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BURNING CALORIES, BURNING OCEAN: METABOLIC RATE IN BIVALVES AS A PREDICTOR OF EXTINCTION SELECTIVITY THROUGH TIME AND DURING RAPID GLOBAL WARMING

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Abstract

Organismal metabolic rate is linked to environmental temperature and oxygen consumption, and as such, may be a useful predictor of extinction risk during major climate-driven crises. However, metabolic attributes can be quantified in many ways, highlighting differing aspects of organisms' ecology. Here, we estimate resting whole-body and mass-specific metabolic rates in post-Carboniferous bivalve taxa using body size and seawater paleotemperature to assess how metabolic rate determines survival both during and outside of intervals of rapid climate warming, or 'hyperthermals'. Accounting for the effects of geographic range size, we find a pattern of preferential extinction of bivalves with lower total calorific needs, largely determined by smaller body size, consistent with the postulated ramping up of ecosystem energetics over the Meso-Cenozoic. Contrary to expectations, extinction selectivity based on total calorific needs and emphasizing body size does not differ between hyperthermals and other time intervals. However, a higher metabolic rate calculated per gram of tissue, which is more determined by environmental temperature than body size, consistently increases the probability of extinction during hyperthermals relative to baseline conditions, particularly within the paleotropics. In tandem with previously documented patterns of extinction selectivity based on relative activity levels, including motility and feeding style, these results enhance our understanding of the role of metabolic activity through time and during climate-driven extinctions. Standardized by mass, per-gram metabolic rate may represent a useful metric through which the effects of anthropogenic climate change on modern marine faunas can be predicted.

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by

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1. Introduction

Rapid climate warming stresses marine organisms through the combined the effects of warming, deoxygenation, CO_2 saturation, and ocean acidification, potentially leading to species range shifts, population declines, and extinctions (Masson-Delmotte et al. 2021). An organism's metabolic activity may influence its vulnerability to warming (Pörtner 2002; Peck et al. 2004; Deutsch et al. 2015), however, evidence is lacking for whether this vulnerability may lead to extinction risk. The fossil record of hyperthermal events, defined as intervals during which average sea surface temperatures in the tropics increased by 2°C or more over a period of less than 100,000 years (Foster et al. 2018), offers a way to test theories of extinction vulnerability, including those hinged upon metabolic rate. Experimental responses of modern marine organisms to climate-related stressors align with patterns of extinction, particularly during hyperthermals, wherein climate sensitivity at the individual level matches extinction selectivity patterns of higher taxa during climate-driven extinctions (Reddin et al. 2020). That hyperthermals approximate the effects of anthropogenic climate change means that understanding how they have impacted organisms and biotas in the past with respect to metabolic rate can provide insight into how it will continue to affect them into the future (Kiessling et al. 2023).

Bivalves as a group are diverse and abundant in both the fossil record (Sepkoski 1984; Alroy 2010) and modern oceans (Appeltans et al. 2012), and the completeness of their fossil record is believed to be relatively high in comparison with other clades (Foote and Sepkoski 1999). Furthermore, many extinct bivalve taxa have close living relatives for which respiration rates and activity levels have been measured. Thus, bivalves serve as a useful model taxon with which to study historical trends in extinction based on metabolic activity. Bivalves are also central to a number of important fisheries and ecosystem services (Wijsman et al. 2019; van der Schatte Olivier et al. 2020; Huang et al. 2023), the likes of which are placed under threat by anthropogenic climate change.

Here, we calculate resting metabolic rates for fossil bivalves based on body size and environmental temperature (Gillooly et al. 2001) to assess how metabolic rate influences the probability of extinction for post-Carboniferous genera, and to determine whether extinction selectivity regimes change during hyperthermal events. We show that bivalve genera with higher calculated metabolic rates are less likely to go extinct overall, but that the direction and magnitude of extinction selectivity during hyperthermals is complex and dependent on which aspect of metabolic rate (whole-body vs. mass-specific) is analyzed. Taxa with higher mass-specific metabolic rates are significantly more likely to go extinct during episodes of climate warming, offering a potential metric with which to identify the marine taxa most at risk under anthropogenic warming.

2. Thermal tolerance and metabolism in animals: the conundrum

Tolerance of climate-related stress in experiments is highly variable across taxa and ecologies. Laboratory experiments on Antarctic marine taxa have shown that, when quantifying activity level through feeding and movement, smaller and more active organisms are more likely to survive short-term warming (Peck et al. 2009). More active marine organisms are also more likely to survive major global change extinctions (Clapham 2017). A greater difference between resting (or basal) and maximum metabolic rate, termed 'aerobic scope' (Peck et al. 2004; Pörtner 2010) also appears to confer further resistance to short-term warming (Peck et al. 2009). Aerobic metabolic activity requires more oxygen in warmer temperatures. The concept of oxygen- and capacity-limited thermal tolerance highlights the linkage between temperature change and biological oxygen supply and demand (Pörtner et al. 2017), a connection that becomes increasingly significant given additional climate-associated stressors such as deoxygenation. In addition, more metabolically active organisms generally have higher CO_2 tolerance (Melzner et al. 2009), making them less vulnerable to hypercapnia as a result of CO_2 buildup in the oceans during hyperthermals (Knoll et al. 1996). More active organisms also tend to have lower skeletal carbonate loads, agreeing with observed patterns of selectivity during the end-Permian mass extinction (Knoll et al. 2007).

To facilitate projections of how anthropogenic warming might change metabolically viable habitat, Deutsch et al. (2015) developed the metabolic index (Φ), defined as the ratio of the temperature-dependent O_2 supply in the environment to the organism's resting O_2 demand. Conditions where demand exceeds supply (i.e., Φ is less than 1) are considered to be metabolically unviable, and organisms in these conditions must either use anaerobic metabolic pathways or suppress aerobic activity, both of which are unlikely to be energetically sustainable in the long term (Deutsch et al. 2015). In this case, however, the prediction for extinction selectivity is the opposite to that extrapolated by Clapham (2017): during times of rapid climate warming, more active organisms, which have greater oxygen demands, should be more vulnerable due to experiencing greater losses of metabolically-viable habitat (Deutsch et al. 2015; Penn and Deutsch 2022). This hypothesized pattern is consistent with elevated extinction rates at high latitudes during the Permian-Triassic event (Penn et al. 2018). Different environmental stressors associated with hyperthermal conditions may act on organism performance in synergistic or, conversely, opposing directions, and on different temporal scales (Reddin et al. 2020). The links between activity level, metabolic rate, and extinction risk during periods of rapid climate warming need greater clarity to help identify the mechanisms leading to organism vulnerability.

