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Organism activity levels predict marine invertebrate survival during ancient global change extinctions

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Abstract

Multi-stressor global change, the combined influence of ocean warming, acidification, and deoxygenation, poses a serious threat to marine organisms. Experimental studies imply that organisms with higher levels of activity should be more resilient, but testing this prediction and understanding organism vulnerability at a global scale, over evolutionary timescales, and in natural ecosystems remain challenging. The fossil record, which contains multiple extinctions triggered by multi-stressor global change, is ideally suited for testing hypotheses at broad geographic, taxonomic, and temporal scales. Here, I assess the importance of activity level for survival of well-skeletonized benthic marine invertebrates over a 100 million-year long interval (Permian to Jurassic periods) containing four global change extinctions, including the end-Permian and end-Triassic mass extinctions. More active organisms, based on a semi-quantitative score incorporating feeding and motility, were significantly more likely to survive during three of the four extinction events (Guadalupian, end-Permian, and end-Triassic). In contrast, activity was not an important control on survival during non-extinction intervals. Both the end-Permian and end-Triassic mass extinctions also triggered abrupt shifts to increased dominance by more active organisms. Although mean activity gradually returned toward pre-extinction values, the net result was a permanent ratcheting of ecosystem-wide activity to higher levels. Selectivity patterns during ancient global change extinctions confirm the hypothesis that higher activity, a proxy for respiratory physiology, is a fundamental control on survival, although the roles of specific physiological traits (such as extracellular pCO_2 or aerobic scope) cannot be distinguished. Modern marine ecosystems are dominated by more active organisms, in part because of selectivity ratcheting during these ancient extinctions, so on average may be less vulnerable to global change stressors than ancient counterparts. However, ancient extinctions

demonstrate that even active organisms can suffer major extinction when the intensity of environmental disruption is intense.

Introduction

Global environmental change subjects marine organisms to the combined stressors of warming ocean temperatures, decreasing pH, and decreasing dissolved oxygen levels (Doney *et al.*, 2012). These stresses, if severe enough, could lead to population declines or even extinction. While these environmental shifts will have negative consequences for many organisms, the traits that make an organism vulnerable or resilient are incompletely understood and, as a result, ecosystem-wide outcomes are challenging to predict in the modern ocean (Queirós *et al.*, 2015). Experimental manipulations are instrumental for understanding the physiological mechanisms, but the rates of change are much greater than expected in nature (Peck *et al.*, 2009), the short timescales often preclude population-level responses or evolutionary change, and the organisms may be removed from ecosystem interactions that also affect their survival (Kroeker *et al.*, 2013). Likewise, natural low-pH vents provide valuable snapshots of communities under stress (Hall-Spencer *et al.*, 2008), but the long-term evolutionary response under ocean-wide acidification remains difficult to assess. The fossil record provides an additional approach to complement the detailed studies of extant organisms, and is ideally suited for examining large-scale or global patterns over evolutionary timescales – spatial and temporal scales that are difficult to assess in the modern ocean (Queirós *et al.*, 2015).

Global change events in Earth’s deep time past provide natural experiments during which marine organisms responded to ocean warming, pH decrease, and other stressors. These events, associated with large-magnitude release of volcanic and volcanic-associated carbon dioxide

(CO_2) from voluminous flood basalt eruptions, often triggered extinctions in the marine realm (Wignall, 2001). In particular, the Permian, Triassic, and Jurassic periods (called "mid-Phanerozoic" here) contained two smaller crises, the Guadalupian and the Toarcian extinctions, as well as the much larger end-Permian and end-Triassic mass extinctions (Fig. 1). Although the rates of environmental change are difficult to constrain (Kemp *et al.*, 2015) and the relative contribution of multiple stressors likely differed among the crises, these mid-Phanerozoic events likely featured ocean warming (Gómez & Goy, 2011; Sun *et al.*, 2012; Schobben *et al.*, 2014), pH decrease (inferred from carbon isotope evidence for ocean-atmosphere pCO_2 increase (Hesselbo *et al.*, 2002, 2007; Payne & Clapham, 2012)), and reduced dissolved oxygen levels (Jenkyns, 1988; Cao *et al.*, 2009; Bond & Wignall, 2010). No single event is a perfect analog for 21st century global change, but consistent patterns of taxonomic or ecological selectivity across multiple extinctions can test whether traits fundamentally influence survival of marine organisms during global change.

