

ABSTRACT

Phanerozoic Trends in the Ecological Tolerance of *Lingula* and Extinction Selectivity of Marine Invertebrates

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Environmental affinity analyses of *Lingula* throughout the Phanerozoic for depth, lithology, grainsize, and latitude using three different affinity metrics reveal that lingulids have high ecological tolerance relative to other brachiopods and marine invertebrates. Lingulids were generalist with regards to depth, grainsize, and latitude, and were siliciclastic specialists throughout much of the Phanerozoic. Generalist behavior was observed for all four metrics following certain mass extinction events such as the end-Permian mass extinction. Logistic regression analyses reveal that generalists and specialists are selected for during many extinction and background times throughout the Phanerozoic. Depth and Lithology ecological tolerance were the most significant determinants of extinction risk. Taxa with a high depth or lithology tolerance were more likely to survive many extinction events, whereas specialist selectivity is more common during background intervals. Overall, ecological tolerance plays a role in determining extinction risk over geologic time and the high ecological tolerance of *Lingula* could provide a mechanism for its longevity and success following mass extinction events.

Phanerozoic Trends in the Ecological Tolerance of *Lingula* and Extinction Selectivity of Marine Invertebrates

by

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CHAPTER ONE

Introduction

The lingulids are an extant group of inarticulate brachiopods that originated in the Early Cambrian. Lingulid brachiopods survived all five first-order mass extinction events and appear to be pervasive during times of ecological or environmental crises. However, the mechanisms favoring the survival of lingulid brachiopods throughout the Phanerozoic are poorly understood (Rodland and Bottjer, 2001; Kowalewski and Flessa, 1996; Smith and Bunje, 1999; Zonneveld et al., 2007; Peng et al., 2007; Simpson and Harnik, 2009; Posenato et al., 2014; Petsios and Bottjer, 2016). Lingulid brachiopods have been identified as “disaster taxa” for the end-Permian mass extinction (Hallam and Wignall, 1997; Rodland and Bottjer, 2001; Peng et al., 2007; Posenato et al., 2014; Petsios and Bottjer, 2016), and as an ecological opportunist by Zonneveld et al. (2007).

Following the 5 first-order mass extinction events there are distinct faunas that proliferate and dominate the marine realm in the immediate aftermath of the extinction (Fischer and Arthur, 1977; Kauffman and Harries, 1996). These faunas are termed “disaster taxa”, and are defined as opportunistic, r-strategists that are facies independent, were not abundant prior to the extinction, and live in high-dominance low-evenness paleocommunities (Fischer and Arthur, 1977; Kauffman and Harries, 1996). The lingulid brachiopods were first demonstrated to be a disaster taxon by Rodland and Bottjer (2001), based on the opportunistic nature of *Lingula* in the aftermath of the end-Permian mass extinction. This study took place in the Dinwoody Formation of Montana and

Wyoming, and it documented that Linguliform brachiopods dominated suboxic, high-organic-matter facies as hypothesized by Wignall and Hallam (1992) and Allison et al.,(1995). Petsios and Bottjer (2016) did a quantitative ecological study of lingulid brachiopods and other bivalve disaster taxa following the EPME. Their methods included assessing the relative abundance of these disaster taxa throughout the Induan, Smithian, and Spathian, as an indicator of ecosystem complexity and recovery (Petsios and Bottjer, 2016). In addition, the abundance of the lingulid trace fossil *Lingulichnus*, or the lingulid dwelling trace, was studied in the Early Triassic (Zonneveld et al., 2007). The presence or absence of lingulid burrows was deemed an insignificant proxy for lingulid abundance and environmental distribution. Peng et al., (2007) and Posenato et al. (2014), are among few other papers to suggest potential mechanisms for lingulid success following the end-Permian mass extinction or the EPME. Lingulid brachiopod ecology throughout the Phanerozoic, besides the Permian and Early Triassic, is poorly documented. However, there are few studies that describe the paleoecology of lingulid-dominated environments in the Cambrian, Ordovician, and Cretaceous (Biernat and Emig, 1993; Holmer and Nakrem, 2012; Ferguson, 1963; Bassett et al., 1999; Zhang et al., 2010; Koevoets et al., 2019). Smith and Bunje, (1999) were one of the few studies to examine changes in lingulid brachiopods throughout the Phanerozoic. They found that richness decreased into the Mesozoic, but morphologic diversity did not decrease until after the Paleozoic. The overall focus on Permian lingulid studies and localized paleoecology studies scattered throughout the Phanerozoic suggests that there are many unanswered questions involving lingulid paleoecology. There is a need to utilize the various studies within the PBDB to

answer questions regarding the opportunistic behavior, and adaptive change of lingulids over time to truly grasp how organisms and ecosystems recover from extinction.

Many biologists have extensively studied modern lingulid ecology, biomineralization and taphonomy, as well as their modern environmental preferences. *Lingularia* and *Lingula* brachiopods that occupy the modern ocean are claimed to be “living fossils” (Biernat and Emig, 1993; Craig, 1952; Ferguson, 1963; Posenato et al., 2014; Petsios and Bottjer, 2016). However, Emig (2003) suggested that although the linguliform body plan is largely unchanged from the Cambrian there are differences in shell shape and overall morphology that suggests that modern organisms are different from those in the Paleozoic. Today, modern lingulid brachiopods are found mostly in shallow, fine-grained, muddy sediments, and are mostly infaunal (Emig, 1997; Hammond, 1983; Worcester, 1969; Allison et al., 1995; Chuang, 1959; Paine, 1963, 1970; Hamlen and Lum, 1962). The lingulids also are tolerant to high salinities and high temperatures but die off at low temperatures less than 18°C (Emig, 1997; Hammen and Lum, 1977; Gunter and Gordon, 1957). In addition, modern lingulid brachiopods are resistant to low dissolved oxygen levels for prolonged periods of time (Emig, 1997). The lingulids possess the blood pigment hemerythrin within their coelomocytes that allow for them to respire during low-tide, and overall suboxic settings (Emig, 1997; Hammond, 1983; Craig, 1952; Paine, 1963, 1970; Hammen, Hamlen and Lum, 1962; Posenato et al., 2014). The lingulids also need to consume 2.5x less oxygen than articulated brachiopods, while still maintaining the same metabolic rate (Emig, 1997; Hamlen and Lum, 1962). Posenato et al. (2014) noted that, following the EPME, lingulid shells were smaller in size and flatter, while the size of the lophophore cavity increased, thus allowing the lingulids to

survive the low-oxygen conditions. The narrower, more pointed shell morphology is also proposed as an adaptation to allow the lingulids to inhabit sandy substrate. However, these postulates are not backed by enough data and could be an avenue for future research. Overall, the studies of modern lingulids provide us with an understanding of lingulid physiology, genetics, and modern ecology, that have implications for potential past survival mechanisms and strategies for the lingulid brachiopods (Luo et al. 2015).

Taphonomic megabiases are also a potential issue with studying Phanerozoic trends especially with chitanophosphatic-shelled organisms like the lingulids (Cusack, Williams, and Buckman, 1999; Williams et al. 1994; Knoll, 2003; Paine, 1963,1970; Gutmann et al., 1978; Watabe and Pan, 1984; Bassett et al., 1999; Allison and Bottjer, 2010). Kowalewski and Flessa, (1996) pioneered the study of these potential megabiases in phosphatic organisms such as the lingulids. They concluded that the apparent decrease in lingulid abundance after the Paleozoic was concordant with the decrease in fossilization potential. Hence, the decline of the lingulids could be a taphonomic artifact (Kowalewski and Flessa, 1996). The modern lingulids have fragile shells that often degrade and fragment in modern oceans reflecting the difficulty of modern lingulids to be preserved as a fossil.

Evidently, the majority of lingulids and disaster taxa related studies focus on one event, usually the EPME, or are making evolutionary and ecological interpretations based on few localities or one Formation except for Kowalewski and Flessa, (1996) and Smith and Bunje, (1999). I aim to document the ecology of lingulids throughout the Phanerozoic using environmental affinity metrics to quantify ecological change.

CHAPTER TWO

Phanerozoic Trends in the Opportunistic Behavior and Ecological Tolerance of *Lingula* Through the Quantitative Analysis of Environmental Affinity

Abstract

Lingulid brachiopods originated in the Cambrian and have survived all five first-order mass extinction events. The genus *Lingula* is widely accepted to be opportunistic, and acts as a “disaster taxon” following, specifically, the end-Permian mass extinction. The ecology of lingulid brachiopods has been studied for the end-Permian mass extinction and for modern lingulids, however, little is known about the ecological history of lingulids throughout the Phanerozoic and for other extinction events. I quantified the ecological tolerance of *Lingula* throughout the Phanerozoic in terms of water depth, substrate, water energy, and latitude, using three substrate affinity metrics. I found lingulids to exhibit generalist behavior in terms of water depth and water energy throughout the Phanerozoic. Lingulids were more specialized with regards to substrate type and latitude. However, lingulids show increased generalist behavior following certain mass extinction events for all four metrics of ecological tolerance. Lingulids were more generalist relative to rhynchonellid and terebratulid brachiopods in terms of water depth, water energy, latitude throughout much of the Phanerozoic and following mass extinctions such as the end-Permian mass extinction.

Introduction

The genus *Lingula* is an extant genus of lingulid brachiopods that originated as early as the Cambrian. The Lingulidae, has survived all five first-order mass extinction events. The lingulids are regarded as a morphologically conserved group with minimal evolutionary change relative to other benthic marine invertebrate groups (Biernat and Emig, 1993; Craig, 1952; Ferguson, 1963; Posenato et al., 2014; Petsios and Bottjer, 2016). However, there are morphological changes throughout the Phanerozoic that are discussed in Emig (2003) and Posenato et al. (2014). These changes include a decrease in shell width and height, a decrease in the width to length ratio, increase in the length of mantle canal, a decrease in the area of the posterior adductor muscle, and the flattening of the pedicle groove within Lingulidae throughout the Phanerozoic (Emig, 2003). In addition, Posenato et al. (2014) noticed a increase in the width to length ratio and an increase in the lophophore cavity for the end-Permian mass extinction.

Modern lingulids differ ecologically and biologically from extant rhynchonelliform and terebratulid brachiopod genera due to their organophosphatic shell, infaunal behavior, and planktonic larval mode (Chuang, 1959, Williams et al., 1994; Posenato et al., 2014). Modern lingulids commonly occupy shallow to moderate water depths from 0 to 60 meters, and are mainly found in fine-grained sand or mud (Emig, 1997; Hammond, 1983; Worcester, 1969; Allison et al., 1995; Chuang, 1959; Paine, 1963, 1970; Hamlen and Lum, 1962). Experimental studies of modern lingulids demonstrated that lingulids can tolerate low to high salinities from 15 g/L to 60 g/L (Emig, 1997). Certain lingulid populations have been found to tolerate temperatures of 1°C up to over 40°C, but typically die off at low temperatures less than 18°C (Emig,

1997; Hammen and Lum, 1977; Gunter and Gordon, 1957). Furthermore, modern lingulid brachiopods are resistant to low dissolved oxygen levels for prolonged periods of time (Emig, 1997). Lingulids only need to consume 2.5x less oxygen than articulated brachiopods to maintain similar metabolic rates (Emig, 1997; Hamlen and Lum, 1962). The lingulids are able to tolerate low-oxygen conditions since they possess an oxygen-binding protein hemerythrin, which allows for respiration during low-tide, and overall suboxic settings (Emig, 1997; Hammond, 1983; Craig, 1952; Paine, 1963,1970; Hammen, Hamlen and Lum, 1962; Posenato et al., 2014). Alisson et al. (1995) suggests that lingulids also have shown resistance to suboxic to anoxic conditions in the geologic past based on the commonality of lingulids within black shale facies throughout the Phanerozoic.

Lingulids have been referred to as a disaster taxon first by Hallam and Wignall (1997) and later by Rodland and Bottjer (2001), Peng et al. (2007), Posenato et al. (2014), and Petsios and Bottjer (2016), and as an ecological opportunist by Zonneveld et al. (2007) for the end-Permian mass extinction. Lingulids occurred in high dominance communities, and proliferated into environments of varying depth and lithology, and become more cosmopolitan in distribution or they had a large, global geographic range following the end-Permian mass extinction (Rodland and Bottjer, 2001; Peng et al., 2007; Posenato et al., 2014; Petsios and Bottjer, 2016). Posenato et al. (2014) noted that, following the end-Permian mass extinction lingulid shells were smaller in size and flatter, while the size of the lophophore cavity increased, thus allowing the lingulids to survive the low-oxygen conditions. The narrower, more pointed shell morphology is also proposed as an adaptation to allow the lingulids to inhabit sandy substrate. Peng et al.

(2007) suggested that the “success” of lingulids following the end-Permian mass extinction could be a result of the shell morphology and composition, and physiology of lingulids that allow them to tolerate shallow to deep water depths and high to low-latitudes.

The high ecological or environmental tolerance of lingulids has mainly been documented in the Triassic and in the modern (Emig, 1997; Rodland and Bottjer, 2001; Peng et al., 2007; Posenato et al., 2014; Petsios and Bottjer, 2016) Relatively little is known about the ecology and environmental tolerance of lingulids throughout the Phanerozoic. This study provides a quantitative estimate for the ecological tolerance of lingulids in terms of water depth (deep vs. shallow), substrate (carbonate vs. siliciclastic), grain size or water energy (fine vs. coarse), and latitude (tropical vs. extratropical) throughout the Phanerozoic. By quantifying the ecological tolerance changes over the Phanerozoic we can better understand the ecological history of such a conservative group as the lingulids. In addition, I aim to elucidate the potential mechanisms for the extreme longevity and relative success of the genus *Lingula* throughout the Phanerozoic.

Methods

A quantitative analysis of the habitat affinity of *Lingula* was performed on a dataset that was downloaded from the Paleobiology Database (paleobiodb.org; PBDB) on February 2, 2021. The initial dataset consisted of marine invertebrate taxa from the Cambrian to Recent. This dataset serves as an external, comparative dataset that I used to assess the affinity of lingulids and other brachiopods genera.

The dataset was filtered to only include occurrences that were identified to the genus level, and only unique occurrences of genera per time bin were included. In addition, only collections from a unique Formation or Member were included in the analysis. This precaution ensures that duplicate occurrences from the same locality are not included (Thompson and Bottjer, 2019). In addition, if a genus occurred more than once within a collection, it was only counted as one occurrence. The dataset was analyzed at the Epoch level since finer scale resolution at the stage level lacked sufficient data. However, the Tertiary was analyzed at the Period level due to data restrictions. Collections with maximum and minimum ages that did not fit within the 2019 International Commission on Stratigraphy age ranges were excluded from study (stratigraphy.org).

Collections were vetted to include detailed facies and lithological descriptions, and that include paleolatitude coordinates. Four datasets were assembled for the entire Phanerozoic that contained only collections that could be assigned to a 1) deep or shallow environment, 2) a carbonate or siliciclastic lithology, 3) a fine or coarse-grain size, and 4) a tropical or extratropical latitude.

Bathymetric Dataset

To calculate bathymetric affinity, I included generic occurrences that could be assigned to a deep or shallow environment. Collections from deltaic, lagoonal, supratidal, intertidal, shallow subtidal, and reef deposits, were deemed to be “shallow” marine environments. Deep offshore subtidal, slope, and deep basinal settings are deemed “deep” marine settings. Collections with no environment listed or non-descriptive environments

such as “marine indeterminate,” “marine,” or “carbonate” were not included in the analysis. The filtering of deep and shallow environments decreased our sample size from 919,179 to 488,588 occurrences or by 47%.

Lithologic Dataset

Lithologic affinity was assessed by assembling a dataset of collections that can be attributed to carbonate or siliciclastic lithologies based on their lithologic description. Based on the Dunham classification (Dunham, 1962), wackestone,” “packstone,” “grainstone,” “rudstone,” “floatstone,” “bafflestone,” “boundstone,” “chalk,” and “marl” were classified as carbonates. Siltstone, sandstone, mudstone, claystone, shale, and conglomerates were classified as siliciclastic. Mixed carbonate and siliciclastic collections were excluded from the dataset. The resulting dataset consisted of 828,174 occurrences of marine organisms, which represents a 10% loss of data.

