**TITLE:** Testing extinction rates across various modes of life in Bivalvia during the end-Cretaceous mass extinction

**KEYWORDS:** bivalve, macroevolution, mass extinctions, extinction selectivity, mode of life, mobility, tiering, feeding strategy

AUTHOR(S): Johanna Sullivan

#### 1. Significance

As Earth enters its sixth mass extinction, understanding extinction selectivity is a major concern. An understanding of the dynamics of extinction selectivity in previous mass extinctions will help us protect modern ecosystems. The end-Cretaceous mass extinction event drove approximately 70% of species to extinction. This pulse event occurred over such a short period of time that it overrode natural selection, providing a good test for the role of certain traits with regard to general survival rates. Results suggest that the tiering and mobility of certain taxa across bivalve genera protected them from suffering the same intensity of extinction as other bivalve groups.

### 2. Abstract

Mass extinctions disrupt the balance of clade richness across the tree of life, dramatically and permanently altering the ecological landscape (Foote, 1997; Jablonski, 2005; Sclafani et al., 2018). Certain groups of organisms are lost to extinction, while others persist through the survival of individual lineages (Jablonski, 2002; Jablonski, 2005; Sclafani et al., 2018; Wan et al., 2021). The difference between survival and extinction could be connected to three key traits-mobility, feeding, and tiering-which combined make up an organism's mode of life (MOL). I analyzed extinction selectivity across all bivalve genera known to exist during the end-Cretaceous mass extinction (KPg) to determine which modes of life fared better and which of the three MOL traits most contributed towards genus survival.

Of the fifteen unique MOLs, and the thirteen MOLs that had enough samples to properly analyze, only one went extinct (immobile, intermediate epifaunal, suspension/photosymbiotic feeder). Despite the relative stability of the MOLs, there were clearly groups hit harder than others. Semi-infaunal suspension feeders suffered the second greatest extinction level regardless of whether the taxa were mobile or sessile (81% for mobile taxa and 72% for sessile taxa) while immobile suspension feeding boring bivalves had the lowest extinction rate (<25%). Separating the three MOL traits, I found tiering to be the most important trait in guarding against extinction with feeding and mobility being of secondary and tertiary importance respectively. More exposed bivalves (intermediate epifaunal or semi-faunal) suffered the greatest extinction rates (100% and 77% respectively) while less exposed bivalves (boring and deep infaunal) had the lowest extinction rates (<25% and 43% respectively). Bivalve groups that relied on a

combination of suspension feeding and photosynthesis (i.e. rudists) suffered a complete extinction whereas groups that used a chemosymbiotic strategy to feed suffered a less than 25% extinction rate. There is also a slight trend towards higher levels of mobility increasing survival rates (58% of immobile bivalves went extinct and 50% of mobile bivalves went extinct). There appears to be intersections between tiering and feeding that affects extinction rates; greater amounts of natural coverage and more reliable sources of food likely protected certain groups against extinction.

#### 3. History and Stratigraphy of the end-Cretaceous

The extinction of the non-avian dinosaurs was long shrouded in mystery. There were numerous creative ideas about this including the idea that rising temperatures stopped the testicals of dinosaurs from functioning. This would have led to an extinction by male sterilization (Gould 1984). The bolide impact theory on dinosaur extinction proposed in the early 1980's by Walter and Lueis Alvarez (Alvarez et. al 1984) was a controversial topic at time of publication (Hoffam and Netecki 1985; Hallem 1987). The Alvarez hypothesis required interdisciplinary collaboration on a scale not yet seen in the paleontological field (Alvarez 1991). Acceptance of the Alvarez Impact Theory has led to a series of planetary projection programs, which aim to prevent a similar impact from occuring again (Smith 1985). The Impact Theory caused quite the sensation amongst the press as it was, literally, out of this world (Angier 1985). Evidence in support of Alvarez's impact theory includes the existence of the Chicxulub Crater off the coast of the Yucatan Peninsula (Henehan, 2019) and the global presence of a layer of rock abundant in shocked quartz (Bohor, B.F. et. al. 1987) and the "tomb stone" layer which contains unusually high levels of iridium, a mineral found more commonly in asteroids than on Earth (Becker 2002).

The Cretaceous/Paleogene (KPg) boundary is denoted by the "tombstone" layer of rock containing a spike of iridium, the disappearance of most Mesozoic megafauna including the non-avian dinosaurs and large marine reptiles (Irizarry, et. al. 2023; Jones, L.H. et. al. 2023), and a negative excursion in oxygen and carbon isotopes (Mount et. al 1986). The GSSP for the KPg boundary was ratified in 1991 and is located in El Kef, Tunisia as documented by the El Kef Coring Project (Molina, E., et. al 2006; Jones, L.H. et. al. 2023). It is located at the base of the Boundary Clay and at El Kef is characterized by a rust colored layer (Molina, E., et. al 2006). The layer contains many key indicators of the K-T boundary including geochemical anomalies, spherules, shocked quartz (Bohor, B.F. et. al. 1987), iridium spikes, and is considered to be isochronous globally in marine and continental sections (Molina, E., et. al 2006; Jones, L.H. et. al. 2023).

The pulse event, hereafter referred to as the 'KPg', occurred roughly 66 Mya (Renne, et al., 2013). The environmental fallout caused by the asteroid impact was immense and drove nearly 70% of Earth's species to extinction (Jablonski D, 1994; Aberhan and Kiessling, 2015; Jones, L.H. et. al. 2023). The impact would have kicked up an enormous dust cloud that rose into

the atmosphere, encircling the planet, and causing volcanic winters for years afterward (Alvarez et. al 1980). Reduced light would have led to a mass die off of photosynthetic organisms such as plants and plankton which led to a complete collapse of the ecological food chain across the planet (Alvarez et. al 1980). Additionally, air pollution brought on by the dust cloud would have caused acid rain to fall around the world, further damaging plant life. The superheated dust and debris falling back to earth would have caused forest fires across the globe. All together, the effects of the Chicxulub impact would have been devastating to marine and terrestrial ecosystems. To anything alive during that time, it would have felt like the end of the world.

#### 4. Introduction

Mass extinctions disrupt and reconfigure the balance of clade richness across the tree of life, often upending ecological hierarchies (Foote, 1997; Jablonski, 2005; Sclafani et al., 2018). Certain modes of life are lost and never regained, while others persist through either the survival of individual lineages or independent re-evolution (Jablonski, 2002; Jablonski, 2005; Sclafani et al., 2018; Wan et al., 2021).

