine Biology* 115: 245–252.
47. Noda, M. 1992. *Inoceramus troegeri* new species (Bivalvia) from the Coniacian Cretaceous of Hokkaido and its systematic implications. *Transactions and Proceedings of the Paleontological Society of Japan New Series* 1992: 1311–1328.
48. Noda, Y. 1992. Neogene molluscan faunas from the Haboro Coal Field, Hokkaido, Japan. *Tohoku University Scientific Report, 2nd Series, number* 62.
49. Palmer, K. V. W. and D. C. Brann. 1965. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. *Bulletins of American Paleontology* 48: 1–1057.
50. Peck, L. S. 1993. The tissues of articulate brachiopods and their value to predators. *Philosophical Transactions of the Royal Society (London) B* 339: 17–32.
51. Pirrie, D. and J. D. Marshall. 1990. Diagenesis of *Inoceramus* and Lower Cretaceous paleoenvironmental geochemistry: a case study from James Ross Island, Antarctica. *Palaios* 5: 336–345.
52. Pisera, A. 1987. Boring and nestling organisms from Upper Jurassic coral colonies from northern Poland. *Acta Palaeontologica Polonica* 32: 83–104.
53. Powell, E. N., A. Logan, R. J. Stanton and D. J. Davies. 1989. Estimating time since death from free amino acid content of the mollusc shell: a measure of time averaging in modern death assemblages? Description of the technique. *Palaios* 4: 16–31.
54. Rossbach, T. J. and J. G. Carter. 1991. Molluscan biostratigraphy of the Lower River Bed Formation at the Martin Marietta Quarry, New Bern, NC. *Journal of Paleontology* 65: 80–118.
55. Sandy, M. R. 1991. Aspects of Middle-Late Jurassic-Cretaceous Tethyan brachiopod biogeography in relation to tectonic and paleoceanographic developments. *Paleogeography, Paleoclimatology, Paleocology* 87: 137–154.
56. Savazzi, E. 1989. Shell torsion and life habit in the recent mytilid bivalve *Modiolus philippinarum*. *Paleogeography, Paleoclimatology, Paleocology* 72: 277–282.
57. Savazzi, E. 1990. Shell biomechanics in the bivalve *Laternula*. *Lethaia* 23: 93–101.
58. Schäfer, W. 1972. Ecology and palaeoecology of marine environments. Oliver and Boyd, Edinburgh.
59. Schonfeld, J., F. Sirocko and N. O. Jørgensen. 1991. Oxygen isotope composition of Upper Cretaceous chalk at Lagerdorf (Northwest Germany): its original environmental signal and palaeotemperature interpretation. *Cretaceous Research* 12: 27–46.
60. Scott, R. W. 1986. Paleobiology of Early Cretaceous protocardids, Caribbean Province. *Journal of Paleontology* 60: 1186–1211.
61. Sepkoski, J. 1992. A compendium of fossil marine animal families. 2nd ed. Milwaukee Public Museum Contributions in Biology and Geology.
62. Simunovic, A. and I. Grubelic. 1992. Biological and ecological studies of the dateshell *Lithophaga lithophaga* L. from the Eastern Adriatic Sea. *Periodicum Biologorum* 94: 187–192.
63. Squires, R. L. and J. L. Goedert. 1991. New Late Eocene molluscs from localized ls deposits formed by subduction-related methane seeps, southwest Washington. *Journal of Paleontology* 65: 412–416.
64. Squires, R. L. and R. Demetron. 1990. New Eocene marine bivalves from Baja California Sur, Mexico. *Journal of Paleontology* 64: 382–391.
65. Stanley, S. M. 1986. Population size, extinction and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* 12: 89–110.
66. Studencka, B. 1991. A new species of genus *Panopea* (Bivalvia) from King George Island, Antarctica. *Polish Polar Research* 12: 363–368.
67. Vietti, R. C. and G. F. Russo. 1987. Molluscs from submarine caves of the Sorrentine Peninsula (Southern Tyrrhenian Sea). *Stygologia* 3: 138–148.
68. Vokes, H. E. and E. H. Vokes. 1992. Neogene paleontology in the Northern Dominican Republic: the genus *Spondylus* (Bivalvia: Spondylidae). *Bulletins of American Paleontology* 102: 5–11.

69. Ward, L. L. and T. R. Waller. 1988. A new species of *Pulvinites* (Mollusca; Bivalvia) from the Upper Paleocene Paspotanam member of the Aquia Formation in Virginia. *Journal of Paleontology* 62: 51–55.
70. Watkins, R. 1990. Pliocene channel deposits of oyster shells in the Salton Trough region, California. *Paleogeography, Paleoclimatology, Paleoecology* 79: 249–262.
71. Wells, P. E. 1987. The stratigraphy and structure of the Mt. Bruce area, northern Wairarapa, Northland, NZ. *Journal of the Royal Society of New Zealand* 17: 101–113.
72. Zitt, J. and O. Nekvasilova. 1987. Epibionts cemented to rocky surfaces and diabase clasts in the Upper Cretaceous 1F Zelezne Hory Mountains, Czechoslovakia. *Casopis Narodniho Muzea v Praze Rada Prirodovedna* 156: 17–34.