3. Quantifying metabolism in fossil organisms

Although activity levels and aerobic scope are related to metabolic rate, a roadblock to studying how metabolism influences extinction risk is an inability to directly measure respiration rates for extinct organisms. Resting whole-body metabolic rate, in Watts or Joules per second, can be estimated from temperature and biomass using a model originally derived by Gillooly et al. (2001) as follows: an organism's whole-body metabolic rate (B) scales with its body mass (M) with an exponent close to 3/4, in other words, $B \propto M^{3/4}$. The relationship between body size, temperature, and resting whole-body metabolic rate can be approximated by the expression,

$$B = B_0 M^{3/4} e^{-E_i/kT} \tag{1}$$

where $e^{-E_i/kT}$ is the Boltzmann’s factor, with E_i being the average activation energy of rate-limiting biochemical reactions, k being Boltzmann's constant, and T being temperature in Kelvin. B_0 is a standard metabolic rate scaling constant, equivalent to the average resting metabolic rate of the higher-order taxon to which the organism belongs. This assumes that resting metabolic rate is taxonomically conserved, a contention supported by, e.g., Saupe et al. (2014), who found that thermal tolerances in mollusks were stable over millions of years covering substantial environmental change. Note that the Gillooly et al. (2001) model estimates resting metabolic rate, and does not explicitly account for variations in activity levels or growth rate except coarsely through the taxon-specific (generally at the ordinal or class level) adjustment of the B_0 coefficient. Previous applications of the Gillooly et al. (2001) model to the fossil record have generally focused on the total energy use of populations and ecosystems, without reference to extinction risk. The three-quarters power scaling of metabolic rate with body mass was used by Finnegan and Droser (2008) to estimate population energy use, with temperature held constant. Finnegan et al. (2011) assessed changes in the energy consumption of marine gastropod assemblages over the Mesozoic Marine Revolution and found that mean per capita metabolic rates of gastropod assemblages rose between the Triassic and Cretaceous, largely driven by increases in body size. Payne et al. (2014) later used the Gillooly et al. (2001) model to establish that, despite being less diverse and abundant, bivalves accounted for a much greater share of metabolic activity than brachiopods in Paleozoic oceans.

Whole-body metabolic rate can be divided by the mass of the organism to yield mass-specific metabolic rate, the metabolic rate of one unit mass of tissue. Mass-specific metabolic rate allows for comparisons of energy expenditure across orders of magnitudes of variation in body size (Makarieva et al. 2008). Mass-specific resting metabolic rate can be approximated by the expression,

$$B = M^{-1} \cdot B_0 M^{3/4} e^{-E_i/kT} = B_0 M^{-1/4} e^{-E_i/kT} \qquad (2)$$

Whereas whole-body metabolic rate ∝ (is proportional to) $M^{3/4}$, mass-specific metabolic rate ∝ $M^{-1/4}$. Assuming consistent values for B_0 and T, a larger organism will have a higher whole-body metabolic rate, but a smaller mass-specific metabolic rate. Whole-body and mass-specific metabolic rate should therefore be inversely correlated with one another. Nearly all prior work using the Gillooly et al. (2001) model with the fossil record has focused on whole-body metabolic rate as an efficient representation of an individual's ecological importance in its community. Given that mass-specific metabolic rates are consistently optimized across the major domains of life (Makarieva et al. 2008), we also assess mass-specific metabolic rate as a potential predictor of extinction selectivity.

Body size is the primary factor governing resting whole-body metabolic rate (Gillooly et al. 2001). Hence, we expect to observe an overall pattern of extinction selectivity similar to that found by Payne and Heim (2020) for body size, wherein organisms with higher whole-body metabolic rates are generally less likely to go extinct, with the opposite trend observed for mass-specific metabolic rate. Reddin et al. (2021) observed extinction selectivity for body size in line with Payne and Heim (2020) but detected a relative shift against larger body sizes in bivalves during hyperthermal-associated stages. We thus expect to observe the preferential extinction of organisms with lower whole-body (total) metabolic rates, and higher mass-specific (per-gram) metabolic rates. Organisms with higher standard metabolic rate scaling constants (B_0) might be more vulnerable during hyperthermals, given that they may have more energetically demanding lifestyles when mass and environmental temperature are standardized.

4. Methodological approach

We downloaded a dataset of Phanerozoic marine animal occurrences from the Paleobiology Database (www.paleobiodb.org, hereafter, 'PBDB') on October 18th, 2023. We binned each occurrence to its respective chronostratigraphic stage, as detailed in the accompanying vignette to the R package *divDyn* (Kocsis et al. 2019), and excluded any unbinned occurrences. We then calculated three-timer sampling completeness of Alroy (2008), and range-based sampling probability using *divDyn* (Kocsis et al. 2019), removing any singletons (taxa with fewer than two occurrences). As the order Unionida is comprised of nearly completely of freshwater bivalves (Lopes-Lima et al. 2017), all genera from this order were excluded from the dataset. We then calculate genus stratigraphic ranges, including last appearance date, by stage using divDyn::modeltab().

Because geographic range size has a known effect on extinction risk (e.g., Payne and Finnegan (2007), we incorporated range size as genus-subsampled maximum great circle distance (GCD) (Foote et al. 2016). Since geographic range size is strongly skewed, we followed Reddin et al. (2021) to bin geographic range into ordinal levels based on the GCD values of each stage. Here, the first bin represents genera with no empirical occurrences during a particular stage (i.e., those interpolated by range-through occurrences), the second representing genera with maximum GCDs of 0 (i.e., those with only a single locality during the stage), the third representing everything else up to the third GCD quartile, and the fourth representing everything above the third quartile. Removing geographic range size from the analysis did not significantly affect our results.

Body size estimates at the genus level were provided by the supplementary data files of Payne and Heim (2020), as measurements of the longest linear dimension (in millimeters) of the largest specimen of each genus. Maximum linear dimensions of bivalve shells are strongly correlated with both shell volume and biomass (Powell 1985). Per Payne et al. (2014), ash-free dry mass (M), in grams, for bivalves scales with the maximum linear dimension of the shell (L) via the following function:

$$M = 1.0 \times 10^{-5} \times L^{2.95} \tag{3}$$

Thus, we estimated M for each genus (in grams) using measurements of maximum shell length.

Based on the compilation of Brey (2001), Payne et al. (2014) used B_0 constants of 1.4×10^{11} W kg$^{-3/4}$ for heterodont bivalves, and 1.3×10^{11} W kg$^{-3/4}$ for all other bivalves. We follow this approach, as did Strotz et al. (2018). We define heterodont bivalves as those included in the molecular phylogeny of Taylor et al. (2007) along with the extinct orders Actinodontida, Hippuritida, and Megalodontida.

Paleotemperature estimates were obtained for each taxon based on its observed distribution over paleogeographic maps. The modern latitude and longitude coordinates associated with each bivalve occurrence listed in the PBDB were used to reconstruct paleolatitude and -longitude coordinates for each occurrence via the R package ‘rgplates’ (Kocsis et al. 2024) with the GPlates desktop application (Müller et al. 2018), using the PaleoMAP model (Kocsis and Scotese 2021). We used these paleocoordinates to retrieve the corresponding annual mean sea surface paleotemperature outputs from HadCML3 climate models run for every five million years (data from Valdes et al. 2017; interpolated by Kocsis et al. 2021). We then calculated the median of all paleotemperature estimates associated with each bivalve genus, irrespective of time, as a relative measure of its thermal preference, which can be done for nearly the entire dataset.

We also correlated our metabolic rate estimates for bivalves with the activity quotient calculated by Clapham (2017). Clapham (2017) assigned activity quotients at the ordinal level for bivalves, whereas our metabolic rate estimates are calculated at the genus level. We compare both whole-body and mass-specific metabolic rate to the activity quotient to explore the nature of their relationships.