The configuration of biodiversity in modern waters reflects the impact of the end-Cretaceous mass extinction (KPg), providing a good test for extinction selectivity amongst modern fauna (Aberhan and Kiessling, 2015). Additionally, this pulse event occurred over such a short period of time that it overrode natural selection, providing a good test for the role of certain traits with regard to general survival rates. Within bivalves 64% of genera were lost, but relatively few families went extinct. The difference between survival and extinction within families could be connected to three key traits-tiering, feeding, and mobility-which combined make up an organism's mode of life (MOL). I analyzed extinction selectivity across all bivalve genera known to exist during the KPg to determine which modes of life fared better and which of the three MOL traits most contributed towards genus survival.

Tiering in this context refers to the position of a marine organism relative to the substratum/water column (i.e. infaunal/epifaunal). In this study tiering is subdivided into six groups: intermediate epifaunal (benthic, extending upward into water column), low-level epifaunal (benthic, not extending upwards into water column), boring (chipping away at and digging into hard rocks), semi-faunal (partly infaunal, party exposed to water column), shallow infaunal (burrowing beneath substrate, living in the top 5 cm of the sediment), and deep infaunal (burrowing beneath substrate, living below the top 5 cm of the sediment). Different tiering positions (infaunal, epifaunal, etc.) may provide greater degrees of protection against environmental pressures leading to certain groups faring better in a global extinction event. (**Figure 1**).



**Figure 1.** Simplified sketch of the different bivalve tiers used in this study. Note that semi-infaunal bivalves actually extend farther up into the water column than most low-lying epifaunal bivalves on account of low-lying bivalves lying flat against the surface. Image credit: J. Sullivan (Adobe Illustrator).

Feeding strategies encompass how organisms acquire the necessary nutrients needed to maintain their own life. Due to time constraints, I only considered the primary method of feeding when assigning genera to feeding methods. However, it is important to note that it is common for bivalve taxa to have a secondary mode of feeding. In this study feeding was subdivided into five groups: carnivore (hunting/eating prey capable of resistance), chemosymbiotic (symbiosis in which bacteria provide chemically-derived energy and nutrients), deposit feeding (capturing loose particles from the substrate), suspension feeding/photosymbiosis (suspension feeding and symbiosis in which one of the participants is capable of photosynthesis), and suspension feeding (capturing food particles from the water). Suspension feeding/photosymbiosis is considered jointly as a single trophic strategy in this study due to the large number of Mesozoic bivalves that relied equally on both methods to gather food. Gathering food and other nutrients is vital to an organism's continued survival and different genera adapt different feeding strategies based on the environment they live in. During a massive upheaval in the global environment, one feeding strategy may become the dominant method as other groups die out due to lack of food.

Mobility refers to the extent that an organism is able to react in response to external stimuli while in its adult stage of life. There is a wide range of mobility, ranging from free-swimming and unattached to immobile and attached. For simplicity's sake and due to time

constraints I only considered whether taxa were mobile or immobile and did not include speed of movement or whether the taxa were normally attached or unattached. Being able to move away from environmental stressors is a key trait numerous organisms have evolved to ensure their survival. By that logic, bivalves that were able to move away from unfit environments during the KPg should have in theory fared better than bivalves that were unable to move.

Past research has shown that across the KPg bivalves lost relatively few MOLs. Despite there being general stability in the presence of MOLs across the KPg, there are distinct shifts in the abundance of certain MOLs across a variety of sites with mobile, shallow infaunal, deposit feeders seeming to fare better than other groups (Aberhan and Kiessling, 2015).

Following the line of research started by Aberhan and Kiessling (2015) and using a modified version of the ecospace model by Bambach et al. (2007), I assigned each bivalve genus that was known to exist during the Maastrictian to a unique MOL. Using Volume N of the *Treatise on Invertebrate Paleontology*, the Paleobiology Database (PBDB), and the Mount Holyoke fossil collection (**Figure 2**), I was able to build a database that encompasses the MOLs of all known bivalve genera that existed during the KPg. With this database I was able to analyze how various MOLs fared across the KPg boundary and test whether certain traits correlate with higher survival rates.

Building off of previous research, I initially thought that mobility would be the most important factor guarding against extinction. However, my results show a more complicated picture with tiering and feeding actually being more important than the ability to move. Of the fifteen unique MOLs, and the thirteen MOLs that had enough samples to properly analyze, only one went extinct (immobile, intermediate epifaunal, suspension feeder). Despite the relative stability of the MOLs, there were clearly groups hit harder than others. Semi-infaunal suspension feeders suffered the second greatest extinction level regardless of whether the taxa were mobile or sessile (81% for mobile taxa and 72% for sessile taxa) while sessile suspension feeding boring bivalves had the lowest extinction rate (<25%). Separating the three MOL traits, I found tiering to be the most important trait in guarding against extinction with feeding and mobility being of secondary and tertiary importance respectively. More exposed bivalves (intermediate epifaunal or semi-faunal) suffered the greatest extinction rates (100% and 77% respectively) while less exposed bivalves (boring and deep infaunal) had the lowest extinction rates (<25% and 43% respectively). Bivalve groups that relied on a combination of suspension feeding and photosynthesis (i.e. rudists) suffered a complete extinction whereas groups that used a chemosymbiotic strategy to feed suffered a less than 25% extinction rate. There is also a slight trend towards higher levels of mobility increasing survival rates (58% of sessile bivalves went extinct and 50% of mobile bivalves went extinct). There appears to be intersections between tiering and feeding that affects extinction rates; greater amounts of natural coverage and more reliable sources of food likely protected certain groups against extinction.

### 5. Materials & Methods

The database was built with data collected from the Paleobiology Database (PBDB), the *Treatise of Invertebrate Paleontology, Volume N*, and the Mount Holyoke College collection (**Figure 2**). Together these sources provided the family and genus name of the bivalve fauna alive during the KPg as well as information about tiering, feeding methods, and level of mobility. These sources also provided temporal ranges for families and genera, which was used to determine the victims and the survivors of the KPg. It was reasoned that the early Danian would have represented a recovery period after the KPg. Therefore, genera that went extinct during the early Danian were counted as victims since they were likely victims of secondary or tertiary extinctions that were still connected to the effects of the main KPg extinction event.