Grainsize Dataset

The grainsize affinity dataset was assembled by compiling collections that were sampled from rocks with a fine or coarse grainsize. Mudstone, wackestone, siltstone, shales, or any rock that has fine grained in its description is classified as fine-grained. Packstone, grainstone, rudstone, floatstone, bafflestone, boundstone, sandstone, conglomerate, and anything described as coarse, is considered coarse grained. The grainsize dataset consists of 491,760 marine occurrences which corresponds to a 46% loss of data.

Latitudinal Dataset

The latitudinal affinity dataset was assembled by including generic occurrences that have paleocoordinates. The paleolatitudes were separated into tropical and extratropical collections based on the paleolatitude. The extent of the tropics was assumed to be 30⁰N and 30⁰S paleolatitude as a base for comparison between high and low latitudes. The latitudinal dataset consists of 888,785 occurrences which is a 3% decrease from the original dataset.

Affinity Calculations

The total amount of unique occurrences in deep vs. shallow, carbonate vs. siliciclastic, fine vs. coarse-grained, and tropical vs. extratropical environments was tallied for each genus within each Epoch. Genera with less than 5 occurrences per time bin were excluded from the quantitative analysis as done in Thompson and Bottjer (2019). Substrate affinity metrics can be sensitive to sample size and to mitigate this sample size bias I only calculated affinity for genera with more than 5 occurrences.

Depth, substrate, water energy, and latitudinal affinity was quantified using standardized relative affinity, a binomial test and a Bayesian statistical metric described by (Miller and Conolly, 2001; Foote, 2006, 2014; Kiessling and Aberhan, 2007, Simpson and Harnik, 2009; Hopkins, 2014; Hopkins et. al, 2014; Thompson and Bottjer, 2019). Affinity was assessed using 3 different methods for each Epoch throughout the Phanerozoic Eon, similar to the methods used in Thompson and Bottjer (2019). The affinity of each genus within the brachiopod Orders Rhynchonellida, and Terebratulida, and for *Lingula*, was calculated if there were more than 5 occurrences of the genus within

each timebin. Previous studies used a minimum of 3 or 4 occurrences to calculate affinity, however I used 5 occurrences to minimize the effect of smaller sample size (Thompson and Bottjer, 2019; Hopkins, 2014).

Standardized Relative Affinity

The standardized relative affinity (SRA) metric was first developed by Miller and Connolly (2001), and was later used in Hopkins (2014), and Thompson and Bottjer (2019). SRA is a relative affinity metric that can be used to compare the affinity for certain environments between different clades. To determine the SRA I calculated the proportion of a genera (A_1) by dividing the number of occurrences within an environment (N_x, N_y), by the total number of occurrences for that genus within each time bin ($N_x + N_y$). The proportion of occurrences was only calculated if there were more than 5 unique occurrences for the genus.

I then used bootstrap subsampling to construct a subsampled dataset for each genus based on the methods modified from Miller and Conolly (2001) and Thompson and Bottjer, (2019). I randomly sampled with replacement up to the total number of occurrences for each genus 1000 times. For Each iteration, I calculated the proportion of occurrences (A_1, A_2) and calculated the mean and standard deviation of the subsampled proportions ($Ntot_1, SD_I$). These values were input into formula [3] to calculate the SRA. All formulas have been modified from Miller and Conolly (2001) and Thompson and Bottjer (2019)

$$A_1 = \frac{N_x}{N_x + N_y} \quad (1)$$

$$A_2 = \frac{N_y}{N_x + N_y} \quad (2)$$

$$SRA = \frac{A_1 + \overline{Ntot_1}}{SD_1} \quad (3)$$

Binomial Test

The binomial test method was used by Foote (2006, 2014), Kiessling and Abernan (2007) and later by Thompson and Bottjer (2019) to quantify substrate affinity. A similar binary affinity method was used by Sclafani et al. (2020). The proportion of substrate occurrences was calculated for all occurrences within a time bin for each depth, lithology, grainsize, and latitude category. The proportion of all occurrences (P_x, P_y) was used as the null hypothesis and I used a one-tailed binomial test to determine if the A_1 and A_2 deviated significantly from the null hypothesis ($\alpha < 0.05$). If a p-value had a value less than 0.05 the affinity was deemed statistically significant for the given substrate, and if neither p-value was significant then no affinity was assigned. This was done following the methods of Foote (2006, 2014) and Thompson and Bottjer (2019) using total collection occurrences instead of using total formation occurrences for each time bin used by Kiessling and Abernan (2007). The binomial test method was only used if the total number of generic occurrences exceeded 5.

Bayesian Method

Simpson and Harnik (2009) calculated substrate affinity using Bayesian inference, and the method was later used by Hopkins (2014), Hopkins et. al, (2014) and Thompson

and Bottjer (2019). This method involves the use of Bayes Theorem to calculate posterior probabilities that a genus has an affinity for a particular substrate. This method also tests the null hypothesis, which is the proportion of total collections per time bin (P_x, P_y). This binomial test is run for both substrates and the resulting $P(E|H1)$ is used to calculate the posterior probability. $P(E|H2)$ was calculated by substituting N_x with N_y . The prior probabilities that a genus was to occur in one substrate over another were assumed to be 0.5 ($P(H1), P(H2)$). It is important to note that this method works under the assumption that the posterior probability is being calculated for the more abundant substrate per time bin. If the posterior probability is calculated for substrate x when substrate y is more abundant the method would generate spurious results (Hopkins, 2014; Thompson and Bottjer, 2019). Since the proportions of substrates fluctuated between time bins (Figures 2.6, 2.7, 2.8, 2.9), I calculated the posterior probability of substrate x only if the proportion substrate x was greater than 0.5. If the proportion of substrate y was greater than 0.5, I calculated the posterior probability for substrate y and used $1-P(H1|E)$ for our plots to ensure that they are on the same scale. A posterior probability of 1 denotes an affinity to the substrate used in the calculation. A posterior probability of 0 indicates that there is an affinity for the other substrate. A posterior probability of 0.5 indicates no affinity for either substrate (Simpson and Harnik, 2009; Hopkins, 2014; Hopkins et. al, 2014; Thompson and Bottjer, 2019). Formulas were adapted from Thompson and Bottjer (2019).

$$P(E|H1) = \binom{N_{tot}}{N_x} P_x^{N_x} (1 - P_x)^{N_{tot}-N_x} \quad (4)$$

$$P(H1|E) = \frac{P(E|H1)P(H1)}{P(E|H1)P(H1)+P(E|H2)P(H2)} \quad (5)$$

Results

Depth Affinity

The depth affinity of lingulid brachiopods was determined for each Epoch within the Phanerozoic using SRA, binomial test, and Bayesian statistical methods. The SRA is interpreted separately from the binomial test and Bayesian methods since the SRA is used to compare the affinity of different clades relative to each other, and the other methods use all marine occurrences within the PBDB (Thompson and Bottjer, 2019).

Standardized relative affinity. The standardized relative affinity of lingulid brachiopods for deep vs. shallow water environments was plotted along with the standard relative affinity of genera within the Orders Rhynchonellida and Terebratulida. These Orders have good fossil records, have a temporal range that encompasses much of the Phanerozoic, and can be found in modern oceans, therefore they are ideal to compare with the lingulid brachiopods. Figure 2.1 shows the SRA of lingulid vs. rhynchonellid and terebratulid genera throughout the Phanerozoic. If the SRA value is greater than 0 that would indicate an affinity for shallow environments. A value less than 0 indicates a shallow affinity, and a value close to 0 indicates no affinity. The affinity of lingulids is assessed relative to the boxplots for rhynchonellid and terebratulid brachiopods seen in Figure 2.1. I interpret the affinity of lingulids in relation to the median line and interquartile range of the other brachiopod Orders. If the lingulids plotted closer to zero than the median of both boxplots I interpret that as lingulids having weaker affinity than the other brachiopods.

Lingulids had SRA values that clustered around 0 throughout the Phanerozoic relative to the terebratulid and rhynchonellid brachiopods (Figure 2.1). In the Middle Devonian, Upper Jurassic and Tertiary, lingulid brachiopods had a greater affinity for deep water environments compared to the other brachiopod Orders. From the Middle Devonian to the Upper Devonian mass extinction interval, the lingulid brachiopods experienced a relative shift from deeper affinity to no affinity following the mass extinction. This weak depth affinity continued into the Mississippian and Permian. Following the end-Permian mass extinction lingulids continued to show a lack of depth affinity relative to the median rhynchonellid and terebratulid values seen in Figure 2.1. In addition, lingulid brachiopods experience a shift from a deeper affinity in the Upper Triassic to no affinity in the Lower Jurassic following the mass extinction event (Figure 2.1). The lingulid brachiopods shift towards a deeper affinity in the Tertiary relative to the other brachiopod Orders. Overall, the relative affinity of rhynchonellids and terebratulids shifted between deep and shallow affinities, and lingulids had weak to no depth affinity throughout the Phanerozoic.

Binomial test and Bayesian. The binomial test method tests the null hypothesis that the proportion of environmental occurrences for a genus equals the proportion of environments within an external dataset within each timebin. The binomial test results in a p-value for each environment where a p-value less than 0.05 was deemed significant (Table 2.1). Lingulid brachiopods had significant affinities for deep environments in the Upper Ordovician, Middle Devonian, Guadalupian, Upper Jurassic, Upper Cretaceous, and Tertiary. A shallow water affinity was observed in the Mississippian. Lingulid

brachiopods were determined to have no significant depth affinity for 15 out of 22 or 68% of Epochs based on the resulting p-values of the binomial test (Table 2.1; Figure 2.2A). In addition, no significant affinity estimates were determined for the End-Ordovician, Late-Devonian, End-Permian, and End-Triassic mass extinctions.

The Bayesian statistical method determines the posterior probability of a genus occurring in a particular environment compared to the null hypothesis of the total proportion of environments within each Epoch. I assigned posterior probabilities of <0.05 and >0.95 as significant affinities based on the methods of Hopkins (2014). Lingulid brachiopods exhibited deep affinity in Middle Devonian, Lower Jurassic, and Upper Jurassic, and a shallow affinity in the Upper Devonian, Mississippian, and Pennsylvanian. No depth affinity was observed for the remaining 16 Epochs (Table 2.1; Figure 2.1, 2.2).

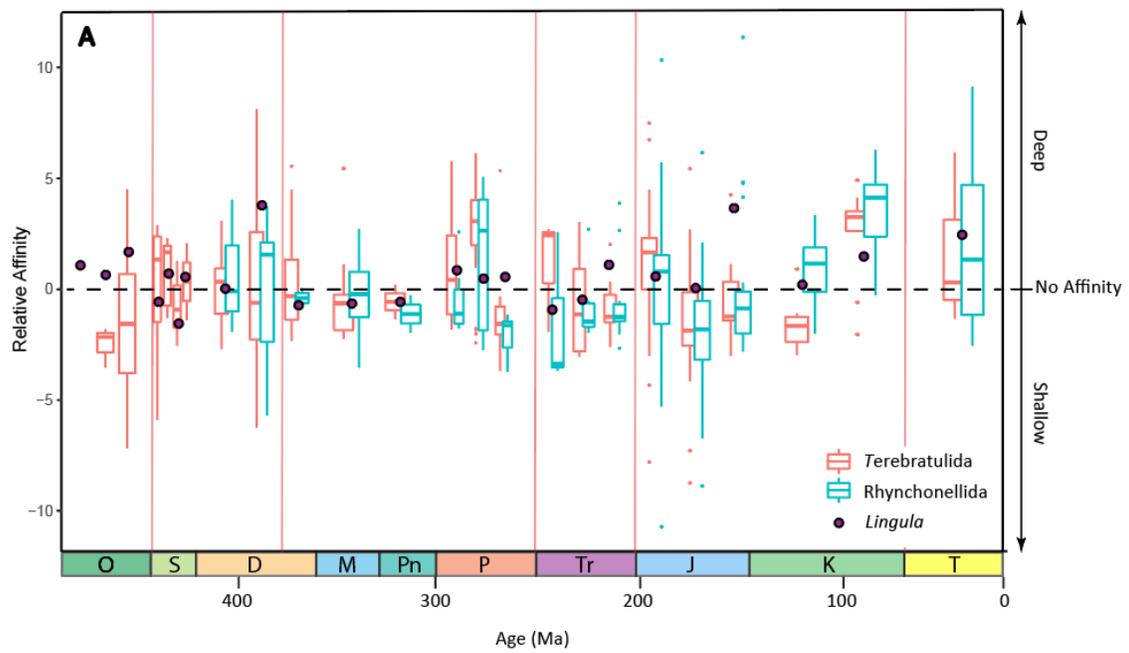


Figure 2.1- Standardized relative affinity of lingulid brachiopods vs. rhynchonellid and terebratulid brachiopods for deep vs. shallow environments. Negative values represent shallow affinity, positive values represent deep and values close to zero represent no affinity.

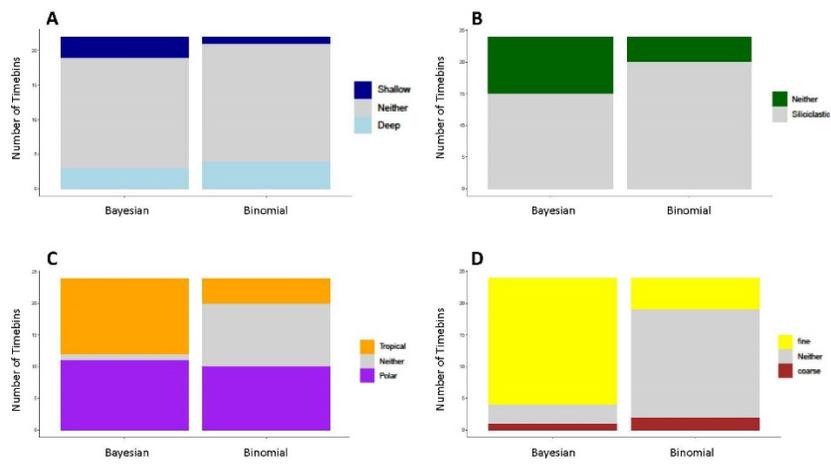


Figure 2.2-Frequency of environmental assignments for lingulid brachiopods for the Bayesian and binomial test methods. A. Shallow vs. deep B. Siliciclastic C. Tropical vs. polar D. Fine vs. coarse-grained. Gray indicates no affinity for either environment or generalist ecology.

Table 2.1- Posterior probability and binomial test results for depth affinity. Significant posterior probabilities over 0.95 and under 0.05 are bolded for each Epoch. Significant p-values are bolded if it is less than 0.05 and p-value<0.05 = x*, p-value<0.01 = x**, p-value<0.001 = x***. All values that are not bolded indicate no significant affinity.

Epoch	Depth Affinity		
	Posterior Probability	Shallow p-value	Deep p-value
Lower Ordovician	0.320	0.969	0.103
Middle Ordovician	0.389	0.914	0.269
Upper Ordovician	0.105	1.000	<0.001***
Llandovery	0.448	0.867	0.265
Wenlock	0.500	0.624	0.650
Ludlow	0.427	0.976	0.086
Pridoli	NA	NA	NA
Lower Devonian	0.724	0.583	0.737
Middle Devonian	0.001	1.000	<0.001***
Upper Devonian	1.000	0.096	0.974
Mississippian	1.000	0.010**	0.996
Pennsylvanian	1.000	0.297	0.886
Cisuralian	0.790	0.961	0.165
Guadalupian	0.500	0.989	0.050*
Lopingian	0.630	0.766	0.514
Lower Triassic	0.733	0.090	0.962
Middle Triassic	0.522	0.065	0.992
Upper Triassic	NA	NA	NA
Lower Jurassic	0.000	0.966	0.105
Middle Jurassic	0.500	0.834	0.436
Upper Jurassic	0.001	1.000	<0.001***
Lower Cretaceous	0.500	0.818	0.353
Upper Cretaceous	0.151	0.989	0.050*
Tertiary	0.177	0.999	0.003**

Lithology Affinity

Standardized relative affinity. The relative lithologic affinity of terebratulid, rhynchonellid and lingulid brachiopods for carbonate vs. siliciclastic lithologies was determined throughout the Phanerozoic. The rhynchonellid and terebratulid brachiopods exhibited similar, relatively carbonate affinities throughout the Phanerozoic. However, in the Lower Devonian and Pennsylvanian, rhynchonellids and terebratulids, respectively, had a greater siliciclastic affinity. The lingulid brachiopods had high siliciclastic affinity relative to the other brachiopod Orders and plotted outside of the minimum affinity values in Figure 2.3 throughout much of the Phanerozoic. Lingulid brachiopods showed no carbonate affinity relative to the terebratulid and rhynchonellid brachiopods. The lingulids showed no relative lithologic affinity in the Lower Ordovician, Lopingian, Lower Triassic, Upper Cretaceous, and Tertiary (Figure 2.3). There was a drastic shift from siliciclastic affinities in the Guadalupian to no affinity in the Lopingian and Lower Triassic, and the other brachiopod Orders had a higher carbonate affinity during this extinction interval.