Extinction selectivity during ancient global change events has often been interpreted in terms of physiological buffering against CO_2 changes, amount of calcification, or the degree of biological control over calcification (Knoll *et al.*, 2007; Clapham & Payne, 2011; Kiessling & Simpson, 2011; Bush & Pruss, 2013), although earlier studies also considered a wider range of physiological traits (Steele-Petrović, 1979; Knoll *et al.*, 1996). The categorization used in these paleontological studies is only approximate because traits such as extracellular acid-base buffering cannot easily be generalized at higher taxonomic levels and can vary widely within groups (Collard *et al.*, 2014). The capacity for acid-base regulation is also unknown in many important fossil groups, including brachiopods, bryozoans, and crinoids, and has been assumed in previous studies to be negligible (Knoll *et al.*, 2007; Clapham & Payne, 2011; Kiessling &

Simpson, 2011). Of groups with known pH buffering capabilities, the categorization used in the previous paleontological studies does not necessarily align with experimental evidence. For example, bivalve molluscs have typically been placed in a category including groups with physiological buffering against CO_2 changes (Knoll *et al.*, 2007; Clapham & Payne, 2011; Kiessling & Simpson, 2011), yet experimental studies suggest that bivalves have only limited ability to compensate for extracellular acid-base changes (Lannig *et al.*, 2010; Heinemann *et al.*, 2012; Parker *et al.*, 2013).

Furthermore, acid-base compensation requires energetically-costly ion transport mechanisms and may incur trade-offs in other aspects of the organism's biology, such as growth or reproduction (Wood *et al.*, 2008; Collard *et al.*, 2014). Other traits, such as inherently high extracellular pCO_2 (or low extracellular pH) may also confer resilience in the face of ocean acidification without imposing additional costs (Collard *et al.*, 2014). Melzner *et al*. (2009) proposed that more active organisms should be less vulnerable during high CO_2 events because of their inherently higher extracellular pCO_2, which would maintain the diffusive gradient between body fluids and seawater even as seawater pCO_2 rises. In addition, active organisms may have better-developed physiological mechanisms for adjusting to exercise-induced acidosis, which may prove advantageous during seawater-driven acidification (Melzner *et al.*, 2009).

Activity level is also proposed to influence survival during rapid warming events. Metabolic oxygen demand increases with increasing temperature in marine invertebrates; as a result, ocean warming can exert stress on marine organisms once oxygen demand exceeds the organism's aerobic scope (Pörtner, 2010). Active organisms, which have the capacity to elevate their metabolic rate during bursts of activity, should on average have higher aerobic scope (the difference between maximum metabolic rate and standard metabolic rate) than sessile organisms

(Pörtner, 2010). Peck *et al*. (2009) developed a semi-quantitative activity quotient and found that more active Antarctic organisms had significantly higher maximum thermal tolerance limits in experimental trials.

Metabolic rates and extracellular pCO_2 levels cannot be assessed directly in fossil species, but the activity quotient of Peck *et al*. (2009) is based on ecological attributes (feeding mode, movement type, movement speed, and movement frequency) that can be applied to extinct organisms. This is an indirect measure of more directly-relevant physiological parameters, but it is an approach that can harness the vast scope of the fossil record to examine ecosystem-wide outcomes among hundreds of calcified taxa at multiple ancient global change events. I used the fossil records of 3986 benthic marine invertebrate genera from the Paleobiology Database (www.paleobiodb.org) to test the hypothesis that more active organisms are also more likely to survive global change stresses, using mid-Phanerozoic extinctions (Guadalupian, end-Permian, end-Triassic, and Toarcian) as test cases.

Materials and Methods

The Paleobiology Database compiles published fossil records into collections that represent fossils obtained from a discrete stratigraphic interval (generally a bed or a few beds representing a short period of sediment deposition) at a single geographic location. The record of a taxon in that collection, which may be resolved to species, genus, or some higher taxonomic level, is termed an occurrence. Using the database API (http://paleobiodb.org/data1.2), I downloaded occurrences of mostly well-skeletonized benthic marine invertebrate groups (brachiopods, bivalves, gastropods, echinoderms, bryozoans, sponges, cnidarians, trilobites, ostracods, and malacostracan crustaceans) spanning the Artinskian (Early Permian, c. 280 Ma) to Bathonian (Middle Jurassic, c. 167 Ma) stages. Only occurrences from marine environments were downloaded, and they were then filtered to select records identified at the genus level or lower, and to exclude occurrences where the genus identification was uncertain (marked with cf., aff., ?, or quotation marks in the database). Occurrences were grouped into geological stages and only those restricted to a single stage were included. The resulting dataset contained nearly 111,000 genus-level occurrences.