We conduct a series of logistic regression models of bivalve genus extinction odds as a function of log metabolic rate and geographic range size, by stage, for each post-Carboniferous stage. Following Reddin et al. (2021), the estimated stage of extinction is considered probabilistic (survival represented by 0, extinction represented by value $0.5 < x < 1$) rather than definite (survival represented by 0, extinction represented by 1), based on the combined sampling completeness of the temporal stage and the clade over all stages. The remainder extinction probability ($1 - x$) falls into the following stage, acknowledging that the youngest known fossils typically fail to represent the true timing of extinction (Signor et al. 1982; Marshall 1990). The resulting extinction selectivity coefficients indicate the mean effect of increasing metabolic rate on extinction risk, in log-odds, during a given stage. Positive values indicate that increasing metabolic rate likewise increases the risk of extinction, while negative values indicate that bivalves with higher metabolic rates are less likely to go extinct than those with lower metabolic rates.

Because clades and traits have different background rates of extinction (Stanley 1985; Raup and Boyajian 1988), we calculate relative hyperthermal vulnerability (RHV), following Reddin et al. (2021), to quantify the significance of any hyperthermal-unique change in extinction rate relative to the group's background rate of extinction. To do this, extinction selectivity coefficients from the logistic regression were synthesized via meta-regression for stages associated with the onset of hyperthermal conditions and, separately, for all other (non-hyperthermal) stages. Stages associated with the continuation rather than onset of hyperthermal conditions were excluded from the calculation of RHV, following Reddin et al. (2021), as the first pulse of hyperthermal-associated extinction is likely to be the most analogous to modern climate change. For the purpose of this study, we focused on the six major post-Paleozoic hyperthermal events as identified by Foster et al. (2018), these being the Permian–Triassic (~252 Ma), Triassic–Jurassic (~201.3 Ma), the end-Pliensbachian–early Toarcian (~183 Ma), the Aptian (~120 Ma), and Cenomanian-Turonian (~94 Ma), and Paleocene-Eocene Thermal Maximum (~55.5 Ma). We calculated RHV as the difference between the average metabolic-rate-based extinction selectivity of stages associated with hyperthermal onsets and of stages not associated with hyperthermals. Following Reddin et al. (2021), we use a 90% confidence interval, as having so few hyperthermals means that it is unlikely for RHV to be significant at the

95% confidence level. Positive RHV values indicate that selectivity against higher metabolic rates is stronger during hyperthermal conditions than during other intervals. We conduct this procedure for both whole-body and mass-specific metabolic rate. Because latitudinally selective extinction patterns have been detected over hyperthermal events, only some aspects of which may be linked to thermal stress (Penn et al. 2018; Reddin et al. 2019, 2022), we repeat the analysis restricting the data solely to tropical bivalve genera (i.e., those whose paleolatitudinal median fell between -30° and 30). All analyses were performed in R using the packages *metafor* (v. 3.8-1) (Viechtbauer 2010), *divDyn* (v. 0.8.2) (Kocsis et al. 2019), and *lme4* (v. 1.1-35.1). Figures were created using the packages *ggplot2* (v. 3.4.2) (Wickham 2016) and *deeptime* (v. 1.0.1) (Gearty 2023).

5. Results

Our PBDB dataset includes 138,419 bivalve occurrences over a total of 1,919 genera. Pectinida, Ostreida, Venerida, and Cardiida are the most well-represented orders in the dataset, both by occurrences and number of genera. Pectinida dominates the Mesozoic, Venerida and Cardiida the Cenozoic, and Ostreida is common throughout.

To assess the relative importance of the standard metabolic rate scaling coefficient (B_0), body mass (M), and average sea surface temperature (T) in estimating metabolic rate using the Gillooly et al. (2001) model, we fit multiple linear regressions to whole-body and mass-specific metabolic rate as a function of each of these parameters, standardized. For whole-body metabolic rate, the coefficient for body mass is by far the largest, indicating that estimates of resting whole-body metabolic rate are largely controlled by body mass; conversely, mass-specific metabolic rate is moderately driven by ambient environmental temperature and uncorrelated with mass

(Table 1). However, bivalves with higher total calorific needs tend to have relatively lower per gram calorific needs (Fig. 1).

Whole-body and mass-specific metabolic rate each show a weak but significant relationship with genus age, recorded as first appearance datum, with total metabolic rate increasing (Fig. 2A), and per-gram metabolic rate decreasing (Fig. 2C), over the course of the Phanerozoic. Likewise, the expected relationship between metabolic rate and paleolatitude is also evident, with taxa living closer to the tropics tending to have higher total and per-gram calorific needs compared to higher-latitude taxa (Fig. 2B,D).

On the whole, bivalves with higher *whole-body* metabolic rates are less likely to go extinct in most post-Carboniferous stages (Fig. 3A). An exception is the Santonian (late Cretaceous)—where only five of the 277 bivalve genera in this stage for which we can estimate metabolic rate went extinct, and the whole-body metabolic rates of those five genera were higher than average. Conversely, bivalves with higher *mass-specific* metabolic rates are generally more likely to go extinct during the post-Carboniferous (Fig. 3B). Similar trends are observed when the above analyses are restricted to tropical latitudes only.

Extinction selectivity based on whole-body metabolic rate during stages associated with hyperthermals is not significantly different from average extinction selectivity during baseline conditions (Fig. 4A). This is the case even when restricting our analysis to the tropics (Fig. 4B). However, extinction selectivity based on mass-specific metabolic rate tends to be stronger during hyperthermal conditions, and this is particularly true in the tropics (Fig. 4C,D). Similar trends are observed when considering only polar taxa as well (i.e., those whose paleolatitudinal median fell outside of -60° and 60°), although the significance of these relationships is limited by the paucity of data on high-latitude bivalves in the fossil record.

6. Discussion

The term 'metabolic rate' is used variably in the paleobiological literature. Descriptive categories associated with motility and feeding (e.g., relative activity levels) are thought to reflect metabolic rate in some way, but comparisons between taxa can be difficult to interpret in part due to wide variation in the frequency and intensity of such behaviors. Resting metabolic rate enables more straightforward comparisons among taxa and can be qualitatively assessed either in terms of (1) the calorific demands of the organism as a whole (whole-body metabolic rate, ~body size) or (2) calorific needs standardized per gram of tissue (mass-specific metabolic rate, ~temperature). Smaller bivalves, with lower whole-body metabolic rates, are more likely to go extinct during post-Carboniferous stages. Meanwhile, bivalves with higher mass-specific rates are more likely to go extinct, with their extinction risk being significantly higher during hyperthermals in the tropics. For each of the two calculated metabolism estimates, we explore biases that might influence our results and then discuss their potential implications for ancient and present-day biodiversity alike.

6.1 Extinction selectivity based on whole-body resting metabolic rate

Because whole-body resting metabolic rate is governed primarily by body mass (Table 1; Gillooly et al. 2001), our observed pattern of extinction selectivity against lower whole-body metabolic rate (Fig. 3A) mirrors the findings of Heim et al. (2015) and Payne and Heim (2020) for body size. Bivalves that are larger, and therefore process more energy per unit time, are less likely to go extinct than smaller genera during most stages (Payne and Heim 2020). Likewise, Malanoski et al. (2024) observed that marine invertebrates with smaller body sizes were more likely to go extinct over geologic time. Although this overlap makes it difficult to discriminate between the evolutionary and ecological influences of body size and caloric needs, it does highlight the mechanistic linkage between these factors that are often considered in isolation. Selectivity in favor of larger bivalves with greater calorific needs is consistent with the 'Seafood through Time' hypothesis of Bambach (1993), which posits that increases in resting metabolic rates and the innovation of more active modes of life led to a ramping up of overall ecosystem energetics and biomass over time. During the proposed Mesozoic Marine Revolution (Vermeij 1993), larger body sizes alongside heightened activity aided both predator and prey in the race for survival. Finnegan et al. (2011) found that mean whole-body metabolic rate in gastropods rose by 150% between the late Triassic and late Cretaceous, a trend driven largely by increases in body size. The observed increase in whole-body metabolic rate runs counter to expectations of preservation bias based on size in the fossil record (Cooper et al. 2006; Valentine et al. 2006), in which we would expect smaller taxa to be vastly underrepresented, particularly in older stages (Hendy 2011).