Binomial test and Bayesian. The binomial test and Bayesian affinity metrics were determined for carbonate vs. siliciclastic environments. The binomial test method yielded significant affinity values for lingulid brachiopods throughout most of the Phanerozoic (Table 2.2; Figure 2.2B). There were 20 of 24 significant siliciclastic affinities and no carbonate affinities for lingulids. No affinity was determined for the Lower Ordovician, Lopingian, Lower Triassic, and Upper Cretaceous (Table 2.2).

The Bayesian affinity metric produced similar results where siliciclastic affinities were most common throughout the Phanerozoic. Lingulid brachiopods had an environmental affinity towards siliciclastics in 15 Epochs and had no affinity for carbonates observed (Figure 2.2B). There was no lithologic affinity in the Lower and Middle Ordovician, Pridoli, Lopingian, Lower Triassic, Upper Triassic, Lower Cretaceous and Upper Cretaceous (Table 2.2).

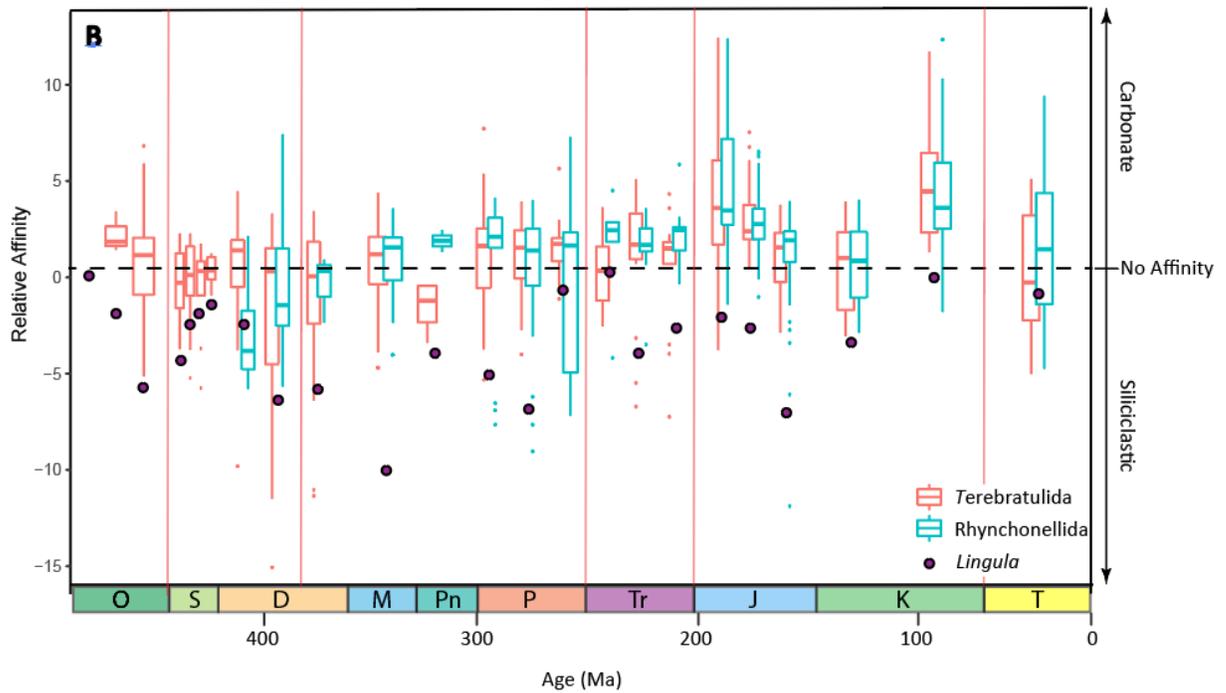


Figure 2.3- Standardized relative affinity of lingulid brachiopods vs. rhychonellid and terebratulid brachiopods for carbonate vs. siliciclastic environments. Negative values represent siliciclastic affinity, positive values represent clastic and values close to zero represent no affinity.

Table 2.2- Posterior probability and binomial test results for lithology affinity. Significant posterior probabilities over 0.95 and under 0.05 are bolded for each Epoch. Significant p-values are bolded if it is less than 0.05 and p-value<0.05 = x*, p-value<0.01 = x**, p-value<0.001 = x***. All values that are not bolded indicate no significant affinity.

Epoch	Lithology Affinity		
	Posterior Probability	Siliciclastic p-value	Carbonate p-value
Lower Ordovician	0.656	0.316	0.862
Middle Ordovician	0.064	0.020*	0.996
Upper Ordovician	0.000	<0.001***	1.000
Llandovery	0.000	<0.001***	1.000
Wenlock	0.003	<0.001***	1.000
Ludlow	0.000	<0.001***	1.000
Pridoli	0.225	0.032*	0.994
Lower Devonian	0.000	<0.001***	1.000
Middle Devonian	0.000	<0.001***	1.000
Upper Devonian	0.000	<0.001***	1.000
Mississippian	0.000	<0.001***	1.000
Pennsylvanian	0.000	<0.001***	1.000
Cisuralian	0.002	<0.001***	1.000
Guadalupian	0.000	<0.001***	1.000
Lopingian	0.795	0.370	0.769
Lower Triassic	0.556	0.834	0.257
Middle Triassic	0.001	<0.001***	1.000
Upper Triassic	0.093	0.031*	0.994
Lower Jurassic	0.142	0.013*	0.994
Middle Jurassic	0.028	0.004**	1.000
Upper Jurassic	0.000	<0.001***	1.000
Lower Cretaceous	0.413	<0.001***	1.000
Upper Cretaceous	0.084	0.140	0.915
Tertiary	0.000	0.050*	0.986

Grainsize Affinity

Standardized relative affinity. Grainsize affinity was calculated for rhynchonellid, terebratulid, and lingulid brachiopods for fine vs. coarse-grained substrate. Lingulid brachiopods exhibited little to no relative affinity throughout most of the Phanerozoic (Figure 2.4). Lingulids had an affinity for fine-grained substrates relative to rhynchonellid and terebratulid brachiopods in the Upper Ordovician, Middle Devonian, and Mississippian (Figure 2.4). There was a relative affinity towards coarse

substrate in the Llandovery. From the Middle to the Upper Devonian extinction interval there was a shift from fine-grained affinity to no affinity. In the Lopingian and Lower Triassic following the end-Permian mass extinction lingulids had no affinity relative to the other brachiopod Orders. The end-Triassic and end-Cretaceous mass extinction events also showed a shift from a more fine-grained affinity to no affinity relative to the other brachiopods.

Binomial test and Bayesian. The grainsize affinity of lingulid brachiopods towards fine vs. coarse-grained substrate was determined using the binomial test and Bayesian methods. The lingulid brachiopods had a significant affinity towards fine-grained substrate in the Upper Ordovician, Middle Devonian, Mississippian, Guadalupian, and Lopingian. In the Llandovery and Upper Jurassic lingulid brachiopods had an affinity for coarse-grained substrates. There was no significant grainsize affinity in the remaining 15 timebins based on the binomial test metric (Table 2.3; Figure 2.2D).

The Bayesian statistical method resulted in the assignment of grainsize affinities for every timebin except for the Cisuralian, Lower Cretaceous, and Tertiary. There are 20 timebins where lingulids exhibit a fine-grained affinity and 1 where there is a coarse-grained affinity in the Upper Jurassic (Table 2.3; Figure 2.2D).

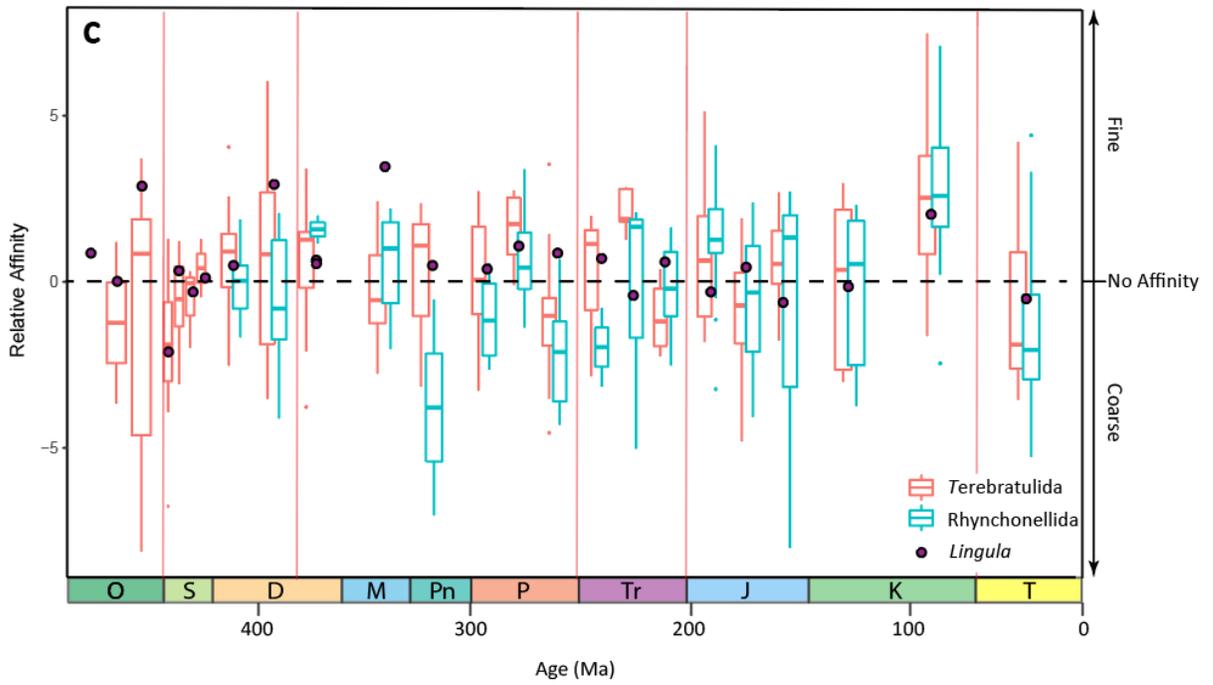


Figure 2.4- Standardized relative affinity of lingulid brachiopods vs. rhynchonellid and terebratulid brachiopods for fine vs. coarse-grained environments. Negative values represent coarse-grained affinity, positive values represent fine-grained affinity and values close to zero represent no affinity.

Table 2.3- Posterior probability and binomial test results for grainsize affinity. Significant posterior probabilities over 0.95 and under 0.05 are bolded for each Epoch. Significant p-values are bolded if it is less than 0.05 and p-value<0.05 = x*, p-value<0.01 = x**, p-value<0.001 = x***. All values that are not bolded indicate no significant affinity.

Grainsize Affinity			
Epoch	Posterior Probability	Coarse p-value	Fine p-value
Lower Ordovician	1.000	1.000	0.226
Middle Ordovician	0.996	0.695	0.606
Upper Ordovician	1.000	1.000	<0.001***
Llandovery	1.000	<0.001***	1.000
Wenlock	1.000	0.730	0.552
Ludlow	1.000	0.383	0.813
Pridoli	1.000	0.857	0.459
Lower Devonian	1.000	0.946	0.111
Middle Devonian	1.000	1.000	<0.001***
Upper Devonian	1.000	0.981	0.051
Mississippian	1.000	1.000	<0.001***
Pennsylvanian	1.000	0.951	0.154
Cisuralian	0.930	0.962	0.196
Guadalupian	0.988	1.000	0.002**
Lopingian	1.000	0.997	0.023*
Lower Triassic	1.000	0.977	0.064
Middle Triassic	0.999	0.395	0.831
Upper Triassic	0.999	1.000	0.104
Lower Jurassic	1.000	0.311	0.825
Middle Jurassic	0.996	0.860	0.458
Upper Jurassic	0.047	0.010**	0.997
Lower Cretaceous	0.882	0.499	0.676
Upper Cretaceous	1.000	0.939	0.116
Tertiary	0.293	0.143	0.948

Latitude Affinity

Standardized relative affinity. The standardized relative affinity of lingulid, terebratulid, and rhynchonellid brachiopods was determined for tropical vs. extratropical environments. In the Ordovician and Silurian lingulid brachiopods exhibit little to no latitudinal affinity except for in the Llandovery where there is a tropical affinity (Figure 2.5). Weak to no affinity is also observed in the Guadalupian, Lopingian, Lower Triassic, and Lower Jurassic associated with the end-Permian and end-Triassic mass extinction

events. Lingulids also show an affinity for tropical latitudes in the Mississippian, and Pennsylvanian. Extratropical affinities are observed for the Devonian, Cisuralian, the Middle and Upper Jurassic, and Lower Cretaceous. There is a shift from tropical affinities in the Paleozoic to more extratropical affinities post-Paleozoic (Figure 2.5).

Binomial test and Bayesian. The latitudinal affinity for lingulid brachiopods was determined by evaluating their affinity towards tropical vs. extratropical environments. The binomial test method resulted in 10 timebins with a significant affinity for extratropical regions (Figure 2.2C). Lingulids had a significant affinity towards tropical regions in the Llandovery, Mississippian, Lopingian, and Lower Triassic (Table 2.4).

The latitudinal affinity calculations for lingulid brachiopods using the Bayesian method resulted in 11 Epochs with tropical affinities in the Paleozoic. There were 11 extratropical occurrences that occurred mainly after the Paleozoic (Table 2.4; Figure 2.2C). Lingulid brachiopods had no latitudinal affinity in the Upper Triassic and Middle Jurassic.