**Figure 2.** *Rastellum diluvianum* (Linnaeus, 1767). Cretaceous (Cenomanian; Tourtia), Essen, Germany. Mount Holyoke College fossil collection No. 4178, gift of the University of Bonn. Note the unusual elongate morphology of this oyster, a shape unknown in the marine biosphere today. *Rastellum diluvianum* is an immobile taxon. Scale bar in centimeters.

Using a modified version of the ecospace model by Bambach et al. (2007), I assigned each bivalve genus to a unique MOL based on its feeding strategy, tiering position, and mobility level. In total, there were fifteen unique MOLs, but only thirteen had enough data to be properly analyzed.

The data was analyzed in RStudio using simple algebra to determine the proportional extinction rates across test groups (**Figure 3**). First, I calculated extinction rates across the thirteen usable MOLs to determine which modes of life suffered the greatest and which ones suffered the least across the KPg. Then I calculated the extinction rates of bivalve genera based solely on feeding, tiering, and mobility in order to determine how much each trait seemed to affect extinction rates.



Figure 3. An example (screenshot from RStudio) of the code used to analyze collected data.

#### 6. Results

Based on my model there is a possibility for sixty MOLs amongst bivalves (**Figure 4**). However, only fifteen of those MOLs have fossil evidence of existing. Of those fifteen, only thirteen had sufficiently large data pools for analysis. Of those thirteen only one, MOL 5 (intermediate epifaunal, suspension feeding, immobile), went extinct. MOL 9 (semi-infaunal, suspension feeder, immobile) and MOL 10 (semi-infaunal, suspension feeder, mobile) suffered the greatest loss without complete extinction with an 81% and a 72% extinction rate respectively. MOL 1 (immobile, boring, suspension feeder) and MOL 2 (deep infaunal, chemosymbiotic feeding, mobile) suffered the least with less than 25% of their genera going extinct. The general trend appears to be that less exposed bivalves, ones that live on top of or under the substrate (low-level epifaunal, shallow/deep infaunal, and boring) suffered less than their more exposed cousins (intermediate epifaunal and semi-infaunal) (**Figure 5**).

	SUS IM	SUS M	DEP IM	DEP M	CHEMO IM	CHEMO M	CAR IM	CAR M	S/P IM	S/P M
BOR	3/ 19									
DE IN		22/ 43		14/ 29		5/22				
SH IN	4/ 15	77/ 139		4/ 12		0/1 (not used)		4/ 8		
SEMI IN	13/ 16	8/ 11								
LL EP	43/ 85	19/ 35						0/ 2 (not used)		
INT EP									39/39	

**Figure 4.** Table showing all possible MOLs for Bivalvia during the late-Cretaceous. BOR = boring, DE IN = deep infaunal, SH IN = shallow infaunal, SEMI IN = semi-infaunal, LL EP = low level epifaunal, INT EP = intermediate epifaunal. SUS IM = immobile suspension feeder, SUS M = mobile suspension feeder, DEP IM = immobile deposit feeder, DEP M = mobile deposit feeder, CHEMO IM = immobile chemosymbiotic feeder, CHEMO M = mobile chemosymbiotic feeder, CAR IM = immobile carnivore, CAR M = mobile carnivore, S/P IM = immobile suspension/photosymbiotic feeder, S/P M = mobile suspension/photosymbiotic feeder. Green squares marked represent MOLs that are represented in the fossil record, ratios in those boxes represent the number of victims over the number of genera present in those MOLs. MOLs with data pools too small to analyze are marked as "(not used)". Empty red squares represent MOLs that are not represented in the fossil record.



**Figure 5.** Proportional extinction rates across 13 unique MOLs. 1 – boring, suspension feeding, immobile. 2 – deep infaunal, chemosymbiotic feeding, mobile. 3 – deep infaunal, deposit feeding, mobile. 4 – deep infaunal, suspension feeding, mobile. 5 – intermediate epifaunal, suspension/photosymbiosis feeding, immobile. 7 – low-level epifaunal, suspension feeding, mobile. 8 – low-level epifaunal, suspension feeding, mobile. 9 – semi-infaunal, suspension feeding, immobile. 10 – semi-infaunal, suspension feeding, mobile. 11 – shallow infaunal, carnivore, mobile. 13 – shallow infaunal, deposit feeding, mobile. 14 – shallow infaunal, suspension feeding, mobile. 15 – shallow infaunal, suspension feeding, mobile.

Of the five unique feeding strategies, suspension/photosynthetic feeders suffered the highest extinction rates amongst genera, going completely extinct. Meanwhile, bivalves that relied solely on suspension feeding lost about 50% of their taxa. Chemosymbiotic feeders suffered the lowest extinction rates, losing less than 25% of genera (**Figure 6**). Note that there are substantially more suspension feeding bivalves present in Cretaceous and modern day oceans than bivalves with other feeding strategies.



**Figure 6.** Proportional extinction rates of bivalve genera based on dominant feeding strategy. CARNIV = carnivore. CHEMO = chemosymbiosis feeder. DEP = deposit feeder. SUS/PHOTO = suspension/photosymbiotic. SUS = suspension feeder.

There is a clear trend between comparatively more "exposed" bivalves and higher extinction rates. Intermediate epifaunal bivalves went completely extinct while semi-infaunal bivalves suffered a 77% extinction rate. Low-level epifaunal bivalves and shallow infaunal bivalves suffered similar levels of extinction with about 50% of their genera going extinct. Deep infaunal bivalves and boring bivalves experienced the lowest extinction rates, losing 43% and 15% percent of their genera respectively (**Figure 7**).



**Figure 7.** Proportional extinction rates of bivalves based on tiering. BOR = boring. DE IN = deep infaunal. INT EP = intermediate epifaunal. LL EP = low-level epifaunal. SEMI-IN = semi-infaunal. SH IN = shallow infaunal.

There appears to be a trend towards immobile bivalves (excepting boring bivalves) experiencing higher extinction rates. Immobile bivalves experienced a 58% percent extinction rate while mobile bivalves experienced a 50% extinction rate (**Figure 8**).



**Figure 8.** Proportional extinction rates between mobile and immobile bivalves shown as a bar graph. N = not mobile. Y = mobile.