Activity quotient is coded at higher taxonomic levels (mostly order and class level), following the scheme used by Peck *et al*. (2009) and using ecology data from the Paleobiology Database, inference from functional morphology, and information about extant members of the group (Table S1). Each attribute (feeding mode, movement type, movement speed, and movement frequency) is scored on an ordinal scale; the quotient is the fourth root of the product of those scores (Peck *et al.*, 2009). Because it is generally not feasible to assess the activity of extinct organisms at finer taxonomic levels, all genera within a higher group are assigned the same activity quotient. As a result, more than 99.5% of occurrences have a recorded activity quotient. This approach undoubtedly overlooks interspecific variability in activity, but differences among groups are likely larger than within-group variability. Furthermore, the activity quotient itself is a broad categorization and is only an approximation of more relevant physiological traits.

I used logistic regression to test whether activity quotient was an important predictor of extinction risk, both during global change extinctions and during background intervals of lower extinction intensity. Extinction can be measured in several ways from stage-level binned data; I used the boundary-crosser method (Foote, 2000) and a variation of the three-timer method (Alroy, 2014). For the boundary-crosser method, I examine only the cohort of genera that cross the bottom boundary of a time interval (i.e., are found both within the interval and in any preceding interval). A boundary-crossing genus is coded as “surviving” if it is present in any succeeding interval and “extinct” if it is not. The three-timer method also considers a cohort of genera that cross the bottom boundary of a time interval, but only those that are present in at least two consecutive intervals (i.e., both within the interval in question and in the immediately preceding interval). A genus from that cohort is coded as “surviving” if it is present in the interval immediately following (it is a “three-timer” sensu Alroy (2014)) and as “extinct” if it is not present in that interval, regardless of its occurrence in subsequent times. Alroy (2014) applied a correction for variable sampling when calculating extinction rates, but this cannot easily be used when coding particular genera as surviving/extinct. Variable sampling probabilities may cause apparent losses that can change estimates of extinction rate, but that effect is unlikely to substantially alter activity-based selectivity patterns.

I also quantified the effects that these crises had on global average activity levels to see if selectivity drove long-term shifts towards communities dominated by more active organisms (Gould & Calloway, 1980; Sepkoski, 1981). I calculated mean activity level of organisms in each time interval in two ways. First, I calculated mean activity on a per-occurrence basis (including an activity value for each occurrence of a genus); this approximates the commonness of each genus and weights common genera more heavily. For ostracods, which are microfossils and are sampled with different protocols from the other macrofossils, variations in the number of occurrences can reflect researcher interest more than true variations in commonness. To account for that, I also calculated mean activity on a per-genus basis, by including one activity value per genus regardless of its number of occurrences.

Results

Extinction selectivity

The Guadalupian (Capitanian stage), end-Permian (Changhsingian and Induan stages), and end-Triassic (Rhaetian stage) extinctions exhibited significant selectivity against less-active genera, regardless of the choice of extinction metric (Fig. 2). Most genus extinctions in the Induan stage occurred in the first 50-100 ka, reflecting the final losses during the end-Permian mass extinction (Shen *et al.*, 2011). Activity level was not a significant predictor of survival during the Pliensbachian or Toarcian stages (the Toarcian extinction occurred within the early part of the Toarcian stage, so . Logistic regression results indicate that the odds of survival increased by approximately 10% for every unit increase in the activity quotient. One unit corresponds to the difference between rhynchonelliform brachiopods and infaunal suspension-feeding bivalves, for example, although it should be noted that the activity quotient is a semi-quantitative score, not a linear scale. In contrast, background extinction, in stages other than the four global change crises, was typically independent of activity quotient or may have preferentially affected more active genera. The Roadian stage of the Permian and Sinemurian stage of the Jurassic are significant with the three-timer method, but it should be noted that the risk of false positive results is elevated when conducting multiple tests (significance in both boundary-crosser and three-timer analyses is more robust). Although active genera were also more likely to survive during the Norian stage (with the boundary-crosser method only; fig. 2b), this may reflect backwards smearing of the end-Triassic extinction in boundary-crosser data (Alroy, 2014) due to incomplete Rhaetian sampling.