The affinity estimates of an organism for a certain depth, substrate, water energy, or latitude has implications for the ecological or environmental tolerance of the organisms. For example, an organism with a high affinity for shallow water environments can be interpreted as having a low depth tolerance. Herein, I identify organisms with a high affinity or low environmental tolerance as specialists, and organisms with a low to no affinity or high environmental tolerance as generalists. For the binomial test, a taxon is identified as a generalist if both p-values exceed 0.05. The posterior probability estimates from the Bayesian affinity metric can be interpreted as generalist if they are between 0.05

and 0.95. However, the closer the posterior probability is to 0.5 the more generalist the organism is since there is an equal probability of occurring in both environments (Hopkins, 2014; Table 2.1, 2.2, 2.3, 2.4)

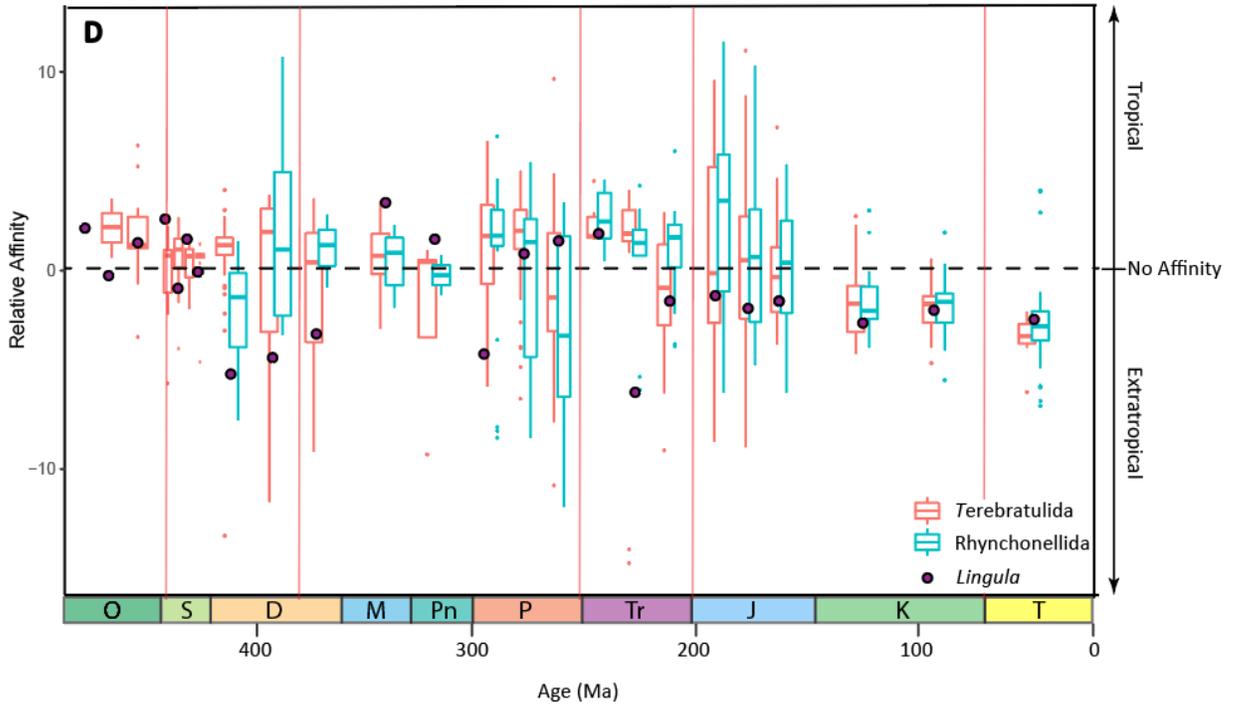


Figure 2.5- Standardized relative affinity of lingulid brachiopods vs. rhynchonellid and terebratulid brachiopods for tropical vs. extratropical environments. Negative values represent extratropical affinity, positive values represent tropical and values close to zero represent no affinity.

Table 2.4- Posterior probability and binomial test results for latitude affinity. Significant posterior probabilities over 0.95 and under 0.05 are bolded for each Epoch. Significant p-values are bolded if it is less than 0.05 and p-value<0.05 = x*, p-value<0.01 = x**, p-value<0.001 = x***. All values that are not bolded indicate no significant affinity.

Epoch	Latitudinal Affinity		
	Posterior Probability	Extratropical p-value	Tropical p-value
Lower Ordovician	1.000	0.975	0.131
Middle Ordovician	0.987	0.355	0.840
Upper Ordovician	1.000	0.871	0.225
Llandovery	1.000	0.994	0.038*
Wenlock	1.000	0.148	0.946
Ludlow	1.000	1.000	0.230
Pridoli	1.000	0.567	0.813
Lower Devonian	0.000	<0.001***	1.000
Middle Devonian	0.000	<0.001***	1.000
Upper Devonian	0.004	<0.001***	1.000
Mississippian	1.000	1.000	<0.001***
Pennsylvanian	1.000	1.000	0.155
Cisuralian	0.012	0.001**	1.000
Guadalupian	0.992	0.978	0.054
Lopingian	1.000	0.998	0.010**
Lower Triassic	1.000	1.000	<0.001***
Middle Triassic	0.000	<0.001***	1.000
Upper Triassic	0.500	0.453	0.731
Lower Jurassic	0.000	0.016*	0.994
Middle Jurassic	0.047	0.132	0.977
Upper Jurassic	0.000	<0.001***	1.000
Lower Cretaceous	0.000	<0.001***	1.000
Upper Cretaceous	0.000	<0.001***	1.000
Tertiary	0.000	0.001**	1.000

Discussion

Depth

Based on the binomial test and Bayesian methods, lingulid brachiopods are predominantly generalist regarding water depth throughout the Phanerozoic (Table 2.1; Figure 2.1, 2.2A). In addition, I found that lingulids exhibit increased generalist depth tolerance following several mass extinction events such as the end-Permian mass extinction. The posterior probability results suggest generalist behavior for the end-

Ordovician, end-Permian, and end-Cretaceous mass extinction event (Table 2.1). The binomial test results suggest generalist behavior following the Late Devonian, end-Permian, and end-Triassic extinctions (Table 2.1). The discrepancy between the binomial test and Bayesian statistical method are partially derived from differences in the proportion of shallow vs. deep environments throughout the Phanerozoic seen in Figure 2.6. Also, the binomial test is more prone to assigning no affinity if the sample size is low and the Bayesian method is less sensitive to low sample sizes (Table 2.5). The differences in the methods usually result in one method assigning an affinity and the other method assigning no affinity, and there are rarely conflicting assignments of affinity.

I determined the standardized relative affinity of lingulid brachiopods relative to genera within the extant brachiopod Orders Rhynchonellida and Terebratulida. I compared lingulids to these Orders to explore how lingulids differ in terms of environmental tolerance to other long-lived brachiopod clades. Lingulids were more generalist throughout most of the Phanerozoic compared to rhynchonellid and terebratulid genera (Figure 2.1). The greater generalist depth tolerance for lingulids was most apparent at extinction boundaries such as the Late Devonian, end-Permian, and end-Triassic (Figure 2.1). The major discrepancy in depth tolerance between lingulids and the other brachiopods during the end-Permian could provide a mechanism for the “success” of lingulids relative to rhynchonellids, and terebratulids in the post-Paleozoic.

The standardized relative affinity metric cannot be directly compared to the binomial test, and Bayesian methods. The Bayesian and binomial test methods leverage an additional dataset that contains all unique marine collections within the PBDB per timebin to calculate the overall proportion of occurrences within each environment.

However, the SRA method uses a bootstrap subsampled dataset for each genus per timebin to calculate the affinity of that genus relative to other genera within the timebin. Therefore, this method does not directly account for potential taphonomic biases that may lead to certain timebins having more of one environment preserved than the other. However, this method is still useful for determining affinity relative to other organisms within each timebin (Hopkins, 2014; Thompson and Bottjer, 2019).

The high proportion of generalist tolerances relative to specialist tolerances observed in both methods suggests that lingulids have a high depth tolerance throughout the Phanerozoic (Table 2.1; Figure 2.1, 2.2A). Lingulids also show high depth tolerances before and after many mass extinction intervals such as the end-Permian. The SRA method further proved that lingulids were more generalist relative to terebratulid and rhynchonelliform brachiopod genera (Figure 2.1). The generalist affinity seen in the Early Triassic corroborates the idea that lingulids were a disaster taxon following the end-Permian mass extinction. Peng et al., (2007) suggests that the apparent ability of lingulids to live in deep and shallow water settings could provide a mechanism for their pervasiveness following the end-Permian mass extinction. Petsios, and Bottjer, (2016), Rodland, and Bottjer, (2001), and Posenato et al., (2014) all indicate the disaster taxon behavior of lingulids following the end-Permian mass extinction and note their ability to thrive in different environments in the extinction aftermath. The depth affinity results show that lingulids are not only generalist in terms of depth tolerance in the Permian, and Triassic. This tolerance for deep and shallow water environments is common during many Epochs throughout the Phanerozoic and for several other mass extinctions (Table 2.1; Figure 2.1). This could have major implications for the ability of lingulids to survive

and thrive following mass extinction events. Several studies suggest that environmental breadth or tolerance could be an important determinant of extinction risk throughout the Phanerozoic and in the modern (Edinger and Risk, 1995; McKinney, 1999; Harnik, Simpson, and Payne, 2012; Heim and Peters, 2011; Foote and Miller, 2013; Saupe et al., 2017). In chapter 3 I further prove the importance of depth tolerance in determining survivorship for several extinction events throughout the Phanerozoic.

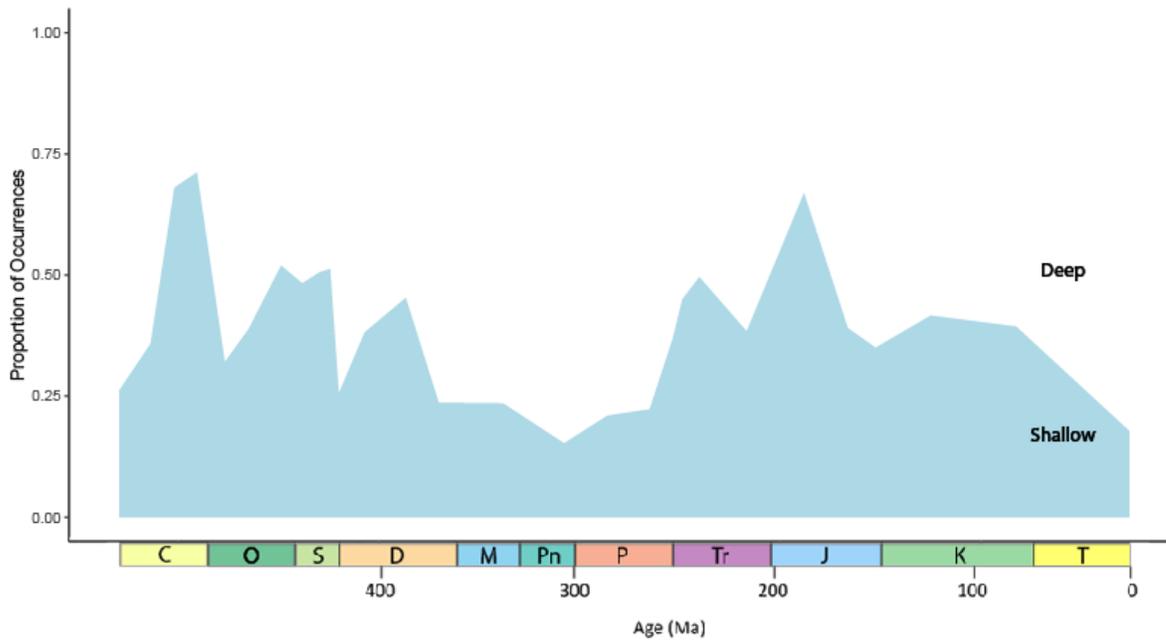


Figure 2.6- Proportion of shallow to deep occurrences plotted at each Epoch throughout the Phanerozoic.

Table 2.5- List of unique lingulid occurrences in deep vs. shallow environments for Epochs from the Lower Ordovician to the Tertiary. AD is the proportion of deep occurrences for lingulid brachiopods, and AS is the proportion of shallow occurrences.

Period	Epoch	Total	Deep	Shallow	AD	AS
Ordovician	Lower Ordovician	11	6	5	0.55	0.45
Ordovician	Middle Ordovician	7	4	3	0.57	0.43
Ordovician	Upper Ordovician	54	41	13	0.76	0.24
Silurian	Llandovery	17	10	7	0.59	0.41
Silurian	Wenlock	8	4	4	0.50	0.50
Silurian	Ludlow	12	9	3	0.75	0.25
Devonian	Lower Devonian	6	2	4	0.33	0.67
Devonian	Middle Devonian	81	60	21	0.74	0.26
Devonian	Upper Devonian	21	2	19	0.10	0.90
Mississippian	Mississippian	86	11	75	0.13	0.87
Pennsylvanian	Pennsylvanian	23	2	21	0.09	0.91
Permian	Cisuralian	7	3	4	0.43	0.57
Permian	Guadalupian	10	5	5	0.50	0.50
Permian	Lopingian	7	3	4	0.43	0.57
Triassic	Lower Triassic	21	8	13	0.38	0.62
Triassic	Middle Triassic	7	1	6	0.14	0.86
Jurassic	Lower Jurassic	18	15	3	0.83	0.17
Jurassic	Middle Jurassic	6	3	3	0.50	0.50
Jurassic	Upper Jurassic	19	15	4	0.79	0.21
Cretaceous	Lower Cretaceous	14	7	7	0.50	0.50
Cretaceous	Upper Cretaceous	10	7	3	0.70	0.30
Tertiary	Tertiary	13	7	6	0.54	0.46

Lithology

The binomial test method resulted in the assignment of lingulids as siliciclastic specialists in almost every Epoch throughout the Phanerozoic for substrate lithology.

However, lingulids had a high lithologic tolerance and were generalist in the Lopingian, and Lower Triassic in association with the end-Permian mass extinction (Table 2.2).

Lingulids were also interpreted as siliciclastic specialist throughout most of the Phanerozoic based on the posterior probability estimates. They possessed high

environmental tolerances and were generalist based on their posterior probabilities for the end-Permian and end-Triassic mass extinctions. Both the binomial test and Bayesian methods did not assign a carbonate affinity at any point throughout the Phanerozoic. The differences in assignments can be attributed to the differences in the proportions of collections in Figure 2.7 and the variability in sample size seen in Table 2.6. However, the two methods were consistent in assigning siliciclastic affinity and there are only minor conflicts where the Bayesian method assigned no affinity when the binomial test assigned siliciclastic affinity.

Using the SRA method, relative to rhynchonellid and terebratulid brachiopods, the lingulids were more specialized towards living in siliciclastic environments throughout much of the Phanerozoic. The lingulids were relatively more generalist in the Lopingian, and Lower Triassic during the end-Permian mass extinction event and in the Upper Cretaceous and Tertiary.

The three methods all showed that lingulids have a high affinity for siliciclastic environments throughout most of the Phanerozoic (Table 2.2; Figure 2.3). This is in agreement with Zonneveld et al. (2007) and Emig (1997) where they noted that lingulids commonly prefer siliciclastics in the modern and geologic past. However, I observed several timebins where lingulids are more generalist with respect to lithology. This generalist behavior is most pronounced in the Lopingian and Lower Triassic where lingulids are regarded as a disaster taxon (Rodland and Bottjer, 2001; Peng et al., 2007; Posenato et al., 2014; Petsios and Bottjer, 2016). The SRA method also showed that lingulids are more generalist during this extinction interval than rhynchonellid and terebratulid brachiopods. These results show that lingulids are capable of inhabiting

carbonate environments and can shift towards being more generalist following extinction events. The agreement of all three methods in assigning lingulids as generalist for the end-Permian mass extinction proves how tolerant they were during this interval.

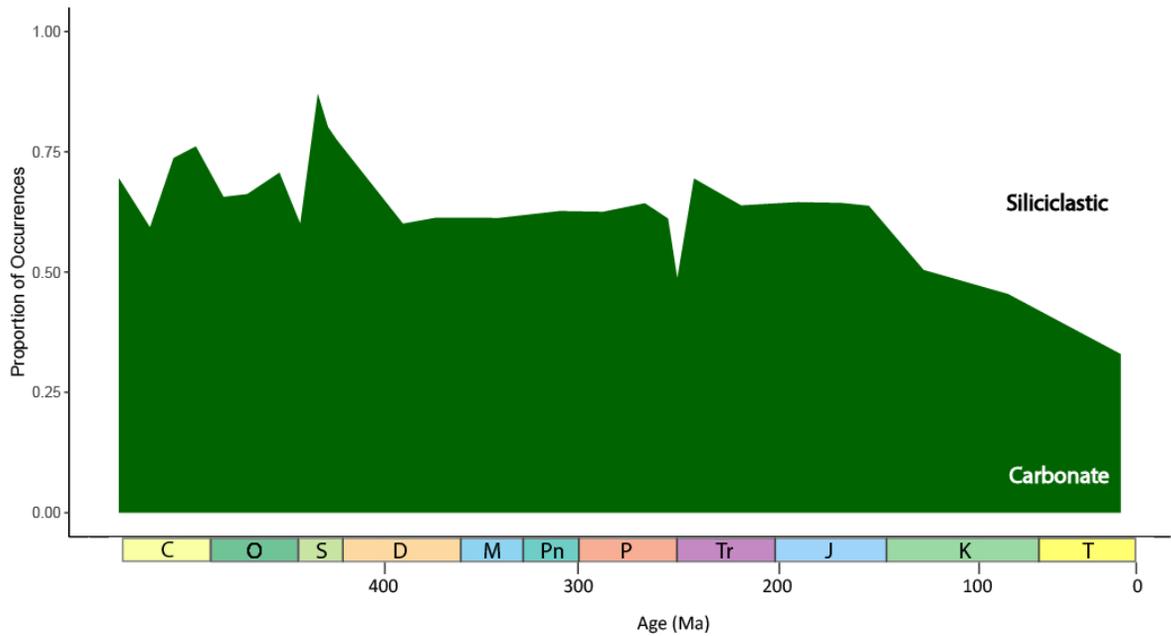


Figure 2.7- Proportion of carbonate to siliciclastic occurrences plotted at each Epoch throughout the Phanerozoic.