Body size is also closely linked to dispersal ability and geographic range size, with larger organisms generally inhabiting larger ranges (Brown et al. 1996). Although a larger geographic range is associated with a reduced risk of extinction (Payne and Finnegan 2007), we accounted for this influence in our logistic regression analyses. Although the effects of body size and geographical range size on extinction risk are interwoven (Harnik 2011), dropping geographic range size from the analysis does not alter the results. The observed pattern of selectivity in favor of larger sizes and higher caloric requirements in bivalves persists even when considering solely tropical genera and occurrences, where predation levels are likely to be more intense (Freestone et al. 2021).

Strotz et al. (2018) found that Pliocene to Recent bivalve and gastropod species with higher whole-body metabolic rates were more likely to go extinct over that interval. While we do observe a positive—albeit not significant—extinction selectivity coefficient for the Pleistocene stage, our findings are overall in opposition to this trend. The inclusion of Recent (Holocene) molluscan faunas in the analysis of Strotz et al. (2018) might account for that difference in that smaller species are easier to recover and identify in the Modern, but less likely to preserve or subsequently be recovered and identified in fossil assemblages (Behrensmeyer et al. 2000; Hendy 2011). Acknowledging the excellent preservation and recovery potential in unlithified Pliocene fossil assemblages of the western Atlantic, this tendency might nonetheless have skewed their results towards smaller, and hence lower metabolic rate, taxa in the Holocene in comparison to extinct taxa. Alternatively, the pattern found by Strotz et al. (2018) is entirely consistent with the postulated drop in production on the Florida platform and western Atlantic between the Pliocene and today (Allmon et al. 1996; Tao and Grossman 2010). Their results could reflect that regional shorter-term environmental shift rather than the global pattern we document over a much longer time interval.

Save for the end-Pliensbachian-early-Toarcian hyperthermal, in which bivalves with higher whole-body metabolic rates are even less likely to go extinct than normal, we find no overall difference in extinction selectivity based on whole-body metabolic rate between stages associated with hyperthermal conditions and those that are not (Fig 4A). Reddin et al. (2021) found a relative increase in extinction risk for bivalves with larger body sizes during hyperthermals, but whole-body metabolic rate evidently does not mirror this tendency as we might expect it to. Although strongly correlated with bivalve body size, whole-body metabolic rate is affected by other factors as well (e.g., environmental temperature, taxon membership). Our results show no clear support for bivalves with greater calorific needs being at greater risk of extinction during past hyperthermal conditions.

6.2. Extinction selectivity based on mass-specific metabolic rate

Mass-specific metabolic rate is influenced more by environmental temperature than by body mass (Table 1). Thus, bivalves that inhabit warmer waters generally have higher mass-specific metabolic rates. The observed trend of selectivity against bivalves with higher mass-specific metabolic rates throughout much of the post-Paleozoic could indicate heightened rates of extinction in warmer, low latitude environments relative to cooler ones and/or the greater prevalence of warm conditions prior to the Neogene (Scotese et al. 2021). However, when our analyses were restricted to tropical latitudes, this pattern of extinction selectivity was even stronger. A similar relationship between temperature and extinction risk was observed by Malanoski et al. (2024), who found that marine invertebrates with higher realized thermal preferences were more likely to go extinct. Higher rates of extinction in the tropics may seem counter to the latitudinal diversity gradient observed in many groups of organisms, including bivalves (Jablonski et al. 2000), but they could be balanced by even higher origination rates in the tropics (Stenseth 1984). Flessa et al. (1996) found that that the median age of recent bivalve genera in the tropics is significantly lower than the median age of contemporary genera from higher latitudes. Jablonski et al. (2006) argued for an "out of the tropics" model of taxon originations in the tropics and subsequent expansion towards the poles. The observed relationship between mass-specific metabolic rate (largely controlled by environmental temperature) and extinction risk may thus be part of the puzzle underlying high rates of tropical turnover. Organisms with lower whole-body (and higher mass-standardized) metabolism generally have shorter lifespans (Speakman 2005), contributing to more rapid evolution and turnover of individuals, populations, and species.

During the majority of the studied hyperthermal intervals, selection against bivalves with higher mass-specific metabolic rates was stronger compared to other time intervals, especially in tropical paleolatitudes. As mass-specific metabolic rate is largely temperature-dependent, this result is consistent with a higher risk of extinction for tropical taxa during warm intervals of the Phanerozoic (Reddin et al. 2019) and during hyperthermal conditions in particular (Reddin et al. 2022). This suggests that the same factors that elevate turnover in warm-water habitats may be at play globally during hyperthermal events, namely, the pervasive effects of thermodynamics on biological rates. Minimal change in extinction selectivity observed across the Paleocene-Eocene Thermal Maximum could be attributed to the low level of mollusk extinctions overall (Ivany et al. 2018), implying that bivalves were not particularly affected by the environmental change during this hyperthermal. However, restricting the analysis to only high-latitude taxa also yields a similar, albeit not significant, increase in the preferential extinction of bivalves with higher mass-specific metabolic rates. This suggests that the lack of a significant pattern in relative hyperthermal vulnerability when considering both tropical and extra-tropical bivalve genera could be an artifact of poor sampling at high latitudes.

To investigate the potential for higher overall turnover in taxa with higher mass-specific metabolic rates, we ran a logistic regression of bivalve origination with respect to mass-specific metabolic rate. Indeed, we observe preferential origination of bivalves with higher mass-specific metabolic rates from the mid-Jurassic onwards, lending further support to the hypothesis of faster turnover among bivalves with higher per-gram metabolic demands. As with extinction, the preferential origination of bivalves with higher mass-specific metabolic rates is further enhanced during hyperthermals, particularly within the tropics. Our results support those of Monarrez et al. (2021), who found differences in both origination and extinction selectivity during the ‘Big Five’ mass extinctions compared to baseline conditions, and further suggest a role for temperature driving turnover of high mass-specific metabolic rate taxa in the tropics.

6.3. An alternate source of B_0 *values*

The B_0 standard metabolic rate coefficient is a taxon-specific normalization constant that attempts to account for physiological differences between different higher-order clades. Payne et al. (2014) and Strotz et al. (2018) used B_0 constants of 1.4×10^{11} W kg$^{-3/4}$ for heterodont bivalves, and 1.3×10^{11} W kg$^{-3/4}$ for all other bivalves, based on the compilation of Brey (2001). An alternate source of standard metabolic rate constants for gastropods was used by Finnegan et al. (2011), taking the average B_0 of multicellular ectotherms of 9.91×10^{7} W/g$^{3/4}$ given by Gillooly et al. (2001) and multiplying by experimentally-derived standard metabolism coefficients for higher-order gastropod taxa provided by Vladimirova (2001). Strotz et al. (2018) applied this method in their analysis of Pliocene to Recent gastropods. Equivalent standard metabolism coefficients for bivalves are provided by Vladimirova et al. (2003), and applying these coefficients does not affect the overall patterns of extinction selectivity based on whole-body and mass-specific metabolic rates. However, estimating resting metabolic rate based on B_0 coefficients from Vladimirova et al. (2003) removes the difference between hyperthermal and baseline extinction selectivity based on mass-specific metabolic rate. B_0 values sourced from Brey (2001) and Vladimirova et al. (2003) are unrelated, meaning that that these two sources likely measure different things.