### 7. Discussion

Past research has shown that the total number of MOLs amongst bivalves remained relatively stable across the KPg (Aberhan and Kiessling, 2015). My results continue to support that claim, with only one of the thirteen unique and usable MOLs going extinct (**Figure 5**). The data also suggests that tiering plays a significant role in the survival of genera. Genera that lived on the seafloor, burrowed underneath the sediment, or dug into hard rocks, in general fared better than genera that extended upward into the water column. When analyzed alongside feeding and mobility, bivalves that lived as either boring, deep infaunal, shallow infaunal, or low-level epifaunal taxa suffered lower extinction rates than bivalves that lived as intermediate epifaunal or semi-infaunal taxa (**Figure 5**). When analyzed by itself, boring bivalves and deep infaunal bivalves experienced the lowest extinction rates (15% and 43% respectively) while shallow

infaunal and low-level epifaunal bivalves both experienced roughly 50% extinction, semi-infaunal bivalves lost over 75% of the total genera, and intermediate epifaunal bivalves went completely extinct (**Figure 7**). It is likely that burrowing deeper into the sediment or carving out homes in hard substrate like rocks provided some genera with a greater degree of protection from external perturbation. Meanwhile, living just on top of or just below the sediment-water interface left those bivalves more exposed to the elements and therefore put them at greater risk. If that was the case then bivalves that were even more exposed, the ones that grew upward into the water column (i.e. intermediate epifaunal and semi-infaunal bivalves), would have been at the highest risk of extinction. This might, at least partially, explain why many widely successful groups of intermediate epifaunal bivalves went extinct and why that mode of life never reappeared.

When feeding strategies were analyzed alongside mobility and tiering, there were some cases where the intersection of feeding and tiering likely played a role in the organisms' survival (**Figure 5**). For example, bivalves that relied both on suspension feeding and photosymbiosis went completely extinct (**Figure 6**). The only bivalves that used this method of feeding were the rudists, which were also the only group of bivalves to build upwards into the water column (intermediate epifaunal). It is a common strategy amongst photosynthetic organisms to grow upwards so that they can better access the sun's rays. If the rudists utilized similar strategies to optimize their own photosynthetic capabilities, then they would have been exposing themselves more to the environment. During the KPg extinction, they would have had less protection than bivalves that remained close to or underneath the ocean floor. Additionally, the cloud of dust and debris kicked up by the asteroid impact blocked the suns' rays for years after the impact, limiting the abilities of photosynthetic organisms to gather food.

Meanwhile, bivalves that relied on chemosymbiosis suffered the lowest rate of extinction, with less than 25% of their genera going extinct (**Figure 6**). Chemosymbiotic bivalves are associated with harsh environments (i.e. areas of low oxygen, hydrocarbon seeps, volcanoes, vents) (Taylor and Glover, 2010). It is likely that a chemosymbiotic lifestyle allowed these bivalves to be more resilient to environmental pressures, because they: 1) were engaging in a type of primary production, and thus had ready access to food sources, and 2) were accustomed to dealing with aqueous fluctuations in redox potential, etc. This would have given them a better chance at surviving a mass extinction. These bivalves also happened to be deep-infaunal bivalves, a tiering group that experienced the second lowest extinction rate across all bivalves (**Figures 5**, 7). Of all the deep infaunal bivalves, chemosymbiotic taxa suffered the lowest extinction rates (<25% extinction), which represents a clear case in how the intersectionality of feeding and tiering affects survival (**Figure 5**). Whereas chemosymbiosis leads bivalves to evolve to be tougher to combat the harsh environments, photosynthesis can leave taxa exposed to environmental pressures. Meanwhile, despite chemosymbiotic bivalves fareing better than bivalves with different feeding strategies when looked at in a vacuum, the group that overall

suffered the lowest extinction rates were suspension feeders as they were boring bivalves (**Figures 5**, 7).

Deposit feeders, suspension feeders, and carnivores all suffered intermediate levels of extinctions; 40% extinction across all carnivores, 43% extinction across all deposit feeders, and 52% extinction across all suspension feeders (**Figure 6**). Deposit feeding, suspension feeding, and carnivory are all versatile modes of feeding that can lead organisms to live in a multitude of environments, leading some populations to be more exposed and others to have more protection. The majority of the bivalves that utilized these modes of feeding were either boring, low-level epifaunal, or shallow/deep infaunal bivalves (**Figure 5**). All of these groups suffered extinction rates around 50% (**Figure 7**). The group of suspension feeders that lived as semi-infaunal organisms experienced much higher mortality (over 75% percent of total genera), likely due to them being more exposed than bivalves living just on top of or under the sediment (**Figure 7**).

There appears to be a slight trend towards mobility guarding against extinction. Across all Bivalvia, 58% percent of immobile bivalves went extinct while only 50% percent of mobile bivalves went extinct (**Figure 8**). However, when analyzed alongside tiering and feeding, being mobile only appeared to be an added protector against extinction in one case. Of the semi-epifaunal suspension feeding bivalves, immobile taxa suffered an 81% extinction rate while their mobile cousins suffered a 72% extinction rate, a nearly 10% percent difference (**Figure 5**). However, there are also examples of mobile taxa suffering higher extinction rates than immobile taxa. Among shallow infaunal suspension feeders, immobile taxa suffered a 26% mortality rate while their mobile counterparts lost over 50% of their genera (**Figure 5**). A similar, though less extreme, example occurs among low-level epifaunal suspension feeders: immobile bivalves lost 50% of their taxa while mobile bivalves lost 54% of their taxa (**Figure 5**). MOL 1 suffered the lowest extinction rate, and those bivalves were all immobile (**Figure 5**). The average adult bivalve will not travel great distances during its lifetime, so compared to traits like feeding and tiering, mobility as an adult may not be as vital in guarding against extinction.