Table 2.6- List of unique lingulid occurrences in carbonate vs. siliciclastic environments for Epochs from the Lower Ordovician to the Tertiary. AC is the proportion of carbonate occurrences for lingulid brachiopods, and AS is the proportion of siliciclastic occurrences.

Period	Epoch	Total	Carbonate	Siliciclastic	AC	AS
Ordovician	Lower Ordovician	11	6	5	0.55	0.45
Ordovician	Middle Ordovician	12	4	8	0.33	0.67
Ordovician	Upper Ordovician	79	29	50	0.37	0.63
Silurian	Llandovery	32	3	29	0.09	0.91
Silurian	Wenlock	17	7	10	0.41	0.59
Silurian	Ludlow	22	8	14	0.36	0.64
Silurian	Pridoli	9	4	5	0.44	0.56
Devonian	Lower Devonian	41	14	27	0.34	0.66
Devonian	Middle Devonian	81	11	70	0.14	0.86
Devonian	Upper Devonian	43	4	39	0.09	0.91
Mississippian	Mississippian	109	13	96	0.12	0.88
Pennsylvanian	Pennsylvanian	39	10	29	0.26	0.74
Permian	Cisuralian	18	3	15	0.17	0.83
Permian	Guadalupian	26	6	20	0.23	0.77
Permian	Lopingian	25	14	11	0.56	0.44
Triassic	Lower Triassic	40	22	18	0.55	0.45
Triassic	Middle Triassic	21	6	15	0.29	0.71
Triassic	Upper Triassic	10	3	7	0.30	0.70
Jurassic	Lower Jurassic	41	19	22	0.46	0.54
Jurassic	Middle Jurassic	8	1	7	0.13	0.88
Jurassic	Upper Jurassic	26	1	25	0.04	0.96
Cretaceous	Lower Cretaceous	20	0	20	0.00	1.00
Cretaceous	Upper Cretaceous	49	18	31	0.37	0.63
Tertiary	Tertiary	21	3	18	0.14	0.86

Grainsize

Lingulid brachiopods were generalist with regards to grainsize for a large proportion of the Phanerozoic based on the binomial test method (Table 2.3; Figure 2.2D). The lingulids exhibited generalist behavior for the Late Devonian, end-Permian, end-Triassic, and end-Cretaceous extinctions. There was also 5 timebins where lingulids were fine-grained specialists, and two timebins where lingulids were coarse-grained

specialists. However, the posterior probability only assigned three intervals where lingulids were generalist, one interval where they were coarse-grained specialists, and they were fine-grained specialists in the remaining intervals. This discrepancy between methods is mainly as result of the small sample size of lingulids for several Epochs such as the Cisuralian, Middle and Upper Triassic which have 7 occurrences (Table 2.7). Despite having the minimum of 5 occurrences in all timebins, the lower sample sizes can result in the binomial test method assigning more generalist occurrences since it is more sensitive to sample size. In addition, there is variability in the proportion of fine occurrences seen in Figure 8 where the proportion of fine occurrences is high throughout much of the Phanerozoic.

The grainsize tolerance for lingulids relative to rhynchonellid and terebratulid brachiopods was high throughout most of the Phanerozoic based on the SRA method. There was a shift in the lingulids towards being more generalist following the Late Devonian, end-Permian, end-Triassic, and end-Cretaceous extinction events (Figure 2.4).

The grainsize tolerance estimates the tolerance of an organism to a particular energy environment. The fine-grained specialists generally prefer low-energy environments, and the coarse-grained specialists, prefer high-energy environments. The binomial test suggests that lingulids are mainly generalist with regards to water energy throughout the Phanerozoic (Table 2.3). The SRA method also resulted in the assignment of lingulids as generalist throughout most of the Phanerozoic relative to other brachiopods. The overall generalist behavior of lingulids suggests that they can tolerate both high and low energy environments. In addition, this increase in generalist behavior is observed at several mass extinction intervals. Lingulids also were more generalist than

other brachiopod genera at several extinction intervals such as the end-Permian extinction. This increased environmental tolerance could provide a survival mechanism for lingulids relative to other brachiopods and other marine invertebrates. However, the Bayesian method resulted in the assignment of lingulids as fine-grained specialists throughout the Phanerozoic. This is concordant with the findings in Zonneveld et al. (2007) and Emig (1997) where they mentioned that lingulids often preferred fine-grained substrates in the Permian and modern day.

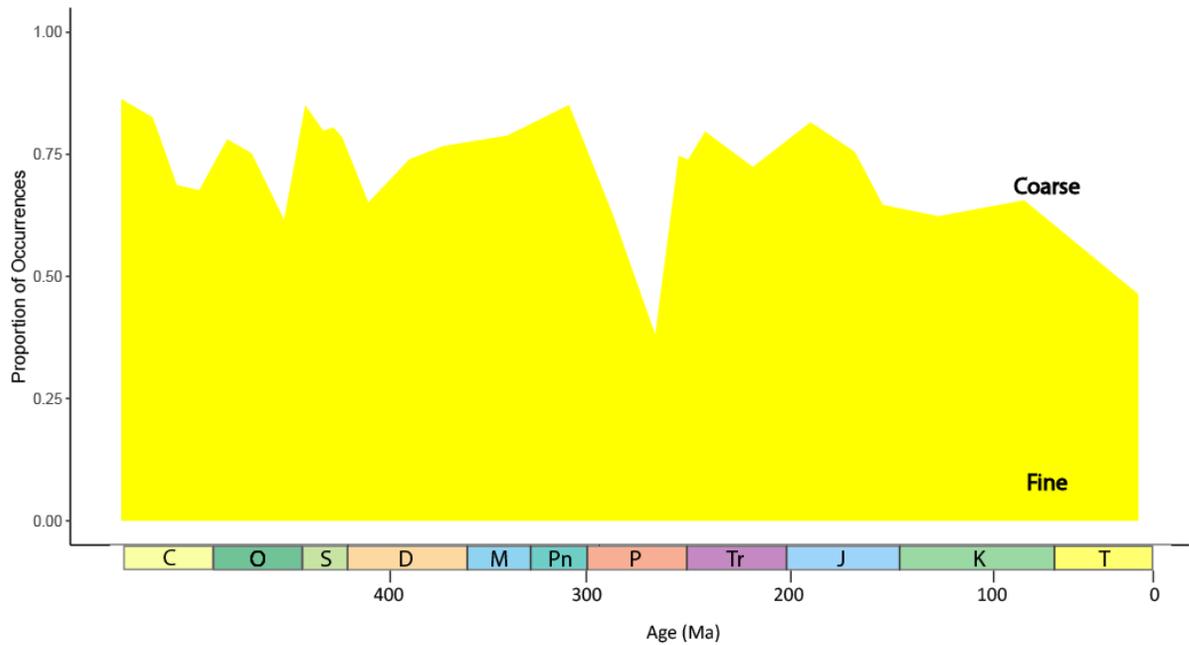


Figure 2.8- Proportion of fine to coarse-grained occurrences plotted at each Epoch throughout the Phanerozoic.

Table 2.7- List of unique lingulid occurrences in fine vs. coarse-grained environments for Epochs from the Lower Ordovician to the Tertiary. AF is the proportion of fine-grained occurrences for lingulid brachiopods, and AC is the proportion of coarse-grained occurrences.

Period	Epoch	Total	Fine	Coarse	AF	AC
Ordovician	Lower Ordovician	6	6	0	1.00	0.00
Ordovician	Middle Ordovician	9	7	2	0.78	0.22
Ordovician	Upper Ordovician	55	49	6	0.89	0.11
Silurian	Llandovery	31	18	13	0.58	0.42
Silurian	Wenlock	12	10	2	0.83	0.17
Silurian	Ludlow	16	12	4	0.75	0.25
Silurian	Pridoli	8	7	1	0.88	0.13
Devonian	Lower Devonian	34	26	8	0.76	0.24
Devonian	Middle Devonian	62	60	2	0.97	0.03
Devonian	Upper Devonian	42	37	5	0.88	0.12
Mississippian	Mississippian	98	96	2	0.98	0.02
Pennsylvanian	Pennsylvanian	30	28	2	0.93	0.07
Permian	Cisuralian	7	6	1	0.86	0.14
Permian	Guadalupian	21	15	6	0.71	0.29
Permian	Lopingian	20	19	1	0.95	0.05
Triassic	Lower Triassic	31	27	4	0.87	0.13
Triassic	Middle Triassic	11	8	3	0.73	0.27
Triassic	Upper Triassic	7	7	0	1.00	0.00
Jurassic	Lower Jurassic	30	23	7	0.77	0.23
Jurassic	Middle Jurassic	7	6	1	0.86	0.14
Jurassic	Upper Jurassic	25	10	15	0.40	0.60
Cretaceous	Lower Cretaceous	20	12	8	0.60	0.40
Cretaceous	Upper Cretaceous	41	31	10	0.76	0.24
Tertiary	Tertiary	14	4	10	0.29	0.71

Latitude

Lingulids showed a mix of specialized tropical and extratropical latitudinal tolerances, and generalist latitudinal tolerances throughout the Phanerozoic. After the Paleozoic lingulids were mostly extratropical specialists. However, this change in tolerance corresponds to a major decrease in the proportion of extratropical environments (Figure 2.9). Lingulids were found in tropical settings in the Mesozoic and Cenozoic,

however they were not numerous enough to affect the affinity assignment for the binomial test and Bayesian methods (Table 2.4). The discrepancy between methods and the variability in assignment is mainly down to the fluctuations in the proportion of tropical environments seen in Figure 2.9. The sample sizes are relatively high compared to the other environmental categories with only the Pridoli and Middle Jurassic having sample sizes lower than 10. Therefore, it is believed that the changes in latitudinal preferences reflect the true environmental tolerance of lingulid brachiopods.

The SRA of lingulids compared to rhynchonellids and terebratulids revealed that the lingulids have similar to more generalist latitudinal tolerances for majority of the Phanerozoic. However, there are several intervals where lingulids were relatively specialized towards living in tropical and extratropical settings. Lingulids were generalist relative to the rhynchonellids and terebratulids for the end-Permian, and end-Triassic extinctions (Figure 2.5).

Overall, the variability in latitudinal tolerance throughout the Phanerozoic suggests that lingulids can tolerate tropical and extratropical environments. Although the binomial test and Bayesian methods both show that lingulids were mostly specialized throughout the Phanerozoic, the SRA suggests that lingulids were generalist relative to rhynchonellid, and terebratulid brachiopods. These methods are fundamentally different and cannot be directly compared since one is a relative metric and the other two rely on an external dataset (Thompson and Bottjer, 2019). However, the SRA tolerance estimates show that lingulids differed ecologically from rhynchonellid, and terebratulid brachiopods for the end-Permian mass extinction event. The latitudinal affinity metric works under the assumption that the palaeolatitudinal extent of the tropics is consistent

throughout the Phanerozoic into the modern. However, as discussed in Hopkins et al., (2014), the tropics are not constant throughout the Phanerozoic and tropical affinity may be overestimated or underestimated in certain intervals. The decreasing proportion of tropical environments throughout the Phanerozoic also may lead to the assignment of extratropical affinities that could represent a taphonomic artifact.

Overall, lingulids show high ecological tolerance with regards to depth, grainsize, and to a lesser extent lithology and latitude. The binomial, Bayesian, and SRA methods all resulted in the assignment of lingulids as generalist throughout the Phanerozoic for water depth for the majority of tested timebins. The binomial test and SRA methods showed the lingulids were generalist throughout most of the Phanerozoic for grainsize or water energy for the majority of tested timebins. The lithology and latitude affinities of lingulids were generalists for several important extinction intervals throughout the Phanerozoic. The lingulids showed increased generalist behavior during extinction events for all four metrics. Most notably, lingulids were more generalist than rhynchonellids and terebratulids in the Lopingian, and Lower Triassic (Figure 2.1, 2.3, 2.4, 2.5).

The generalist behavior and “success” of the lingulids relative to other brachiopods following the end-Permian and other extinctions is most likely a result of physiological and ecological differences. Peng et al. (2007) mentioned that the lingulids likely thrived during the aftermath of the end-Permian mass extinction due to their organophosphatic shell and infaunal ecology. Clapham and Payne (2011) show that the end-Permian mass extinction was mainly physiologically selective due to low-oxygen, high-CO₂, high temperature stress, and ocean acidification as a result of Siberian Trap volcanism (Chen and Benton, 2012). I hypothesize that the extreme tolerance of *Lingula*

to suboxic to anoxic conditions, variable temperatures, salinities, and water depth that is observed in the modern was similar in the geologic past. This tolerance to harsh conditions would give lingulids the advantage during times of extinction.

The increase in generalist behavior for lingulids after mass extinction is likely due to the adaptive filling of empty niches that are available after the extinction event that they were not able to fill before the extinction due to competitive exclusion. The proliferation of a taxon into new environments shortly after mass extinction events can be attributed to successful survival and adaptation of that lineage. Lingulids mainly exhibit ecological success and adaptations towards generalist life habit following the end-Permian mass extinction. However, I observe increased generalist behavior in lingulids following other extinction events as well.

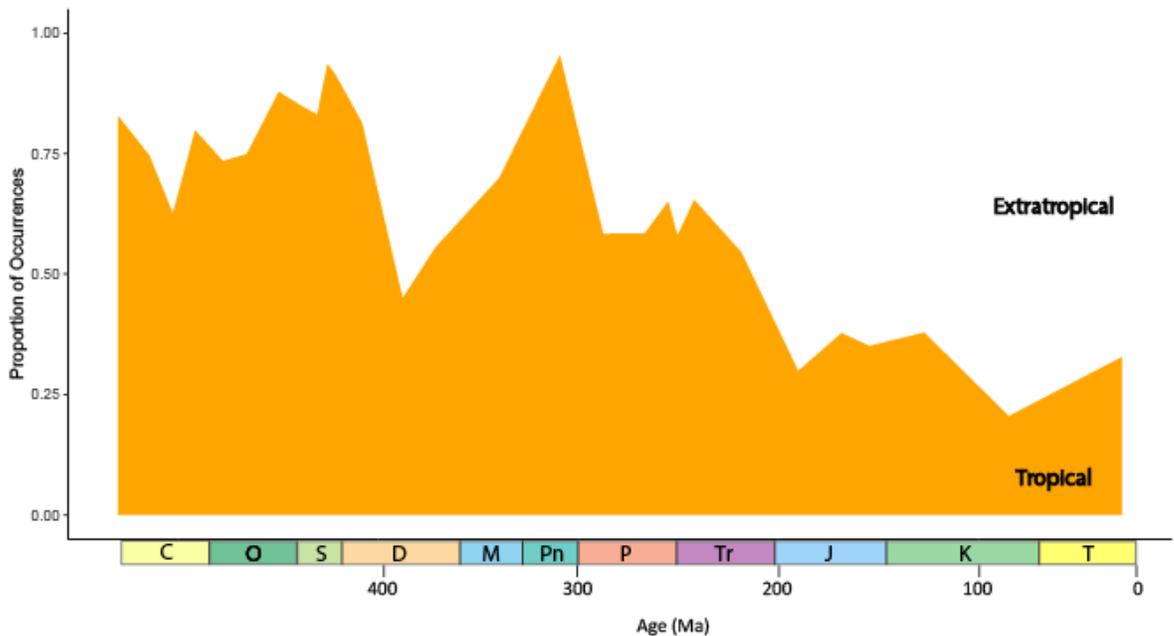


Figure 2.9- Proportion of tropical to extratropical occurrences plotted at each Epoch throughout the Phanerozoic.