Because whole-body metabolic rate is so heavily dependent on body mass, the sourcing of B_0 values was of little consequence for previous work focusing on whole-body metabolic rate. However, since the alternate metric of mass-specific metabolic rate significantly reduces the importance of body mass in the Gillooly et al. (2001) equation, the influence of B_0 values increases. Brey (2001) consists of a compilation of resting metabolic rates for marine invertebrates; B_0 values are determined by controlling for latitude, depth, and body mass. The coefficients provided by Brey (2001) split the dataset into heterodont and non-heterodont bivalves. Vladimirova et al. (2003) instead combined experimental rates of oxygen consumption for select bivalve taxa with published data on energy metabolism to obtain clade-specific mass-dependent coefficients of resting metabolic rate. B_0 values from Vladimirova et al. (2003) provide greater taxonomic resolution that might better reflect the range of variation in resting metabolic rates within Bivalvia. Indeed, using these values results in the B_0 coefficient having a much larger effect on mass-specific metabolic rate (Table 2). However, the relatively low number of measurements combined with the limited number of orders and families represented means that we have less confidence in assigning B_0 values from Vladimirova et al. (2003) in our dataset.

Given the uncertainty associated with assigning B_0 values, we can alternatively ignore the effects of the taxon-specific normalization coefficient altogether and simply run the analysis holding B_0 constant for all bivalves. This approach yields a pattern of RHV resembling that obtained from using values from Brey (2001) for heterodont and non-heterodont bivalves. In other words, the significance of mass-specific metabolic rate as a predictor of extinction selectivity persists even when considering only the mass- and temperature-dependent variation in resting metabolic rate. However, because the coefficients of Brey (2001) and Vladimirova et al. (2003) are unrelated, future analyses must take care when choosing which method to employ in estimating resting metabolic rate. Additional experimental constraints on B_0 for a range of taxa would be most welcome in the effort to understand the propensity for extinction based on metabolic rate.

6.4. Potential sources of bias

Preservation biases are well-known in the fossil record, including the preferential loss of, e.g., small, fragile, and aragonitic shells both before and after burial (Hendy 2011). This likely manifests in our dataset as the dominance of calcite-shelled ostreids and pectenids for much of the record, particularly in the pre-Cretaceous. Given the minimal impact of B_0 values sourced from Brey (2001) on resting metabolic rate, the effect of this overrepresentation of non-heterodont bivalves is likely to be minimal. Conversely, the experimental respiration rates of Vladimirova et al. (2003) indicate that the subclass Pteriomorphia, including the families Ostreidae and Pectinidae, has the overall highest level of energy metabolism standardized by mass, and hence using their coefficients could skew the calculations of extinction selectivity based on metabolic rates. Independent of taxonomy, the relationships among metabolism, lifespan, and growth rates in bivalves (e.g., Ridgway et al. 2011; Moss et al. 2016), however, mean that the effects of size bias on whole-body metabolic rate in particular cannot be ignored. Payne and Heim (2020) found that the preferential extinction of smaller-bodied taxa persists even when accounting for a size bias using a capture-mark-recapture analysis. Thus, the observed higher risk of extinction in bivalves with lower whole-body metabolic rates, largely controlled by body size, is likely true.

Our analysis uses maximum shell length as a proxy for body size, and so in effect considers only fully mature, adult shells. However, metabolic rate and energy uses varies considerably over the course of an organism’s lifespan (Pörtner 2010), and many bivalves, e.g., Pacific oysters, *Crassostrea gigas*, exhibit some degree of plasticity in terms of metabolic rate over ontogeny (Dupoué et al. 2023). Juvenile bivalves are at particular risk from the effects of warming, acidification, and hypoxia (Bressan et al. 2014; Stevens and Gobler 2018), suggesting that a more complete understanding of the interplay between life history and resting metabolic rate is important. Such an analysis is unfortunately limited by the availability of requisite data over large taxonomic groups. If selection is strongest early in bivalve life histories, our patterns based on adult body sizes could be misleading.

Another potential concern is the use of sea surface temperature as the input for environmental temperature in the Gillooly et al. (2001) metabolic rate model, despite the fact that bivalves are benthic organisms and temperature generally decreases with depth on the shelf. Here, sea surface temperature serves as a proxy for the distribution of energy on the planet. While not an exact match for true environmental temperature in which the organisms were living, variations in sea surface temperature estimates as applied to occurrences and calculated for genera should nonetheless approximate the geographic component of environmental temperature. Future work could potentially involve sensitivity analyses incorporating average thermocline depth and estimated habitat depth, but this is beyond the scope of this study.

Geographical sampling bias in our dataset poses particular concern for the determination of last appearance dates. Taxa with wider geographic ranges are both less likely to go extinct and more likely to be sampled independent of any real difference in extinction risk (Payne and Finnegan 2007). The inclusion of geographic range size in our logistic regression analyses reduces the confounding effects of range size on extinction risk. Nevertheless, geographical sampling biases remain strong in the fossil record, heavily influencing observed patterns of diversity and turnover (Alroy 2008; Vilhena and Smith 2013; Close et al. 2020; Antell et al. 2024). The strong relationship between metabolic rate and paleolatitude (Fig. 2D) agrees with observed trends of shorter lifespans and faster growth rates among lower-latitude bivalves (Moss et al. 2016), but variable oversampling of the tropics could nonetheless influence our results.

Restricting our analysis to the more consistently well-sampled tropical bivalves obviates this potential problem, where relative hyperthermal vulnerability based on metabolic rate shows even stronger and more distinct trends.

6.5. The utility of metabolic rate for predicting extinction risk

Prior work on assessing metabolism and extinction selectivity in the fossil record has investigated metabolic rate and energetics in a variety of ways. Using activity level scoring based on styles of feeding and movement, Clapham (2017) argued that more active organisms were more likely to survive during climate driven extinctions. Using the same measures of activity, Reddin et al. (2021) found that higher activity levels were associated with higher survival odds in general, but this effect was less pronounced during hyperthermals than non-hyperthermals. These results imply that raw extinction selectivity in the fossil record may not be the best indicator about changes in extinction risk associated specifically with warming, whereas relative changes in extinction risk during past hyperthermals could be more useful Our findings expand upon this to argue that extinction risk based on individuals' total calorific needs (whole-body metabolic rate) does not differ significantly during and outside of hyperthermal intervals, whereas selection against higher calorific needs per gram of tissue is stronger during hyperthermal conditions. The activity quotient calculated by Peck et al. (2009) and used by Clapham (2017) is not strongly correlated with either whole-body or mass-specific metabolic rate as calculated here (although these studies were done at a higher taxonomic resolution than ours). As a measure of feeding and movement (i.e., sporadic expenditures of energy), the activity quotient likely does not reflect resting conditions to the extent that basal/resting metabolic rate does. Organisms score high in the activity quotient if they are capable of large bursts of energy, irrespective of their resting metabolic rate.