#### 8. Conclusions

Initially my hypothesis was that mobility would be the most important factor for avoiding extinction. However, of the three traits studied (tiering, feeding, and mobility), tiering appears to be the most important with regards to survival across the KPg. Bivalves that lived in environments that provided inherent protections experienced lower rates of extinction than bivalves that lived in environments that left them more exposed (**Figures 5**, 7). Feeding strategy seems to be secondary, with some modes of feeding suffering lower extinction rates and others experiencing much higher extinction rates (**Figures 5**, 6). Chemosymbiotic bivalves suffered the lowest levels of extinction across bivalves when only feeding was considered (**Figure 6**). However, when MOLs were looked at holistically, the group that fared the best were from MOL 1 and were suspension feeders who lived by boring into hard substrate and rocks (**Figure 5**). Across all of Bivalvia mobile bivalves suffered a lower extinction rate than immobile bivalves,

but when considered alongside feeding and tiering, mobility was not shown to be a definitive trait that protected against extinction. There are examples of mobile bivalves suffering lower extinction rates than immobile bivalves—as in the case with the semi-infaunal suspension feeders—but more often mobile genera suffered higher extinction rates than immobile genera, and the bivalve group that suffered the lowest rate of extinction overall were boring, *immobile*, suspension feeders (**Figure 5**).

When it comes to surviving a mass extinction as a bivalve, location and natural protection seems to be the most important factor with feeding strategy being of secondary importance and mobility not greatly affecting overall survival.

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#### 10. References

Aberhan, M., & Kiessling, W. (2015). Persistent ecological shifts in marine molluscan assemblages across the end-Cretaceous mass extinction. *Proceedings of the National Academy of Sciences U.S.A*, *112*(23), 7207–7212. https://doi.org/10.1073/pnas.1422248112

Angier, N., (1985). "Did Comets Kill the Dinosaurs? A Bold New Theory About Mass Extinctions". *Time*. Volume 125, number 18, pages 72-83.

Alvarez et. al., (1980). "Extraterrestrial Cause for Cretaceous-Tertiary Extinction". *Science*. Volume 208, number 4448, pages 1095-1108.

Alvarez, W., et. al. (1984), "Impact Theory of Mass Extinctions and the Invertebrate Fossil Record". *Science*. Volume 223, number 4641, pages 1135-1141.

Alvarez, W., (1991). "The Gentle Art of Scientific Trespassing". *GSA Today*. Volume 1, number 2, pages 1-34.

Bambach, R.K., Bush, A.M., Erwin, D.H., "Autecology and the filling of ecospace: Key metazoan radiations". *Palaeontology* 50, 1–22 (2007). https://doi.org/10.1111/j.1475-4983.2006.00611.x

Becker, Luann (2002). "Repeated Blows" (PDF). *Scientific American*. **286** (3): 77–83. Bibcode:2002SciAm.286c..76B. doi:10.1038/scientificamerican0302-76. PMID 11857903. Retrieved April 26, 2023.

Bohor, B.F., et. al. (1987). "Shocked Quartz in the Cretaceous-Tertiary Boundary Clays: Evidence for a global distribution". *Science*. Volume 236, pages 705-709.

Foote, M. (1997). The evolution of morphological diversity. *Annual Review of Ecology and Systematics*, 28(1), 129–152. <u>https://doi.org/10.1146/annurev.ecolsys.28.1.129</u>

Gould, S.J., (1984). "Sex, Drugs, Disasters, and the Extinction of Dinosaurs". *Discover*. Volume 5, number 3, pages 67-72.

Hallem, A., (1987), "End-Cretaceous Mass Extinction Event: Argument for Terrestrial Causation". *Science*. Volume 238, pages 1237-1242.

Henehan, M.J., (2019). "Rapid Ocean Acidification and Protracted Earth System Recovery Followed the end-Cretaceous Chicxulub Impact". *Proceedings of the National Academy of Sciences (USA)*. Volume 116, number 45, pages 22500-22504.

Hoffman, A., Netecki, M.H., (1985). "Reception of the Asteroid Hypothesis of Terminal Cretaceous Extinctions". *Geology*. Volume 13, pages 884-887.

Irizarry, K.M., et. al., (2023). "Faunal and Stratigraphic Analysis of the Basal Cretaceous-Paleogene (K-Pg) Boundary Event Deposits, Brazos River, Texas USA". *Palaeogeography, Palaeoclimatology, Palaeoecology*. Volume 610. doi: https://doi.org/10.1016/j.palaeo.2022.111334

Jablonski, D. (2002). "Survival without recovery after mass extinctions". *Proceedings of the National Academy of Sciences*. Volume 99, number 12, pages 8139–8144. https://doi.org/10.1073/pnas.102163299

Jablonski, D. (2005). "Mass extinctions and macroevolution". *Paleobiology*, Volume 31, number 5, pages 192–210. https://doi.org/10.1666/0094-8373(2005)031[0192:MEAM]2.0.CO;2

Jones, L.H., et. al., (2023). "Stratigraphy of the Cretaceous/Paleogene (K/Pg) boundary at the Global Stratotype Section and Point (GSSP) in El Kef, Tunisia: New insights from the El Kef Coring Project". *GSA Bulletin* 2023; doi: https://doi.org/10.1130/B36487.1

Moore, R. C. (1953). *Treatise on invertebrate paleontology : prepared under the guidance of the Joint Committee on Invertebrate Paleontology*. Geological Society of America and University of Kansas Press [Lawrence].

Mount, J.F., et al. (1986). "Carbon and Oxygen Isotope Stratigraphy of the Upper Maastrichtian, Zumaya, Spain: A Record of Oceanographic and Biologic Changes at the end of the Cretaceous". *Palaios*. Volume 1, pages 87-92.

Mount Holyoke College Fossil Collection. Accessed from September 2022-May 2023.

Paleobiology Database (2022). *The Paleobiology Database*. Accessed from September 2022–May 2023. <u>https://paleobiodb.org/#/</u>

Renne; et al. (2013). "Time Scales of Critical Events Around the Cretaceous-Paleogene Boundary". *Science*. Volume 339, number 6120, pages 684–687. Bibcode:2013Sci...339..684R. doi:10.1126/science.1230492. PMID 23393261. S2CID <u>6112274</u>

Sclafani, J. A., Congreve, C. R., Krug, A. Z., & Patzkowsky, M. E. (2018). "Effects of mass extinction and recovery dynamics on long-term evolutionary trends: A morphological study of Strophomenida (Brachiopoda) across the Late Ordovician mass extinction". *Paleobiology*, Volume 44, number 4, pages 603–619. https://doi.org/10.1017/pab.2018.24

Smith, J.V., (1985). "Protection of the Human Race Against Natural Hazards (Asteroids, Comets, Volcanoes, Earthquakes)". *Geology*. Volume 13, pages 675-678.