Table 2.8- List of unique lingulid occurrences in tropical vs. extratropical environments for Epochs from the Lower Ordovician to the Tertiary. AT is the proportion of tropical occurrences for lingulid brachiopods, and AE is the proportion of extratropical occurrences.

Period	Epoch	Total	Tropical	Extratropical	AT	AE
Ordovician	Lower Ordovician	12	11	1	0.92	0.08
Ordovician	Middle Ordovician	12	8	4	0.67	0.33
Ordovician	Upper Ordovician	80	73	7	0.91	0.09
Silurian	Llandovery	32	31	1	0.97	0.03
Silurian	Wenlock	17	12	5	0.71	0.29
Silurian	Ludlow	22	22	0	1.00	0.00
Silurian	Pridoli	9	8	1	0.89	0.11
Devonian	Lower Devonian	41	16	25	0.39	0.61
Devonian	Middle Devonian	105	10	95	0.10	0.90
Devonian	Upper Devonian	43	9	34	0.21	0.79
Mississippian	Mississippian	109	93	16	0.85	0.15
Pennsylvanian	Pennsylvanian	39	39	0	1.00	0.00
Permian	Cisuralian	29	8	21	0.28	0.72
Permian	Guadalupian	28	21	7	0.75	0.25
Permian	Lopingian	25	22	3	0.88	0.12
Triassic	Lower Triassic	41	39	2	0.95	0.05
Triassic	Middle Triassic	30	7	23	0.23	0.77
Triassic	Upper Triassic	16	8	8	0.50	0.50
Jurassic	Lower Jurassic	42	6	36	0.14	0.86
Jurassic	Middle Jurassic	8	1	7	0.13	0.88
Jurassic	Upper Jurassic	34	3	31	0.09	0.91
Cretaceous	Lower Cretaceous	21	0	21	0.00	1.00
Cretaceous	Upper Cretaceous	52	1	51	0.02	0.98
Tertiary	Tertiary	23	1	22	0.04	0.96

Conclusions

Lingulid brachiopods are environmentally and ecologically tolerant of different water depths, and to a lesser extent grainsizes throughout the Phanerozoic. Lingulids are specialized for living in siliciclastic environments, tropical or extratropical environments throughout the Phanerozoic. However, lingulids commonly are generalist during certain major mass extinction events such as the end-Permian mass extinction. I observed increased generalist behavior for depth, substrate, and water energy during the end-

Permian mass extinction and other extinction events such as the end-Ordovician, Late Devonian, and end-Triassic extinction events.

The SRA method showed that lingulids are generalist relative to the extant brachiopod Orders Rhynchonellida, and Terebratulida for depth, water energy, and latitude for many geologic Epochs throughout the Phanerozoic. I also observed a shift in lingulids towards being more generalist for several mass extinctions and for all four metrics. The most pronounced shift towards generalist behavior coincides with the end-Permian mass extinction and can be observed for depth, substrate, water energy, and latitude.

The high ecological and environmental tolerance of lingulids in the Lopingian, and Lower Triassic could provide an explanation for why lingulids were more successful than the rhynchonelliform brachiopods. This high ecological tolerance could also have implications for the evolutionary longevity of the genus *Lingula* and could suggest that lingulids are more resistant to extinctions relative to other benthic marine invertebrates.

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CHAPTER THREE

“Survival of the Tolerant” – A Logistic Regression Analysis of Ecological Tolerance Selectivity Throughout the Phanerozoic

Abstract

Environmental tolerance and ecological breadth are important predictors of extinction risk in Modern ecosystems, and generalist taxa have been posited to be resistant to extinction relative to specialists. Differential survivorship of ecologically stenotopic or eurytopic taxa has likely had significant macroevolutionary effects following both background extinction and mass extinction events throughout the Phanerozoic, but quantifying environmental tolerance in the fossil record is not straightforward. Herein, I utilize several environmental proxies to assess the ecological tolerance of marine genera, quantitatively assigning taxa as specialist or generalist taxa using a binomial test to assess whether there was significant environmental affinity compared to the proportion of environments within the paleobiology database per timebin . I used multiple logistic regression to quantify the depth, substrate, energy level and latitude selectivity towards generalists vs. specialists for background and mass extinction intervals. I found that depth and substrate were the most important variables in determining survivorship throughout the Phanerozoic. Generalist taxa for depth and substrate selectively survived certain mass extinction intervals, and the selective survival of specialists was more common during background intervals. Overall, selectivity based on environmental tolerance is a significant determinant of extinction risk for many background and extinction intervals throughout the Phanerozoic. The difference in

selectivity between mass extinctions and background intervals suggests that different extinction causal mechanisms manifest as different selectivity regimes for mass extinction and background extinction throughout the Phanerozoic.

Introduction

Extinction selectivity is highly variable throughout the Phanerozoic and plays a pivotal role in shaping evolutionary history. By determining the selectivity regimes during mass extinction events and background times, we can better understand the nature of mass extinction intervals and their potential causes relative to background times (Payne and Finnegan, 2007; Clapham and Payne, 2011). There are several potential determinants of extinction risk for marine taxa during both background and mass extinction events. Limited geographic range has been identified as the primary determinant of extinction risk throughout the Phanerozoic (Jablonski and Raup, 1965; Payne and Finnegan, 2007; Harnik, Simpson, and Payne, 2012; Heim and Peters, 2011; Orzechowski et al., 2015; Collins et al., 2019; Casey et al. 2021). Ecological breadth or environmental tolerance has also been hypothesized to be an important determinant of survivorship (Edinger and Risk, 1995; McKinney, 1999; Harnik, Simpson, and Payne, 2012; Heim and Peters, 2011; Foote and Miller, 2013; Saupe et al., 2017). Several biotic crises throughout the Phanerozoic exhibit a proliferation of eurytopic or generalist taxa relative to stenotopic or specialist taxa following the extinction event (Erwin, 1998; Harries et al., 1996). Extinction selectivity can force a shift toward a prevalence of eurytopic taxa following both major and minor extinction events, however, there have been few attempts to quantify environmental tolerance selectivity throughout the entirety

of the Phanerozoic at the ecosystem level. Kammer et al., 1998 identified eurytopic crinoids by calculating the mean facies occurrences per species or eurytopy index, and using canonical correspondence analysis to further identify eurytopic taxa. They found that eurytopic crinoid clades had longer longevities during the Mississippian. Endinger and Risk (1995) found the selective survival of eurytopic brooding corals in the Oligocene. They qualitatively assigned taxa as eurytopic if they were tolerant of myriad environments. Harnik Simpson, and Payne (2012) and Foote and Miller (2013) considered environmental breadth selectivity and concluded that environmental breadth was the second most important predictor of survivorship and for early clade survival. Foote and Miller (2013), Harnik, Simpson, and Payne (2012), and Heim and Peters (2011) used environmental breadth or the number of unique environmental occurrences to quantify environmental tolerance. However, environmental breadth does not account for nuances in abundance distribution within the organism's preferred range, and treats low-abundance populations on the fringe of their ecological tolerance limits as equally important in determining ecological tolerance as those occurring in high-abundance populations. In order to also incorporate abundance distributions within ecological niches, I instead utilize the binomial test method of Foote (2006;2014) to quantify the affinity of an organism for a particular water depth, substrate lithology, energy level, and latitude as a proxy for ecological or environmental tolerance. This allows us to identify taxa with statistically significant affinities as "specialist" and with no affinity as "generalist".

Methods

Occurrences of marine invertebrate taxa were downloaded from the Paleobiology Database on April 20, 2021 (PBDB; <http://www.paleodb.org>) ranging in age from the Cambrian to the Pleistocene. Each genus-level occurrence was assigned to a deep or shallow environment, carbonate or siliciclastic lithology (as a proxy for substrate preference), fine- or coarse-grained sediment, or tropical vs. extratropical latitude based on the reported lithological descriptions and environmental interpretations reported in the PBDB (after Thompson and Bottjer (2019), Sclafani et al. (2020), Hopkins et al. (2014) and Foote (2006;2014). Occurrences with sufficient environmental and lithologic information were tallied for each unique genus within 95 stages over the Phanerozoic. Only genera with a minimum of 5 occurrences per timebin were included for analysis, for a total of 18,768 unique occurrences representing 5,248 unique genera.

The relative number of occurrences of each environmental or lithological assignment (deep vs. shallow; carbonate vs. siliciclastic, fine-grained vs. coarse-grained) was calculated per stage using unique collection occurrences from the PBDB. These proportions per timebin were used as the null hypothesis for a one-tailed binomial test, following the methods of Foote (2006), as a means to account for differential representation or preservation of depositional settings between time bins (Foote, 2014; Peters, 2008). A binomial test was performed for each genus per time bin to determine if a significant affinity for one or the other environment could be detected ($\alpha = 0.05$). If environmental affinity was non-significant, the taxon was interpreted as having no affinity. Genera with significant affinities were regarded as specialist and genera with no significant affinity were treated as generalist. This method generates categorical tolerance

assignments (Foote, 2006; 2014), and is therefore ideal for logistic regressions, compared to other commonly used methods for assigning environmental tolerance in the fossil record (Miller and Connolly, 2001; Simpson and Harnik, 2009; Hopkins. 2014; Hopkins et al., 2014)

Logistic regression was performed with depth, substrate, grainsize, and latitude tolerance as the predictors and extinction or survival within each timebin as the response variable in a binomial glm with a logit link function based on the methods of Payne and Finnegan (2007). I calculated the log-odds ratios and the $\ln(\log\text{-ratios})$ or log-odds to represent the selectivity of each model towards different affinity metrics. The models were evaluated against the null model in which selectivity is equal to zero and models with p-values greater than 0.05 were deemed significant.

Results

Depth tolerance was found to be the most significant predictor of extinction risk throughout the Phanerozoic with 33 out of 95 stages showing a significant association between survivorship and depth affinity (Figure 3.1A; Table 3.1,A1). The end-Ordovician, Late Devonian and end-Permian mass extinctions showed significant selectivity based on depth tolerance at the extinction boundary or during the stage immediately following the extinction boundary (the recovery intervals). The end-Triassic, and end-Cretaceous extinctions did not exhibit any selectivity towards generalists or specialist in regards to depth tolerance (Figure 3.1A; Table 3.1). The preferential survival of generalist taxa over specialist taxa is also observed for several smaller biotic crises (after Bond and Grasby, 2017) such as the Botomian, Sheinwoodian, Homerian, Givetian,

Serpukhovian, Carnian, and Cenomanian (Figure 3.1A; Table 3.1). For all minor and major extinction intervals, there was 13 intervals in which generalists preferentially survived, and 1 interval in the Frasnian where specialists preferentially survived (Table 3.1). Statistically significant selective extinction of generalists is more commonly observed during background stages such as during the Katian, Moscovian, Ladinian, Bathonian, and Kimmeridgian stages.

Substrate tolerance was found to be the second most prominent predictor of extinction over the Phanerozoic with 28 stages showing significant extinction selectivity. Selective extinction of substrate lithology specialists was observed in 17 stages, and selective extinction of substrate lithology generalists was observed in 11 stages (Figure 3.1B; Table 3.1,A2). Substrate-based extinction selectivity was most common during the background intervals and recovery stages following biotic crises. Selective survival of generalists is observed in the Serpukhovian, and in the stages following the end-Ordovician and EPME (Table 3.1).

Grain-size tolerance was a significant determinant of extinction in 26 stages, with 15 favoring the survival of grain-size generalist and 11 favoring grain-size specialist (Figure 3.1C; Table 3.1,A3). The end-Triassic boundary and recovery stages following the late Devonian and end-Cretaceous mass extinctions exhibited selective extinction of grain-size specialist. Grainsize tolerance was most commonly significant during background times and increased in significance into the Cenozoic with 9 out of 13 significant associations between grainsize affinity and survival in the Tertiary.

Latitudinal tolerance was the least significant predictor of extinction throughout the Phanerozoic with 22 stages with significant latitude tolerance selectivity (Figure

3.1D, Table 3.1,A4). The end-Ordovician, and the stages following the EPME and End-Cretaceous showed significant latitude tolerance selectivity (Table 3.1).

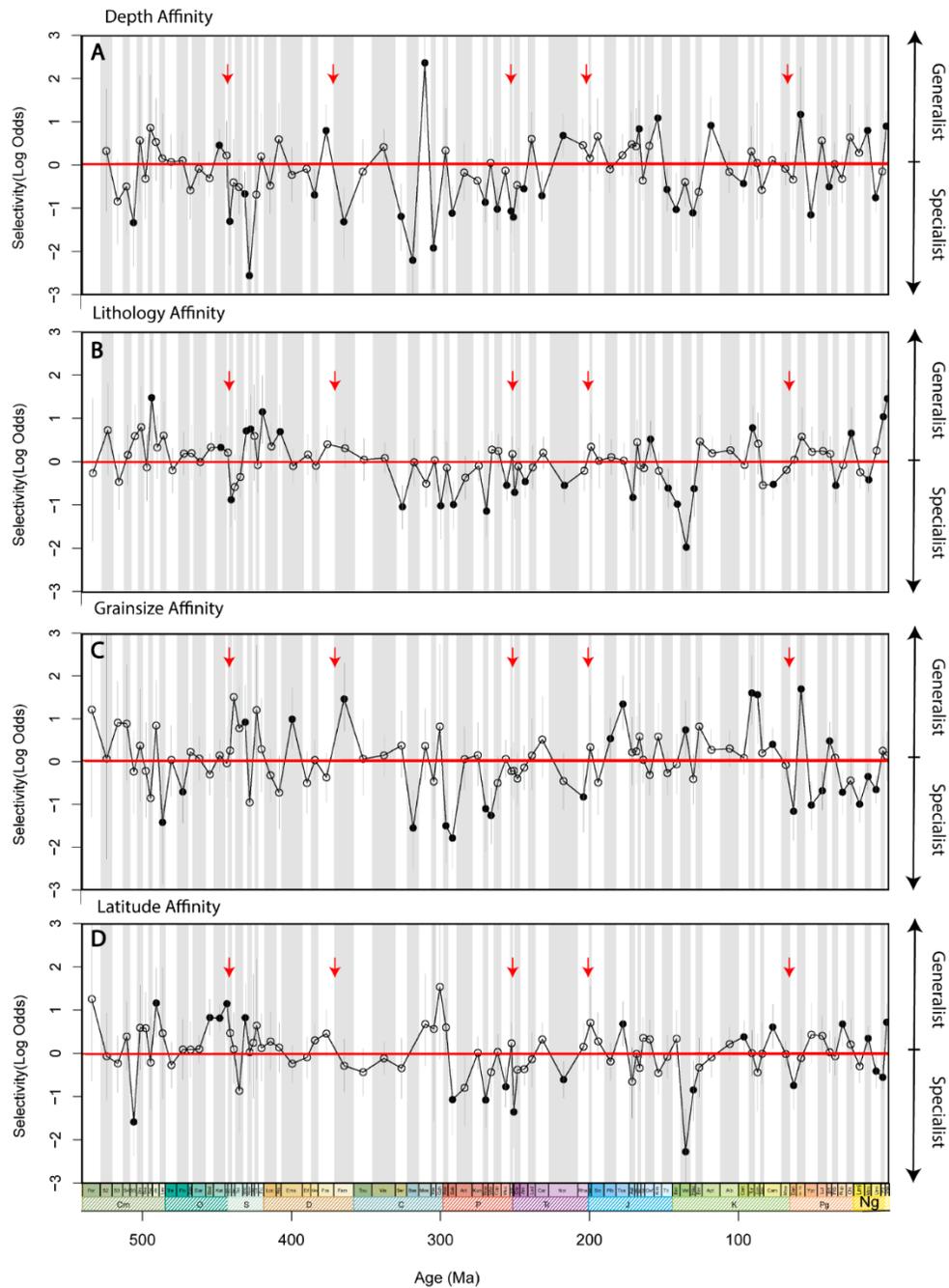


Figure 3.1- Environmental tolerance selectivity trends throughout the Phanerozoic. Selectivity is plotted as log-odds where a positive log-odds indicates where specialists preferentially survive, a negative log-odds indicates where generalists preferentially survive and a log-odds of zero means there is no effect on survivorship. Stages in which ecological tolerance has a significant effect on survivorship ($p < 0.05$) are indicated by solid circles, and gray lines indicate the 95% confidence interval. A. Depth affinity selectivity B. Lithology affinity selectivity C. Grainsize affinity selectivity D. Latitude affinity selectivity. Figure was plotted using the r package divDyn (Kocsis et al., 2019).