Body size and environmental temperature affect extinction selectivity in opposite directions: a larger body mass decreases extinction risk (Payne and Heim 2020), while warmer environmental temperatures increase it (Mayhew et al. 2012; Reddin et al. 2019, 2022). Though metabolism in the fossil record has previously been assessed solely via whole-body metabolic rate, mass-specific metabolic rate shows a clearer and more interpretable pattern of extinction selectivity during hyperthermal events, likely due to mass and temperature acting in the same direction alongside their underlying metabolic implications. Mass-specific metabolic rate is strikingly similar across the major domains of life (Makarieva et al. 2008) and may be more directly relevant to assess the physiological consequences of warming, anoxia, acidification, and hypercapnia for organisms during periods of rapid climate warming. Laboratory studies on modern snow crabs (*Chionoecetes opilio*) show that energetic needs increase with both mass and temperature, while energetic input (i.e., caloric consumption) also increases with mass but displays a unimodal peak with regards to temperature, decreasing especially rapidly as temperatures get too hot (Foyle et al. 1989). Because mass increases both energetic need and input, the effects on net energy flow are minimal in comparison to temperature. In contrast, the combination of simultaneously high energetic needs and low energetic input as organism performance (e.g., feeding success) decreases at high temperatures may be what drives population loss during hyperthermal conditions. Snow crabs experienced a major population collapse in 2021 linked to mass starvation as a consequence of a marine heat wave (Szuwalski et al. 2023). Similar temperature-dependent energetic misbalances may explain why increasing mass-specific metabolic rate might increase extinction risk during hyperthermal conditions. Alaska's Bering Sea snow crab season was recently closed for the second year in a row (Alaska Department of Fish and Game 2023) as a direct result of these die-offs, banning the harvesting of this commercially important taxon. Such examples of lost ecosystem services highlight the importance of understanding metabolism-driven responses to climate change.

7. Conclusion

As human activity continues to influence the Earth's climate, marine organisms will increasingly face climate-related stressors that may threaten their survival. Our results suggest that bivalves with higher mass-specific metabolic rates, especially those that live in warmer environments, are at greater risk of extinction than lower metabolic rate bivalves. This distinction becomes more pronounced during hyperthermals. Our findings are consistent with the existing body of literature concerning body size, temperature, and extinction rates, but provide a more direct link between metabolic activity and survival. The effects of climate change on metabolic rate selectivity may be even more severe among taxa less resilient than bivalves. Future work should include mass-specific metabolic rate as a relevant predictor for how marine ectotherms will perform in conditions of warming, anoxia, and acidification.

8. Appendix

Table 1: The influence of standard metabolic rate scaling coefficients (B_0), body mass (M), and average sea surface temperature (T) on whole-body and mass-specific metabolic rate. Standardized coefficients are from multiple linear regressions, one regression per row. B_0 values are sourced from either (A) Brey (2010), (B) Vladimirova et al. (2003), or (C) are alternatively set constant at 9.91 × 10^7 W/$g^{3/4}$, the average B_0 of multicellular ectotherms given by Gilooly et al. (2001) for all genera. Whole-body metabolic rate is mainly determined by body mass, whereas mass-specific metabolic rate is more temperature dependent. The data here are each post-Carboniferous genus that had all variables calculated (n = 1111).

(A) B_0 values from Brey (2010)					
	B_0	M	T	**Adjusted R-squared**	**p-value**
Whole-body Metabolic Rate	0.0094	0.97	0.024	0.95	< 0.0001
Mass-specific Metabolic Rate	0.020	-0.070	0.51	0.22	< 0.0001
(B) B_0 values from Vladimirova et al. (2003)					
	B_0	M	T	**Adjusted R-squared**	**p-value**
Whole-body metabolic rate	0.015	0.95	0.030	0.91	< 0.0001
Mass-specific metabolic rate	0.31	-0.055	0.48	0.29	< 0.0001
(C) B_0 eliminated altogether					

	B_0	M	T	**Adjusted R-squared**	**p-value**
Whole-body metabolic rate		0.98	0.024	0.96	< 0.0001
Mass-specific metabolic rate		-0.070	0.51	0.22	< 0.0001

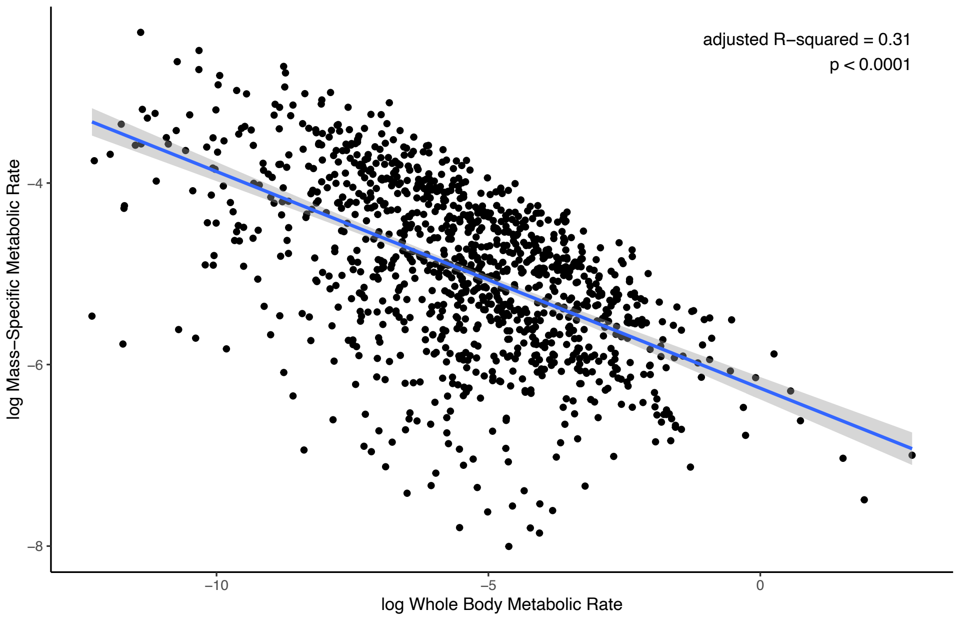

Figure 1: Relationship between log whole-body and log mass-specific metabolic rate in bivalves. The data here are each post-Carboniferous genus that had all values calculated (n = 1111). Bivalves with larger body sizes and thus higher total calorific needs tend to have lower per gram calorific needs.