Taylor, J.D., Glover, E.A. (2010). "Chemosymbiotic Bivalves. In: Kiel, S. (eds) The Vent and Seep Biota". *Topics in Geobiology*, Volume 33, pages 107-135. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-9572-5\_5

Wan, J., Foster, W. J., Tian, L., Stubbs, T. L., Benton, M. J., Qiu, X., & Yuan, A. (2021). "Decoupling of morphological disparity and taxonomic diversity during the end-Permian mass extinction". *Paleobiology*. Volume 47, number 3, pages 402–417. <u>https://doi.org/10.1017/pab.2020.57</u>

## **Supplemental Material**

### S1. Supplemental Data

- S1.1. To see my completed dataset, please follow the following link: <u>https://docs.google.com/spreadsheets/d/e/2PACX-1vT45\_pDsrFSAwn-7o4Je8Lfb7ld2qZM</u> <u>9Fmwa2YDh tYOYd9h kKza21RR9Pvib3NnUZi-UYEdu9d62h/pubhtml</u>
- S1.2. The Paleobiology Database can be accessed through this link: <u>https://paleobiodb.org/#/</u>
- S1.3. *The Treatise of Invertebrate Paleontology, Volume N*, is available for loan from the Mount Holyoke College Library

### **S2.** Supplemental Methods

### Copy of R-Code:

S2.1.1. {

- S2.1.2. #Sullivan Thesis Code
- S2.1.3.
- S2.1.4. #install.packages('ggplot2')
- S2.1.5. #install.packages('ggpubr')
- S2.1.6. #install.packages('ggrepel')
- S2.1.7. #install.packages('geomorpj')
- S2.1.8. #install.packages('Morpho')
- S2.1.9. #install.packages('imager')
- S2.1.10. #install.packages('cowplot')
- S2.1.11. #install.packages('grid')
- S2.1.12. #install.packages('jpeg')
- S2.1.13. #install.packages('png')
- S2.1.14. #install.packages('parallel')
- S2.1.15. #install.packages('DT')
- S2.1.16. #install.packages('googlesheet4')
- S2.1.17. #install.packages('tidyverse')
- S2.1.18. # library(ggpubr)
- S2.1.19. library(ggplot2)
- S2.1.20. library(ggrepel)
- S2.1.21. library(geomorph)
- S2.1.22. library(Morpho)
- S2.1.23. library(imager)
- S2.1.24. library(cowplot)
- S2.1.25. library(grid)
- S2.1.26. library(jpeg)
- S2.1.27. library(png)
- S2.1.28. library(parallel)

- S2.1.29. library(DT)
- S2.1.30. library(googlesheets4)
- S2.1.31. library(tidyverse)
- S2.1.32.
- S2.1.33. MOBILITY <-

read\_sheet('https://docs.google.com/spreadsheets/d/1U9Psur8mCVl2nkero670oQPe6IjQ
50uodE6EVCcpfRY/edit#gid=0',

S2.1.34. sheet='DATA',na=c("NA","#N/A","")) S2.1.35. S2.1.36. } S2.1.37. S2.1.38. df <- MOBILITY S2.1.39. S2.1.40. df %>% S2.1.41. count(Family) S2.1.42. S2.1.43. df %>% S2.1.44. count(Family, Tiering, Feeding) S2.1.45. S2.1.46. df %>% S2.1.47. group by(Family) %>% count(Tiering,Feeding, 'Genus Mobile', 'Gensus-V-or-S') %>% S2.1.48. S2.1.49. spread(`Gensus-V-or-S`,n,fill=0) S2.1.50. S2.1.51. MOL <- df %>% S2.1.52. group by(`Gensus-V-or-S`) %>% S2.1.53. count(Tiering,Feeding,'Genus Mobile') %>% S2.1.54. spread(`Gensus-V-or-S`,n,fill=0) %>% mutate(ntot.mol=S+V, S2.1.55. propext=V/ntot.mol) %>% S2.1.56. S2.1.57. mutate(MOL, mol=paste(Tiering,Feeding,`Genus Mobile`)) S2.1.58. S2.1.59. #define new column S2.1.60. X <- c('1','2','3','4','5','6','7','8', S2.1.61. S2.1.62. '9','10','11','12','13','14','15') S2.1.63. S2.1.64. MOL new <- cbind(MOL,X)S2.1.65. S2.1.66.

S2.1.67.	#MOL Graphs
S2.1.68.	
S2.1.69.	Plot1 <- ggplot(MOL_new, aes(x=X,y=propext)) +
S2.1.70.	geom_col() +
S2.1.71.	labs(x='Mode of Life',y='Proportional Extinction') +
S2.1.72.	theme(axis.title = element_text(size = $20$ ),
S2.1.73.	axis.text.x = element_text(size=15, color = 'black'),
S2.1.74.	axis.text.y = element_text(size=15, color = 'black'))
S2.1.75.	
S2.1.76.	#Edited MOL
S2.1.77.	
S2.1.78.	MOLV2 <- MOL_new %>% slice(1,2,3,4,5,7,8,9,10,11,13,14,15)
S2.1.79.	
S2.1.80.	Plot1.2 <- ggplot(MOLV2, aes(x=factor(X, X),y=propext)) +
S2.1.81.	geom_col() +
S2.1.82.	<pre>labs(x='Mode of Life',y='Proportional Extinction') +</pre>
S2.1.83.	theme(axis.title = element_text(size = 20),
S2.1.84.	<pre>axis.text.x = element_text(size=15, color = 'black'),</pre>
S2.1.85.	axis.text.y = element_text(size = 15, color = 'black'))
S2.1.86.	
S2.1.87.	#Feeding
S2.1.88.	
S2.1.89.	df %>%
S2.1.90.	count(Feeding)
S2.1.91.	
S2.1.92.	df %>%
S2.1.93.	group_by(Feeding) %>%
S2.1.94.	summarise(n = n()) $\% > \%$
S2.1.95.	mutate(Freq = n/sum(n))
S2.1.96.	
S2.1.97.	FEED <- df %>%
S2.1.98.	group_by(Feeding) %>%
S2.1.99.	count(`Gensus-V-or-S`) %>%
S2.1.100.	spread(`Gensus-V-or-S`,n,fill=0) %>%
S2.1.101.	mutate(ntot.fee=S+V,
S2.1.102.	propext=V/ntot.fee) %>%
S2.1.103.	ungroup()
S2.1.104.	
S2.1.105.	#Feeding graphs
S2.1.106.	