Table 3.1- Extinction selectivity from Cambrian till the Pleistocene. Only Stages with at least one significant p-value ($\alpha < 0.05$) were included. Geologic context denotes whether the Stage represents a background, extinction, or mass extinction interval. Minor biotic crises and mass extinction intervals were determined from Bond and Grasby (2017). Depth, lithology, grainsize, and latitude survivors indicate whether there was preferential survival of generalists, specialists, or NA if there is no effect on survival.

Stage	Geologic context	Depth survivors	Lithology survivors	Grainsize survivors	Latitude survivors
Stage 5	end-Botomian extinction	generalist	generalist	NA	generalist
Jiangshanian	Dresbachian extinction	NA	specialist	NA	specialist
Lawsonian	Background	NA	NA	generalist	NA
Floian	Background	NA		generalist	NA
Sandbian	Background	NA	specialist	NA	specialist
Katian	Background	specialist	specialist	NA	specialist
Hirnantian	end-Ordovician mass extinction	NA	specialist	NA	specialist
Rhuddanian	end-Ordovician mass extinction	generalist	NA	NA	NA
Sheinwoodian	Ireviken event	generalist	specialist	specialist	specialist
Homerian	Mulde event	generalist	NA	NA	NA
Emsian	Background	NA	NA	specialist	NA
Givetian	Thaganic event	generalist	NA	NA	NA
Frasnian	late-Devonian mass extinction	specialist	NA	NA	NA
Famennian	late-Devonian mass extinction	generalist	NA	specialist	NA
Serpukhovian	late-Serpukhovian extinction	generalist	NA	NA	NA
Bashkirian	Background	generalist	NA	generalist	NA
Moscovian	Background	specialist	NA	NA	NA
Kasimovian	Background	generalist	NA	NA	NA
Asselian	Background	NA	NA	generalist	NA
Sakmarian	Background	generalist	generalist	generalist	generalist
Roadian	Background	generalist	generalist	generalist	generalist
Wordian	Background	NA	NA	generalist	NA
Capitanian	Capitanian extinction	generalist	NA	NA	NA
Wuchiapingian	Background	NA	generalist	NA	generalist
Changhsingian	end-Permian mass extinction	generalist	NA	NA	NA
Induan	Smithian-Spathian extinction	generalist	generalist	NA	generalist
Anisian	Background	generalist	NA	NA	NA
Carnian	Carnian extinction	generalist	NA	NA	NA
Norian	Background	specialist	generalist	NA	generalist
Rhaetian	end-Triassic mass extinction	NA	NA	generalist	NA
Pliensbachian	Early Jurassic extinction	NA	NA	specialist	NA

Table 3.1- Extinction selectivity from Cambrian till the Pleistocene continued.

Stage	Geologic context	Depth survivors	Lithology survivors	Grainsize survivors	Latitude survivors
Toarcian	Background	NA	specialist	specialist	specialist
Bathonian	Background	specialist	NA	NA	NA
Kimmeridgian	Background	specialist	NA	NA	NA
Tithonian	Background	generalist	NA	NA	NA
Berriasian	Background	generalist	NA	NA	NA
Valanginian	Background	NA	generalist	specialist	generalist
Hauterivian	Background	generalist	generalist	NA	generalist
Aptian	Background	specialist	NA	NA	NA
Cenomanian	Cenomanian extinction	generalist	specialist	NA	specialist
Turonian	Background	NA	NA	specialist	NA
Coniacian	Background	NA	NA	specialist	NA
Campanian	Background	NA	specialist	specialist	specialist
Danian	End-Cretaceous mass extinction	NA	generalist	generalist	generalist
Selandian-Thanetian	Background	specialist	NA	specialist	NA
Ypresian	PETM	generalist	NA	generalist	NA
Lutetian	Background	NA	NA	generalist	NA
Bartonian	Background	generalist	NA	specialist	NA
Rupelian	Background	NA	specialist	generalist	specialist
Lower Miocene	Background	NA	NA	generalist	NA
Middle Miocene	Background	specialist	specialist	generalist	specialist
Upper Miocene	Background	generalist	generalist	generalist	generalist
Pliocene	Background	NA	generalist	NA	generalist
Pleistocene	Background	specialist	specialist	NA	specialist

Discussion

For the four environmental tolerance metrics tested, mass extinction intervals appear to operate under different selectivity regimes than background extinction intervals (Table 2.1). This is consistent with the findings in Erwin (1998), Harries et al. (1996) Payne and Finnegan (2007), Clapham and Payne (2011), and Harnik, Simpson, and Payne (2012). I found that tolerance with respect to water depth is the most important

determinant of survivorship during mass extinction intervals and the selectivity was greater than the surrounding background stages. The depth tolerance selectivity trends differed to geographic range selectivity where mass extinctions were less selective than surrounding background stages (Payne and Finnegan, 2007; Clapham and Payne, 2011). This selectivity pattern varies based on the nature of the biotic crisis and for different affinity metrics throughout the Phanerozoic (Figure 3.1).

Biotic crises such as the end-Ordovician, late-Devonian, Serpukhovian, and EPME, have been documented to mark transitions from stenotopic taxa to more cosmopolitan, eurytopic taxa (Erwin, 1998; Harries et al., 1996; Stanley and Powell, 2003; Dai and Song, 2020;). The end-Ordovician extinction was selective towards generalists for depth and lithology following the extinction and was selective towards specialists for latitude affinity (Figure 3.1; Table 3.1). This suggests that there was an advantage to being tolerant of different substrates, and water depths, and specialized taxa were selected against in the aftermath of the extinction. For the Late Devonian extinction, specialist taxa were selected for in the Frasnian for depth tolerance and in the Fammenian for grainsize tolerance. The selectivity towards specialists in the Frasnian could be suggest that there was an advantage to living in one substrate or water depth over another. Whereas in the aftermath, generalist depth affinities were selected for suggesting that there was stress on both shallow and deep-water environments and the most environmentally tolerant organisms survived. The Serpukhovian extinction had a strong selectivity towards generalist depth affinities, lithologies and grainsize. This strong selectivity could suggest that environmental stresses affected taxa at various water depths and various substrates and the generalist taxa were favored. The EPME was selective

towards generalist depth, lithology, and latitude tolerance at the extinction interval or in the aftermath. The preference of generalist taxa and the emergence of generalist disaster taxa is well known at the EPME (Erwin, 1998; Petsios and Bottjer, 2019). Yin et al. (2006) noted an increase in eurytopic taxa in the Capitanian and leading up to the EPME. These results show that the shift towards generalist or eurytopic taxa following the EPME was driven by the selectivity of the extinction against specialists. However, Clapham and Payne (2011) showed that geographic range, and physiology were also selected for during the EPME. The lack of strong ecological affinity selectivity for the end-Triassic and end-Cretaceous suggests that there are other variables influencing survivorship which could indicate different causal mechanisms of these extinctions. Bond and Wignall (2008) noted that many eurytopic bivalve taxa suffered high extinction intensities for the end-Triassic in addition to stenotopic taxa. Jablonski and Raup (1995) also determined that water depth was not an important determinant of extinction risk in the end-Cretaceous and geographic range was the most important determinant.

Generalist latitude tolerance was the least important metric throughout the Phanerozoic this is likely due to tropical and extratropical environments having conflicting selectivity regimes leading to no significant advantage for specialists or generalists. Grainsize tolerance also was not very selective throughout the Phanerozoic. Depth tolerance and lithologic affinity were the most selective metrics throughout the Phanerozoic. This suggests that organisms that can tolerate both deep and shallow, and carbonate and siliciclastic environments are more likely to survive during mass extinction intervals. The selectivity towards generalist taxa occurred for mass extinctions and biotic crises with varying causal mechanisms and extinction intensities. The selectivity towards

specialists during background intervals could suggest that the causes of extinction are fundamentally different than during mass extinction intervals.

Conclusions

Eurytopic or generalist taxa have been selected for at many background and mass extinction intervals throughout the Phanerozoic. This corroborates the idea that ecologically tolerant taxa are more resilient during major biotic crises proposed by McKinney et al. (1997). Depth, substrate, and to a lesser extent latitudinal, tolerance are important determinants of extinction risk, especially during mass extinction intervals. The ecological tolerance selectivity regime can indicate underlying causal mechanisms and the nature of environmental perturbations during extinction and background intervals. The importance of ecological tolerance as a determinant of extinction survivorship over the Phanerozoic suggests that we should incorporate ecological tolerance as a determinant of extinction risk for the modern biotic crisis.

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CHAPTER FOUR

Conclusions

Lingulid brachiopods are environmentally and ecologically tolerant of different water depths, and to a lesser extent grainsizes throughout the Phanerozoic. Lingulids typically are generalist during certain major mass extinction events such as the end-Permian mass extinction. There is also an apparent shift towards increased generalist behavior following certain mass extinction events. I observed increased generalist behavior for depth, substrate, and water energy during the end-Permian mass extinction and other extinction events such as the end-Ordovician, Late Devonian, and end-Triassic extinction events. The SRA method further corroborated the other affinity metric results. Lingulids were more generalist compared to rhynchonellid and terebratulid brachiopods in terms of water depth, water energy, and latitude for most of the Phanerozoic, and following mass extinction events.

The SRA method showed that lingulids are generalist relative to the extant brachiopod Orders Rhynchonellida, and Terebratulida for depth, water energy, and latitude for many geologic Epochs throughout the Phanerozoic. I also observed a shift in lingulids towards being more generalist for several mass extinctions and for all four metrics. The most pronounced shift towards generalist behavior coincides with the end-Permian mass extinction and can be observed for depth, substrate, water energy, and latitude.

Eurytopic or generalist taxa have been selected for or against at many background and mass extinction intervals throughout the Phanerozoic. Depth, substrate, and to a lesser extent latitudinal, tolerance have been important determinants of extinction risk, especially during mass extinction intervals, throughout the Phanerozoic. Generalist taxa with regards to water depth preferentially survived many extinction events and specialist taxa preferentially survived during several background Stages. The importance of depth, substrate, and latitudinal tolerance in determining extinction risk throughout the Phanerozoic suggests that it may play a role in determining extinction risk for the modern biotic crisis.

Since lingulids are fairly generalist with regards to depth, water energy, and latitude during many extinction events and background times, this could provide a survival mechanism for lingulid brachiopods relative to other brachiopods. This difference in ecological tolerance between lingulids and other brachiopods is most pronounced at the end-Permian mass extinction, and most likely played a role in their survival and success in the aftermath as a disaster taxon. The extinction selectivity results suggests that taxa that are tolerant of myriad water depths are more likely to survive several mass extinction events, and background intervals. Overall, environmental affinity can reveal important ecological information, and can be an important determinant of extinction risk throughout the Phanerozoic. Through the study of long-ranging taxa such as the lingulid brachiopods we can further elucidate the mechanisms of survival and clade longevity.

APPENDIX

APPENDIX

Supplementary Tables

Table A1- Selectivity (Log-Odds), lower and upper confidence intervals and p-values for depth selectivity

Stage	Depth Affinity Selectivity			
	Selectivity	Low C. I.	High C. I.	p-val
Stage 2	0.3	-1.071	1.707	0.666
Stage 3	-0.844	-1.82	0.1	0.082
Stage 4	-0.508	-1.552	0.55	0.339
Stage 5	-1.329	-2.322	-0.355	0.007
Drumian	0.539	-0.842	2.014	0.449
Guzhangian	-0.33	-1.237	0.625	0.483
Paibian	0.827	-0.302	2.015	0.158
Jiangshanian	0.505	-0.381	1.498	0.286
Lawsonian	0.131	-0.863	1.147	0.797
Tremadocian	0.051	-0.558	0.67	0.87
Floian	0.083	-0.547	0.714	0.797
Dapingian	-0.593	-1.242	0.037	0.068
Darriwilian	-0.101	-0.48	0.277	0.6
Sandbian	-0.32	-0.731	0.091	0.127
Katian	0.429	0.06	0.799	0.023
Hirnantian	0.201	-0.547	0.974	0.603
Rhuddanian	-1.3	-2.283	-0.429	0.005
Aeronian	-0.413	-1.431	0.575	0.412
Telychian	-0.521	-1.133	0.082	0.092
Sheinwoodian	-0.674	-1.19	-0.167	0.01
Homerian	-2.533	-4.39	-1.258	0.001
Ludfordian	-0.689	-1.508	0.074	0.085
Pridoli	0.178	-0.811	1.154	0.72
Lochkovian	-0.486	-1.129	0.143	0.133
Pragian	0.564	-0.194	1.393	0.16
Emsian	-0.242	-0.854	0.376	0.439
Eifelian	-0.106	-0.724	0.501	0.733
Givetian	-0.697	-1.299	-0.111	0.021
Frasnian	0.764	0.187	1.354	0.01
Famennian	-1.308	-2.162	-0.526	0.002
Tournaisian	-0.17	-0.882	0.555	0.641
Visean	0.388	-0.021	0.797	0.063

Table A1- Depth selectivity continued.

Stage	Selectivity	Low C. I.	High C. I.	p-val
Serpukhovian	-1.187	-1.961	-0.442	0.002
Bashkirian	-2.183	-2.941	-1.491	0
Moscovian	2.303	0.715	5.197	0.026
Kasimovian	-1.905	-2.832	-1.038	0
Asselian	0.31	-0.543	1.277	0.498
Sakmarian	-1.113	-1.726	-0.511	0
Artinskian	-0.191	-0.838	0.486	0.569
Kungurian	-0.375	-0.863	0.122	0.134
Roadian	-0.866	-1.316	-0.426	0
Wordian	0.03	-0.529	0.605	0.917
Capitanian	-1.022	-1.504	-0.546	0
Wuchiapingian	-0.145	-0.641	0.357	0.569
Changhsingian	-1.067	-1.562	-0.582	0
Induan	-1.204	-1.99	-0.474	0.002
Olenekian	-0.476	-1.001	0.043	0.073
Anisian	-0.558	-1.108	-0.025	0.043
Ladinian	0.574	-0.038	1.191	0.066
Carnian	-0.717	-1.301	-0.16	0.013
Norian	0.651	0.164	1.144	0.009
Rhaetian	0.431	-0.165	1.038	0.159
Hettangian	0.132	-0.62	0.892	0.73
Sinemurian	0.632	-0.214	1.5	0.145
Pliensbachian	-0.113	-0.631	0.391	0.664
Toarcian	0.206	-0.265	0.68	0.392
Aalenian	0.453	-0.267	1.201	0.223
Bajocian	0.403	-0.413	1.264	0.341
Bathonian	0.801	0.202	1.445	0.011
Callovian	-0.371	-0.821	0.071	0.103
Oxfordian	0.417	-0.031	0.872	0.07
Kimmeridgian	1.05	0.553	1.575	0
Tithonian	-0.574	-1.072	-0.092	0.021
Berriasian	-1.03	-1.982	-0.202	0.021
Valanginian	-0.405	-0.959	0.136	0.145
Hauterivian	-1.107	-1.899	-0.398	0.004
Barremian	-0.63	-1.465	0.143	0.121
Aptian	0.88	0.283	1.523	0.005
Albian	-0.176	-0.646	0.295	0.462
Cenomanian	-0.44	-0.864	-0.015	0.042
Turonian	0.29	-0.254	0.854	0.303
Coniacian	0.025	-1.251	1.409	0.969

Table A1- Depth selectivity continued.