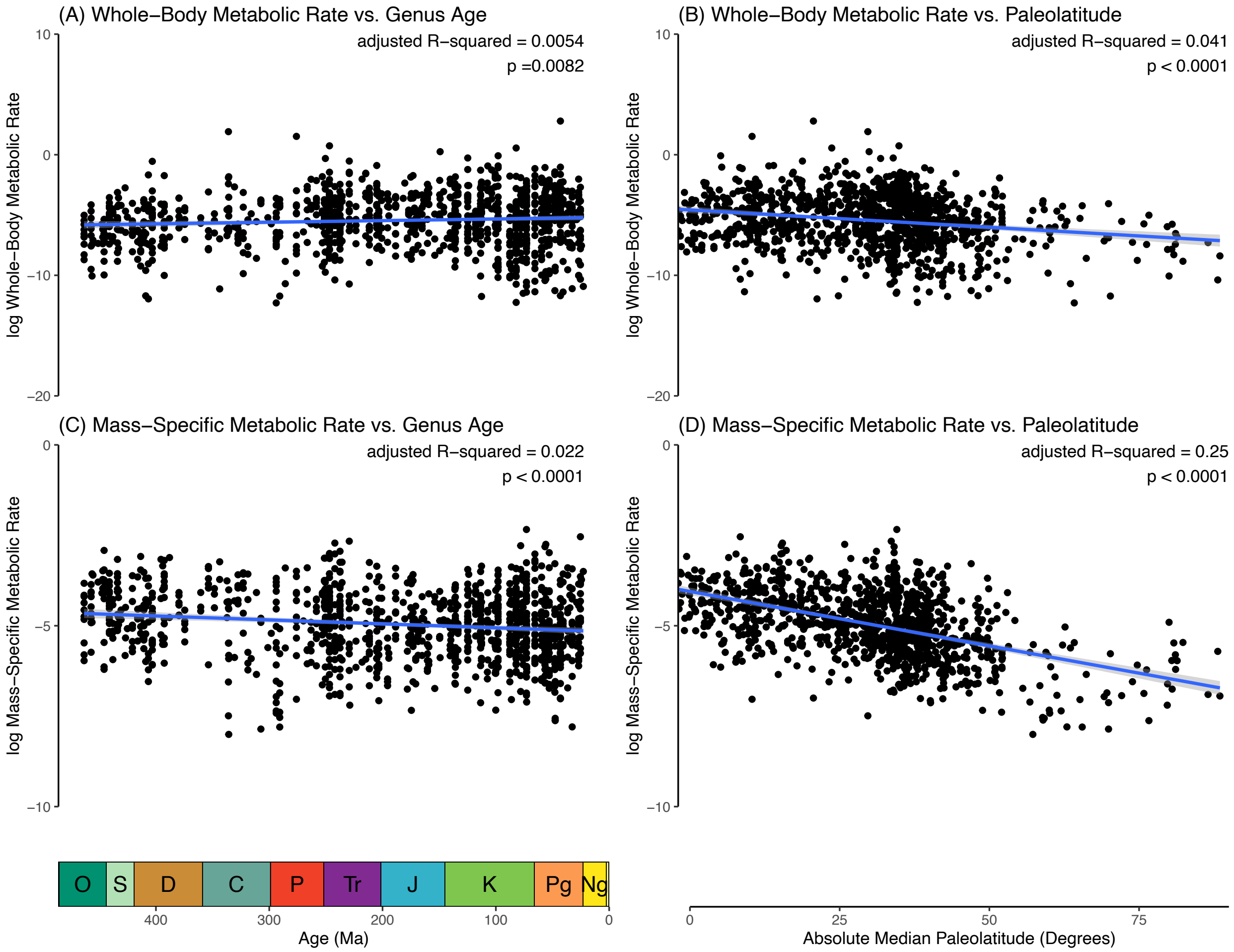

Figure 2: Relationships between metabolic rate and genus age (first appearance datum), or absolute paleolatitude. A, whole-body metabolic rate versus genus age. B, whole-body metabolic rate vs. absolute genus median paleolatitude. C, mass-specific metabolic rate versus genus age. D, mass-specific metabolic rate vs. absolute paleolatitude. Whole-body metabolic rate decreases, and mass-specific metabolic rate increases, with genus age. Both whole-body and mass-specific metabolic rates decrease with absolute paleolatitude. The data here are each post-Carboniferous genus that had all values calculated (n = 1111).

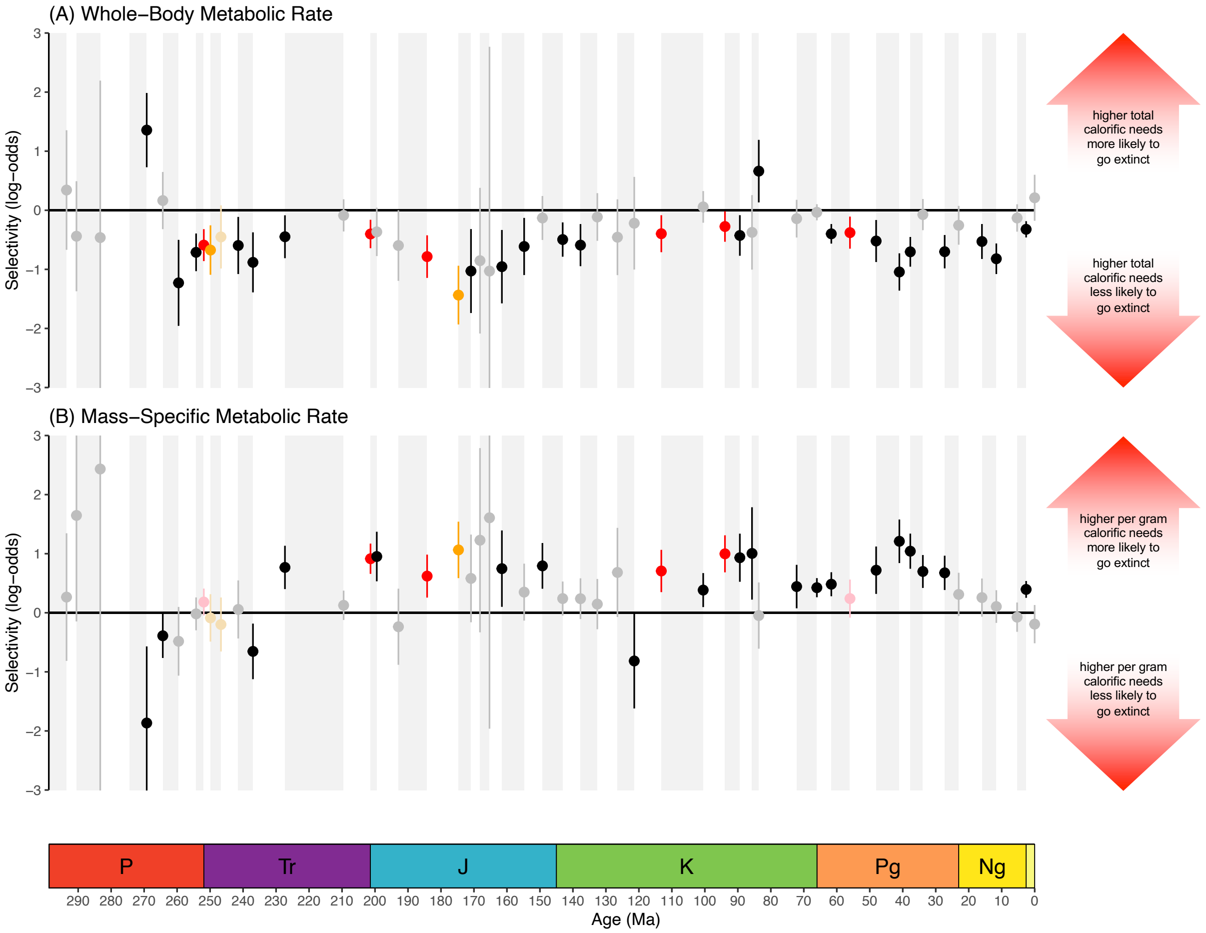

Figure 3: Regression coefficients from logistic regression analyses of extinction as a function of (A) whole-body and (B) mass-specific metabolic rate in bivalves. Error bars indicate 90% confidence intervals. Stages associated with the onset (red) or continuation (orange) of hyperthermal conditions are colored. Data points whose error bars intersect the x-axis (statistically insignificant selectivity) are grayed out. A higher whole-body metabolic rate is generally associated with a reduced risk of extinction in the post-Paleozoic. The inverse trend is observed when basal metabolic rate is standardized by mass, with a higher mass-specific metabolic rate generally associated with an increased risk of extinction in the post-Paleozoic.