S2.1.107.	Plot2 <- ggplot(FEED, aes(x=Feeding,y=propext)) +
S2.1.108.	geom_col() +
S2.1.109.	<pre>labs(x='Feeding Method',y='Proportional Extinction') +</pre>
S2.1.110.	theme(axis.title = element_text(size = 20),
S2.1.111.	<pre>axis.text.x = element_text(size=15, color = 'black'),</pre>
S2.1.112.	axis.text.y = element_text(size = 15, color = 'black'))
S2.1.113.	
S2.1.114.	#Tiering
S2.1.115.	
S2.1.116.	df %>%
S2.1.117.	count(Tiering)
S2.1.118.	
S2.1.119.	df %>%
S2.1.120.	group_by(Tiering) %>%
S2.1.121.	summarise(n = n()) %>%
S2.1.122.	mutate(Freq = n/sum(n))
S2.1.123.	
S2.1.124.	TIER <- df %>%
S2.1.125.	group_by(Tiering) %>%
S2.1.126.	count(`Gensus-V-or-S`) %>%
S2.1.127.	spread(`Gensus-V-or-S`,n,fill=0) %>%
S2.1.128.	mutate(ntot.tie=S+V,
S2.1.129.	propext=V/ntot.tie) %>%
S2.1.130.	ungroup()
S2.1.131.	
S2.1.132.	#Tiering Graph
S2.1.133.	
S2.1.134.	Plot3 <- ggplot(TIER, aes(x=Tiering,y=propext)) +
S2.1.135.	geom_col() +
S2.1.136.	labs(x='Tiering',y='Proportional Extinction') +
S2.1.137.	theme(axis.title = element_text(size = 15),
S2.1.138.	<pre>axis.text.x = element_text(size=12, color = 'black'),</pre>
S2.1.139.	axis.text.y = element_text(size = 12, color = 'black'))
S2.1.140.	
S2.1.141.	#Mobility
S2.1.142.	
S2.1.143.	df %>%
S2.1.144.	count(`Genus Mobile`)
S2.1.145.	
S2.1.146.	mob <- df %>%

S2.1.147.	group_by(`Genus Mobile`) %>%
S2.1.148.	count(`Gensus-V-or-S`) %>%
S2.1.149.	spread(`Gensus-V-or-S`,n,fill=0) %>%
S2.1.150.	mutate(ntot.mob=S+V,
S2.1.151.	propext=V/ntot.mob) %>%
S2.1.152.	ungroup()
S2.1.153.	
S2.1.154.	#Mobility graph
S2.1.155.	
S2.1.156.	Plot4 <- ggplot(mob, aes(x=`Genus Mobile`,y=propext)) +
S2.1.157.	geom_col() +
S2.1.158.	labs(x='Mobility',y='Proportional Extinction') +
S2.1.159.	theme(axis.title = element_text(size = $15$ ),
S2.1.160.	<pre>axis.text.x = element_text(size=12, color = 'black'),</pre>
S2.1.161.	axis.text.y = element_text(size = 12, color = 'black'))
S2.1.162.	
S2.1.163.	#old code
S2.1.164.	#total extinction data
S2.1.165.	
S2.1.166.	T_EXT <- MOBILITY %>%
S2.1.167.	group_by(Family) %>%
S2.1.168.	count(`Gensus-V-or-S`) %>%
S2.1.169.	spread(`Gensus-V-or-S`,n,fill=0) %>%
S2.1.170.	mutate(ntot.fam=S+V,
S2.1.171.	propext=V/ntot.fam) %>%
S2.1.172.	ungroup()
S2.1.173.	
S2.1.174.	#total mobility data
S2.1.175.	
S2.1.176.	T_MOB <- MOBILITY %>%
S2.1.177.	group_by(Family) %>%
S2.1.178.	count(`Genus Mobile`) %>%
S2.1.179.	spread(`Genus Mobile`,n,fill=0) %>%
S2.1.180.	mutate(ntot.fam=Y+N,
S2.1.181.	propimob=N/ntot.fam) %>%
S2.1.182.	ungroup()
S2.1.183.	
S2.1.184.	#join data
S2.1.185.	
S2.1.186.	TDATA <- left_join(T_EXT,T_MOB,by='Family')

S2.1.187.	
S2.1.188.	#total graph
S2.1.189.	
S2.1.190.	Total <- ggplot(TDATA, aes(x=propext,y=propimob)) +
S2.1.191.	geom_count(shape=10) +
S2.1.192.	geom_smooth(method='lm') +
S2.1.193.	<pre>scale_size_continuous(range=c(4,10), name = 'No. of families\noccupying</pre>
space	)') +
S2.1.194.	labs(x = 'Proportional Extinction',
S2.1.195.	y = 'Proportion of Immobile Genera') +
S2.1.196.	theme(axis.title = element_text(size = $15$ ),
S2.1.197.	<pre>axis.text.x = element_text(size=10, color = 'black'),</pre>
S2.1.198.	<pre>axis.text.y = element_text(size = 10, color = 'black')) +</pre>
S2.1.199.	theme(legend.box.background=element_rect(color='black'),
S2.1.200.	<pre>legend.title = element_text(size=15, color = 'black'),</pre>
S2.1.201.	<pre>legend.text = element_text(size=15, color = 'black'),</pre>
S2.1.202.	legend.key.size = unit(1, 'cm'),
S2.1.203.	legend.position = "bottom")
S2.1.204.	
S2.1.205.	#FW data
S2.1.206.	
S2.1.207.	FW <- MOBILITY %>%
S2.1.208.	filter(Tiering=='FW IN')
S2.1.209.	
S2.1.210.	#FW extinction data
S2.1.211.	
S2.1.212.	FW_EXT <- FW %>%
S2.1.213.	group_by(Family) %>%
S2.1.214.	count(`Gensus-V-or-S`) %>%
S2.1.215.	spread(`Gensus-V-or-S`,n,fill=0) %>%
S2.1.216.	mutate(ntot.fam=S+V,
S2.1.217.	propext=V/ntot.fam) %>%
S2.1.218.	ungroup()
S2.1.219.	
S2.1.220.	#FW mobility data
S2.1.221.	
S2.1.222.	FW_MOB <- FW %>%
S2.1.223.	group_by(`Family`) %>%
S2.1.224.	count(`Genus Mobile`) %>%
S2.1.225.	spread(`Genus Mobile`,n,fill=0) %>%