Stage	Selectivity	Low C. I.	High C. I.	p-val
Santonian	-0.587	-1.221	0.019	0.062
Campanian	0.092	-0.299	0.481	0.645
Maastrichtian	-0.1	-0.474	0.273	0.599
Danian	-0.349	-1.021	0.328	0.308
Selandian-Thanetian	1.13	0.261	2.215	0.021
Ypresian	-1.151	-1.761	-0.569	0
Lutetian	0.534	-0.006	1.118	0.061
Bartonian	-0.513	-0.935	-0.088	0.017
Priabonian	0	-0.471	0.486	0.999
Rupelian	-0.332	-0.873	0.212	0.228
Chattian	0.609	-0.047	1.344	0.083
Lower Miocene	0.257	-0.278	0.844	0.366
Middle Miocene	0.767	0.259	1.334	0.005
Upper Miocene	-0.761	-1.105	-0.411	0
Pliocene	-0.166	-0.439	0.108	0.233
Pleistocene	0.861	0.515	1.205	0

Table A2- Selectivity (Log-Odds), lower and upper confidence intervals and p-values for lithology selectivity

Lithology Affinity Selectivity				
Stage	Selectivity	Low C. I.	high C. I.	p-val
Stage 2	-0.044	-1.036	0.937	0.929
Stage 3	-0.209	-0.864	0.417	0.52
Stage 4	0.402	-0.372	1.196	0.312
Stage 5	-1.538	-2.316	-0.763	0
Drumian	0.601	-0.346	1.573	0.217
Guzhangian	0.594	-0.239	1.408	0.155
Paibian	-0.186	-1.24	0.858	0.726
Jiangshanian	1.164	0.393	1.963	0.003
Lawsonian	0.476	-1.014	1.967	0.517
Tremadocian	-0.246	-0.766	0.278	0.356
Floian	0.108	-0.578	0.797	0.757
Dapingian	0.105	-0.51	0.739	0.74
Darriwilian	0.118	-0.192	0.429	0.455
Sandbian	0.833	0.438	1.248	0
Katian	0.821	0.525	1.117	0

Table A2- Lithology continued

Stage	Selectivity	Low C. I.	High C. I.	p-val
Bashkirian	-2.183	-2.941	-1.491	0
Moscovian	2.303	0.715	5.197	0.026
Kasimovian	-1.905	-2.832	-1.038	0
Asselian	0.31	-0.543	1.277	0.498
Sakmarian	-1.113	-1.726	-0.511	0
Artinskian	-0.191	-0.838	0.486	0.569
Kungurian	-0.375	-0.863	0.122	0.134
Roadian	-0.866	-1.316	-0.426	0
Wordian	0.03	-0.529	0.605	0.917
Capitanian	-1.022	-1.504	-0.546	0
Wuchiapingian	-0.145	-0.641	0.357	0.569
Changhsingian	-1.067	-1.562	-0.582	0
Induan	-1.204	-1.99	-0.474	0.002
Olenekian	-0.476	-1.001	0.043	0.073
Anisian	-0.558	-1.108	-0.025	0.043
Ladinian	0.574	-0.038	1.191	0.066
Carnian	-0.717	-1.301	-0.16	0.013
Norian	0.651	0.164	1.144	0.009
Rhaetian	0.431	-0.165	1.038	0.159
Hettangian	0.132	-0.62	0.892	0.73
Sinemurian	0.632	-0.214	1.5	0.145
Pliensbachian	-0.113	-0.631	0.391	0.664
Toarcian	0.206	-0.265	0.68	0.392
Aalenian	0.453	-0.267	1.201	0.223
Bajocian	0.403	-0.413	1.264	0.341
Bathonian	0.801	0.202	1.445	0.011
Callovian	-0.371	-0.821	0.071	0.103
Oxfordian	0.417	-0.031	0.872	0.07
Kimmeridgian	1.05	0.553	1.575	0
Tithonian	-0.574	-1.072	-0.092	0.021
Berriasian	-1.03	-1.982	-0.202	0.021
Valanginian	-0.405	-0.959	0.136	0.145
Hauterivian	-1.107	-1.899	-0.398	0.004
Barremian	-0.63	-1.465	0.143	0.121
Aptian	0.88	0.283	1.523	0.005
Albian	-0.176	-0.646	0.295	0.462
Cenomanian	-0.44	-0.864	-0.015	0.042
Turonian	0.29	-0.254	0.854	0.303
Coniacian	0.025	-1.251	1.409	0.969
Santonian	-0.587	-1.221	0.019	0.062
Campanian	0.092	-0.299	0.481	0.645

Table A2- Lithology continued

Stage	Selectivity	Low C. I.	High C. I.	p-val
Maastrichtian	-0.1	-0.474	0.273	0.599
Danian	-0.349	-1.021	0.328	0.308
Selandian-Thanetian	1.13	0.261	2.215	0.021
Ypresian	-1.151	-1.761	-0.569	0
Lutetian	0.534	-0.006	1.118	0.061
Bartonian	-0.513	-0.935	-0.088	0.017
Priabonian	0	-0.471	0.486	0.999
Rupelian	-0.332	-0.873	0.212	0.228
Chattian	0.609	-0.047	1.344	0.083
Lower Miocene	0.257	-0.278	0.844	0.366
Middle Miocene	0.767	0.259	1.334	0.005
Upper Miocene	-0.761	-1.105	-0.411	0
Pliocene	-0.166	-0.439	0.108	0.233
Pleistocene	0.861	0.515	1.205	0

Table A3- Selectivity (Log-Odds), lower and upper confidence intervals and p-values for grainsize selectivity

Grainsize Affinity Selectivity				
Stage	Selectivity	Low c. I.	high C. I.	p-val
Stage 2	0.057	-2.217	3.166	0.963
Stage 3	0.875	-0.007	1.816	0.058
Stage 4	0.854	-0.438	2.188	0.192
Stage 5	-0.234	-1.195	0.69	0.623
Drumian	0.355	-0.906	1.643	0.58
Guzhangian	-0.22	-1.277	0.886	0.686
Paibian	-0.836	-2.897	0.861	0.363
Jiangshanian	0.812	-0.191	1.832	0.113
Lawsonian	-1.386	-2.785	-0.088	0.042
Tremadocian	0.031	-0.8	0.812	0.94
Floian	-0.696	-1.399	-0.008	0.049
Dapingian	0.213	-0.773	1.313	0.685
Darriwilian	0.063	-0.439	0.566	0.804
Sandbian	-0.299	-0.767	0.178	0.215
Katian	0.134	-0.221	0.489	0.458
Hirnantian	-0.045	-0.82	0.779	0.911
Rhuddanian	0.243	-0.449	0.966	0.499
Aeronian	1.459	0.191	3.312	0.054
Telychian	0.75	-0.065	1.694	0.09
Sheinwoodian	0.886	0.135	1.729	0.028
Homerian	-0.934	-1.872	0.06	0.055

Table A3- Grainsize continued.

Stage	Selectivity	Low c. I.	high C. I.	p-val
Ludfordian	1.163	0.05	2.635	0.068
Pridoli	0.274	-0.699	1.423	0.605
Lochkovian	-0.318	-0.918	0.29	0.301
Pragian	-0.711	-1.537	0.124	0.091
Emsian	0.955	0.289	1.675	0.007
Eifelian	-0.494	-1.179	0.211	0.161
Givetian	0.028	-0.428	0.485	0.903
Frasnian	-0.368	-0.926	0.187	0.194
Famennian	1.415	0.681	2.228	0
Tournaisian	0.055	-0.772	0.952	0.9
Visean	0.135	-0.322	0.59	0.56
Serpukhovian	0.357	-0.382	1.144	0.356
Bashkirian	-1.514	-2.451	-0.664	0.001
Moscovian	0.349	-0.417	1.203	0.393
Kasimovian	-0.459	-1.292	0.441	0.294
Asselian	-1.465	-2.308	-0.638	0.001
Sakmarian	-1.742	-2.432	-1.09	0
Artinskian	0.049	-0.641	0.787	0.892
Kungurian	0.139	-0.554	0.878	0.702
Roadian	-1.078	-2.043	-0.171	0.022
Wordian	-1.23	-1.878	-0.612	0
Capitanian	-0.492	-1.095	0.098	0.104
Wuchiapingian	0.053	-0.374	0.482	0.806
Changhsingian	-0.226	-0.769	0.301	0.407
Induan	-0.214	-0.86	0.434	0.516
Olenekian	-0.394	-0.975	0.167	0.174
Anisian	-0.14	-0.651	0.367	0.59
Ladinian	0.132	-0.65	0.965	0.746
Carnian	0.495	-0.367	1.471	0.285
Norian	-0.449	-1.094	0.202	0.173
Rhaetian	-0.812	-1.609	-0.001	0.046
Hettangian	0.32	-0.661	1.473	0.55
Sinemurian	-0.481	-1.217	0.284	0.207
Pliensbachian	0.515	0.041	0.994	0.034
Toarcian	1.299	0.712	1.943	0
Aalenian	0.204	-0.537	1.002	0.6
Bajocian	0.224	-0.523	1.025	0.566
Bathonian	0.565	-0.117	1.322	0.12
Callovian	0.034	-0.488	0.576	0.899
Oxfordian	-0.308	-0.764	0.15	0.185

Table A3- Grainsize continued.

Stage	Selectivity	Low c. I.	high C. I.	p-val
Kimmeridgian	0.563	-0.123	1.322	0.124
Tithonian	-0.266	-0.756	0.225	0.287
Berriasian	-0.07	-0.747	0.624	0.841
Valanginian	0.714	0.104	1.374	0.027
Hauterivian	-0.403	-0.973	0.169	0.165
Barremian	0.79	-0.156	1.92	0.128
Aptian	0.258	-0.201	0.728	0.276
Albian	0.29	-0.118	0.706	0.167
Cenomanian	0.076	-0.293	0.448	0.686
Turonian	1.553	0.835	2.399	0
Coniacian	1.511	0.417	2.971	0.016
Santonian	0.186	-0.383	0.778	0.527
Campanian	0.384	0.015	0.755	0.042
Maastrichtian	-0.083	-0.389	0.222	0.593
Danian	-1.136	-1.789	-0.533	0
Selandian-Thantetian	1.641	0.7	2.863	0.002
Ypresian	-0.996	-1.561	-0.456	0
Lutetian	-0.669	-1.103	-0.241	0.002
Bartonian	0.459	0.041	0.897	0.035
Priabonian	0.082	-0.366	0.544	0.724
Rupelian	-0.702	-1.202	-0.219	0.005
Chattian	-0.438	-0.979	0.1	0.11
Lower Miocene	-0.974	-1.389	-0.571	0
Middle Miocene	-0.347	-0.649	-0.044	0.025
Upper Miocene	-0.645	-0.956	-0.334	0
Pliocene	0.238	-0.065	0.548	0.127
Pleistocene	0.13	-0.449	0.688	0.652

Table A4- Selectivity (Log-Odds), lower and upper confidence intervals and p-values for latitude selectivity

Latitude Affinity Selectivity				
Stage	Selectivity	Low c. I.	high C. I.	p-val
Stage 2	-0.044	-1.036	0.937	0.929
Stage 3	-0.209	-0.864	0.417	0.52
Stage 4	0.402	-0.372	1.196	0.312
Stage 5	-1.538	-2.316	-0.763	0
Drumian	0.601	-0.346	1.573	0.217
Guzhangian	0.594	-0.239	1.408	0.155
Paibian	-0.186	-1.24	0.858	0.726

Table A4- Latitude continued.

Stage	Selectivity	Low c. I.	high C. I.	p-val
Jiangshanian	1.164	0.393	1.963	0.003
Lawsonian	0.476	-1.014	1.967	0.517
Tremadocian	-0.246	-0.766	0.278	0.356
Floian	0.108	-0.578	0.797	0.757
Dapingian	0.105	-0.51	0.739	0.74
Darriwilian	0.118	-0.192	0.429	0.455
Sandbian	0.833	0.438	1.248	0
Katian	0.821	0.525	1.117	0
Hirnantian	1.149	0.319	2.073	0.009
Rhuddanian	0.482	-0.146	1.129	0.137
Aeronian	0.115	-0.673	0.951	0.78
Telychian	-0.829	-1.788	0.116	0.084
Sheinwoodian	0.829	0.131	1.597	0.025
Homerian	0.046	-0.672	0.776	0.9
Ludfordian	0.651	-0.551	2.165	0.33
Pridoli	0.14	-0.61	0.916	0.718
Lochkovian	0.29	-0.348	0.964	0.383
Pragian	0.154	-0.403	0.723	0.591
Emsian	-0.215	-0.634	0.203	0.313
Eifelian	-0.071	-0.545	0.403	0.769
Givetian	0.318	-0.056	0.699	0.098
Frasnian	0.469	-0.053	1.009	0.082
Famennian	-0.26	-0.854	0.347	0.395
Tournaisian	-0.405	-0.938	0.12	0.133
Visean	-0.092	-0.458	0.273	0.621
Serpukhovian	-0.315	-1.003	0.36	0.362
Bashkirian	16.477	-77.406	NA	0.987
Moscovian	0.686	-0.265	1.819	0.188
Kasimovian	0.577	-1.518	3.603	0.623
Asselian	0.61	-0.021	1.273	0.063
Sakmarian	-1.03	-1.841	-0.325	0.007
Artinskian	-0.762	-1.622	-0.024	0.058
Kungurian	0.034	-0.341	0.403	0.859
Roadian	-1.039	-1.666	-0.472	0.001
Wordian	-0.405	-0.963	0.117	0.139
Capitanian	0.052	-0.35	0.454	0.801
Wuchiapingian	-0.737	-1.204	-0.287	0.002
Changhsingian	0.249	-0.21	0.709	0.287
Induan	-1.31	-2.12	-0.561	0.001
Olenekian	-0.352	-0.908	0.217	0.219

Table A4- Latitude continued.

Stage	Selectivity	Low c. I.	high C. I.	p-val
Anisian	-0.337	-0.712	0.036	0.077
Ladinian	-0.111	-0.744	0.501	0.725
Carnian	0.337	-0.044	0.722	0.084
Norian	-0.576	-0.991	-0.163	0.006
Rhaetian	0.172	-0.373	0.721	0.537
Hettangian	0.716	-0.079	1.552	0.083
Sinemurian	0.295	-0.353	0.954	0.375
Pliensbachian	-0.163	-0.589	0.26	0.451
Toarcian	0.688	0.185	1.199	0.008
Aalenian	-0.623	-1.449	0.149	0.124
Bajocian	0.009	-0.508	0.527	0.972
Bathonian	-0.31	-0.823	0.193	0.231
Callovian	0.372	-0.09	0.836	0.115
Oxfordian	0.339	-0.089	0.774	0.123
Kimmeridgian	-0.425	-0.906	0.044	0.079
Tithonian	-0.056	-0.538	0.425	0.819
Berriasian	0.352	-0.284	0.992	0.278
Valanginian	-2.213	-3.45	-1.249	0
Hauterivian	-0.81	-1.514	-0.145	0.02
Barremian	-0.3	-0.976	0.372	0.381
Aptian	-0.069	-0.526	0.388	0.765
Albian	0.234	-0.147	0.616	0.23
Cenomanian	0.396	0.031	0.762	0.034
Turonian	0.027	-0.488	0.538	0.917
Coniacian	-0.413	-1.29	0.46	0.353
Santonian	0.013	-0.666	0.727	0.97
Campanian	0.618	0.131	1.139	0.016
Maastrichtian	0.005	-0.287	0.297	0.973
Danian	-0.71	-1.254	-0.168	0.01
Selandian-Thanetian	-0.087	-0.708	0.566	0.788
Ypresian	0.445	-0.197	1.159	0.194
Lutetian	0.419	-0.014	0.864	0.061
Bartonian	0.046	-0.418	0.532	0.848
Priabonian	-0.046	-0.469	0.387	0.833
Rupelian	0.685	0.187	1.215	0.009
Chattian	0.223	-0.346	0.821	0.452
Lower Miocene	-0.273	-0.647	0.092	0.146
Middle Miocene	0.361	0.092	0.632	0.009
Upper Miocene	-0.382	-0.772	-0.01	0.049
Pliocene	-0.523	-0.795	-0.255	0
Pleistocene	0.728	0.331	1.149	0

Table A5- Binomial test affinity values calculated for marine invertebrate genera within each stage. The total occurrences are listed for each genus followed by the occurrences in each environment. The p-values are posted for each environment, and a p-value < 0.05 indicates an affinity for the environment.

<https://baylor-ir.tdl.org/bitstream/handle/2104/11609/Table%20A5.csv>

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