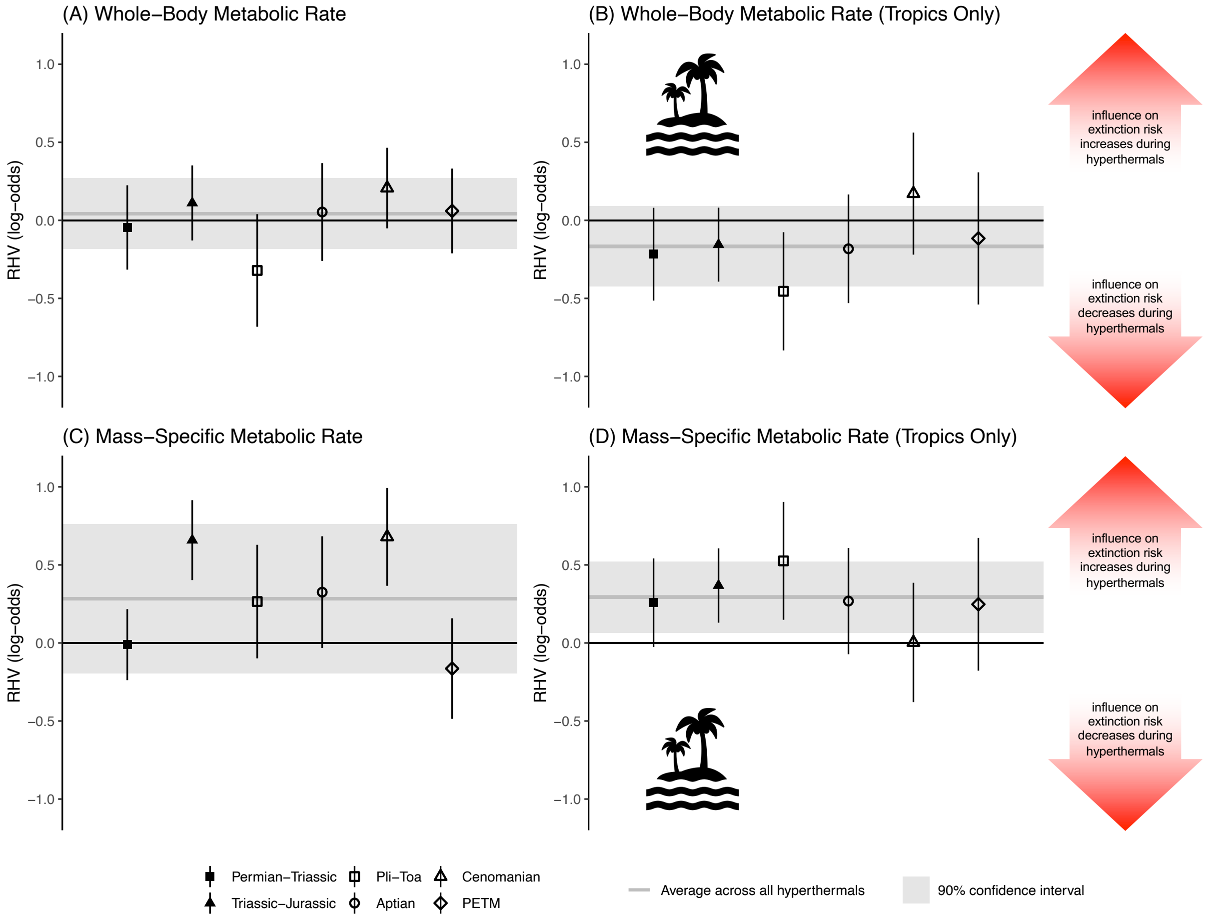

Figure 4: Relative hyperthermal vulnerability (RHV) of metabolic rate in bivalves, showing any deviation of hyperthermal extinction selectivity (individual events in black and mean across all events in grey) from baseline selectivity (i.e., RHV = 0). A, whole-body metabolic rate. B, whole-body metabolic rate, tropical genera only. C, mass-specific metabolic rate. D, mass-specific metabolic rate, tropical genera only. Mean extinction risk for bivalves with higher whole-body metabolic rates is decreased during stages associated with hyperthermal onset compared to baseline conditions among tropical bivalves, though not significantly so. Mean extinction risk during stages associated with hyperthermal onset for bivalves with higher mass-specific metabolic rates per gram of tissue is increased compared to baseline conditions,

significantly so when considering solely genera with median paleolatitudes within 30° of the equator and occurrences within this range.

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EDUCATION

M.S.	Earth Sciences Advisor: Linda C. Ivany	Syracuse University	2024
B.A.	*Magna Cum Laude* Biological Sciences Earth and Atmospheric Sciences	Cornell University	2021

AWARDS AND HONORS

Daniel F. Merriam Endowed Scholarship	Syracuse University Earth & Environmental Sciences	2024
Outstanding Teaching Assistant Award	Syracuse University Graduate School	2024
Marjorie Hooker Geology Award	Syracuse University Earth & Environmental Sciences	2023
Einhorn Discovery Grant	Cornell University College of Arts & Sciences	2019

PUBLICATIONS

Gavirneni, S., Ivany, L., and Reddin, C., Burning calories, burning ocean: metabolic rate in bivalves as a predictor of extinction selectivity through time and during rapid global warming. For submission to *Paleobiology*, expected May 2024.

PUBLISHED ABSTRACTS

Gavirneni, S., Ivany, L., and Reddin, C., 2023, Burning calories, burning ocean: the effects of metabolic rate on selectivity during hyperthermal-driven extinctions: Geological Society of America Abstracts with Programs, v. 55, no. 6, https://doi.org/10.1130/abs/2023AM-392718.

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RESEARCH EXPERIENCE

Research Intern	Paleontological Research Institution Historical Oyster Body Size Project	2018–2019
Shoals Research Apprenticeship	Shoals Marine Laboratory	2018

TEACHING EXPERIENCE

Graduate Teaching Assistant EAR 105: Earth Science EAR 111: Climate Change EAR 210: History of Earth and Life EAR 317: Sedimentary Processes and Systems	Syracuse University	2021–2024
Undergraduate Teaching Assistant BIOEE 1780: Evolutionary Biology and Diversity	Cornell University	2018

SERVICE

Diversity, Equity, and Inclusion Committee	Syracuse University Earth & Environmental Sciences	2021–2024
Biological Sciences Student Advisor	Cornell University Office of Undergraduate Biology	2019–2021

OUTREACH

Natural Science Explorers Program	Northside Learning Center	2024
Clark's Reservation Outreach	Pine Grove Middle School	2023

SKILLS

Programming Languages and Software: R, Python, MATLAB, SAS

Languages: English, French

ACTIVITIES

President	Cornell Mafia Club	2020–2021
Treasurer	Cornell Mafia Club	2019–2020
Event Supervisor	Science Olympiad at Cornell	2017–2021