S2.1.226.	mutate(ntot.fam=Y,
S2.1.227.	propimob=Y/ntot.fam) %>%
S2.1.228.	ungroup()
S2.1.229.	
S2.1.230.	#Join FW data
S2.1.231.	
S2.1.232.	FW_DATA <- left_join(FW_EXT,FW_MOB,by='Family')
S2.1.233.	
S2.1.234.	
S2.1.235.	#filter OUT FW data
S2.1.236.	
S2.1.237.	MARINE <- MOBILITY %>%
S2.1.238.	filter(Tiering!='FW IN')
S2.1.239.	
S2.1.240.	# extinction Data
S2.1.241.	
S2.1.242.	M_EXT <- MARINE %>%
S2.1.243.	group_by(Family) %>%
S2.1.244.	count(`Gensus-V-or-S`) %>%
S2.1.245.	spread(`Gensus-V-or-S`,n,fill=0) %>%
S2.1.246.	mutate(ntot.fam=S+V,
S2.1.247.	propext=V/ntot.fam) %>%
S2.1.248.	ungroup()
S2.1.249.	
S2.1.250.	# mobility data
S2.1.251.	
S2.1.252.	M_MOB <- MARINE %>%
S2.1.253.	group_by(Family) %>%
S2.1.254.	count(`Genus Mobile`) %>%
S2.1.255.	spread(`Genus Mobile`,n,fill=0) %>%
S2.1.256.	mutate(ntot.fam=Y+N,
S2.1.257.	propimob=N/ntot.fam) %>%
S2.1.258.	ungroup()
S2.1.259.	
S2.1.260.	# join data (Ext and Mob)
S2.1.261.	
S2.1.262.	MDATA <- left_join(M_EXT,M_MOB,by='Family')
S2.1.263.	
S2.1.264.	#df <- data.frame(propext,propimob)
S2.1.265.	

S2.1.266.	#cor(propext, propimob)
S2.1.267.	
S2.1.268.	# extinction levels vs. immobility
S2.1.269.	
S2.1.270.	<pre>#ggplot(MDATA, aes(x=propimob,y=propext)) +</pre>
S2.1.271.	#geom_point(shape=10,size=10) +
S2.1.272.	#geom_abline(intercept=0,slope=1,lty=2,col='grey60') +
S2.1.273.	#geom_smooth(method='lm')
S2.1.274.	
S2.1.275.	<pre>#ggplot(MDATA, aes(x=propext,y=propimob)) +</pre>
S2.1.276.	<pre># geom_point(shape=10,size=10) +</pre>
S2.1.277.	<pre># geom_abline(intercept=0,slope=1,lty=2,col='grey60') +</pre>
S2.1.278.	<pre># geom_smooth(method='lm')</pre>
S2.1.279.	
S2.1.280.	#Marine Graph
S2.1.281.	
S2.1.282.	Marine <- ggplot(MDATA, aes(x=propext,y=propimob)) +
S2.1.283.	geom_count(shape=10) +
S2.1.284.	geom_smooth(method='lm') +
S2.1.285.	<pre>scale_size_continuous(range=c(4,10), name = 'No. of families\noccupying</pre>
space'	)+
S2.1.286.	labs(x = 'Proportional Extinction',
S2.1.287.	y = 'Proportion of Immobile Genera') +
S2.1.288.	theme(axis.title = element_text(size = $15$ ),
S2.1.289.	axis.text.x = element_text(size=10, color = 'black'),
S2.1.290.	axis.text.y = element_text(size = 10, color = 'black')) +
S2.1.291.	theme(legend.box.background=element_rect(color='black'),
S2.1.292.	legend.title = element_text(size=15, color = 'black'),
S2.1.293.	legend.text = element_text(size=15, color = 'black'),
S2.1.294.	legend.key.size = unit(1, 'cm'),
S2.1.295.	legend.position = "bottom")
S2.1.296.	
S2.1.297.	P_Blank <- ggplot(MDATA, aes(x=propext,y=propimob)) +
S2.1.298.	geom_point(shape=NA) +
S2.1.299.	labs(x='Proportional Extinction',
S2.1.300.	y='Proportion of Immobile Genera') +
S2.1.301.	theme(legend.position = 'none') +
S2.1.302.	theme(axis.title = element_text(size = $15$ ),
S2.1.303.	axis.text.x = element_text(size=10, color = 'black'),
S2.1.304.	axis.text.y = element_text(size = 10, color = 'black'))

S2.1.305.	
S2.1.306.	plot_grid(T_Proposal,P_Blank,nrow = 2,labels = 'auto')
S2.1.307.	
S2.1.308.	# tiering data
S2.1.309.	
S2.1.310.	# feeding data
S2.1.311.	
S2.1.312.	# lifestyle data
S2.1.313.	
S2.1.314.	LS <- MOBILITY %>%
S2.1.315.	group_by(Family) %>%
S2.1.316.	count('Feeding')
S2.1.317.	
S2.1.318.	# join data (LF and Ext)
S2.1.319.	
S2.1.320.	LSDATA <- left_join(LS,EXT,by='Family')
S2.1.321.	
S2.1.322.	# lifestyle vs. propotional extinctions
S2.1.323.	
S2.1.324.	ext_ls <- ggplot(LSDATA,aes(x=propext, y=Lifestyle)) +
S2.1.325.	geom_count(shape=10) +
S2.1.326.	<pre>scale_size_continuous(range=c(4,10), name = 'No. of families\noccupying</pre>
space')	
S2.1.327.	
S2.1.328.	# join data (LS and Mob)
S2.1.329.	
S2.1.330.	x <- left_join(LS,MOB,by='Family')
S2.1.331.	
S2.1.332.	test1 <- ggplot(x,aes(x=Lifestyle,y=N)) +
S2.1.333.	geom_col()
S2.1.334.	
S2.1.335.	test2 <- ggplot(x,aes(x=Lifestyle,y=Y)) +
S2.1.336.	geom_col()
S2.1.337.	
S2.1.338.	plot_grid(test1,test2)

# **S1.** Supplemental Results



**Supplemental Figure 1.** Proportional extinction rates between mobile and immobile bivalves shown as a scatter plot. Points sized by the number of families occupying that space. Blue line represents the trend line.