Trends in activity level

Due to the numerical dominance of brachiopods, mean activity level was consistently low during the Permian, both when assemblage-wide mean activity is weighted by occurrence counts (Fig. 3a) or only using a single value per genus regardless of its number of occurrences (Fig. 3b). Although the Guadalupian extinction exhibited significant selectivity against less active organisms, there is no noticeable shift in mean occurrence-weighted activity level across the event. Genus-weighted activity may have increased in the late Permian, consistent with extinction selectivity, but any shift is small if present, likely the result of the small magnitude of extinction among marine invertebrates overall (Clapham *et al.*, 2009). Activity levels increased markedly in the Changhsingian, but that shift is an artifact of intensive sampling of ostracods in the latest Permian (there is nearly a fourfold increase in the number of ostracod occurrences from the preceding Wuchiapingian stage). After excluding ostracods, occurrence-weighted activity levels in both the Wuchiapingian and Changhsingian are consistent with earlier Permian values and there is no significant trend over time (a non-significant decrease of 0.0009 activity units per Myr, $R^2 = 0.01$, $p = 0.81$). In contrast, there was a small increase in mean activity level from the middle Permian to the late Permian when assemblage-wide mean activity is weighted by genus rather than by occurrence (Fig. 3b). Mean activity increased from 1.78-1.87 in the late early and middle Permian (1.95 in the Kungurian) to 2.07 in the Wuchiapingian and 2.08 in the Changhsingian.

The end-Permian mass extinction, approximately 252 Ma, triggered a large increase in the mean activity of benthic macroinvertebrates as measured by occurrence-weighted mean activity (Fig. 3a, excluding ostracods) or by genus-weighted mean activity (Fig. 3b). If ostracods are included, occurrence-weighted mean activity reached Triassic levels by the Changhsingian but, as discussed earlier, that increase is an artifact of publication quantity; the increase does not occur in genus-weighted results or when ostracods are excluded from occurrence-weighted values. Increased mean activity values primarily resulted from a shift from brachiopod to mollusk dominance (Gould & Calloway, 1980; Fraiser & Bottjer, 2007), as well as the intense and selective extinction of other predominantly sessile groups like crinoids, bryozoans, and corals (Payne & Clapham, 2012).

Mean activity may have trended to lower values during the Triassic as part of post-extinction biotic recovery. Although the slope of the occurrence-weighted trend, excluding ostracods, does not differ significantly from zero (a decrease of 0.003 activity units per Myr, $R^2 = 0.14$, $p = 0.41$), the data are noisy and the statistical power with only seven data points is low. However, the decrease as measured by genus-weighted mean activity is stronger (a decrease of 0.007 activity units per Myr, $R^2 = 0.52$, $p = 0.07$). Furthermore, independent evidence indicates that less active groups, such as brachiopods, crinoids, and corals, became more abundant (Stanley, 2003; Clapham & Bottjer, 2007; Greene *et al.*, 2011), suggesting that the trend toward lower mean activity is likely real.

Mean activity level also increased following the end-Triassic mass extinction as a result of the selective losses during the crisis. The magnitude of the increase was smaller than at the end-Permian event, likely because the end-Triassic extinction was less intense and because latest Triassic communities already contained a higher proportion of active organisms. Mean activity levels may have decreased slightly through the Early and Middle Jurassic, although the slope is shallower than the Triassic decrease. The trend in occurrence-weighted data, excluding ostracods, does not differ significantly from zero (a decrease of 0.001 activity units per Myr, $R^2 = 0.03$, $p = 0.72$). The trend in genus-weighted data is slightly stronger (a decrease of 0.003 activity units per Myr, $R^2 = 0.45$, $p = 0.1$). Despite changes like the increased prominence of low-activity corals after an Early Jurassic low in reef-building (Stanley, 2003), the overall trend towards lower mean activity is weak.

Consistent with the lack of observed selectivity, there is only weak evidence for a long-term shift in mean activity associated with the Toarcian extinction. Activity increased in occurrence-weighted data (Fig. 3a, although actual values are comparable to earlier Jurassic stages), but decreased in genus-weighted data (Fig. 3b). The timing of the extinction, within the early Toarcian rather than at a stage boundary, also complicates analysis because some Toarcian occurrences are derived from pre-extinction strata. The Pliensbachian-Toarcian boundary does not exhibit any clearer of a shift, however. Mean activity instead decreased from the Pliensbachian to Toarcian when ostracods are excluded from occurrence-weighted data, increased slightly when ostracods are included (Fig. 3a), and exhibited a more pronounced increase in the genus-weighted data (Fig. 3b). Middle Jurassic activity values are also consistent with a single Jurassic trend to lower mean activity. Although a transient shift following the extinction cannot be ruled out, especially because the Toarcian data point mixes pre- and post-extinction occurrences, the small magnitude of extinction suggests that long-term global effects may have been minimal.

Discussion

Biotic selectivity of global change

The pattern of extinction from the Permian through Jurassic supports the hypothesis of Peck *et al.* (2009) that an organism’s activity quotient is an important predictor of survival during global change events. Active organisms were preferentially likely to survive the

Guadalupian, end-Permian, and end-Triassic extinctions, despite activity levels being largely unimportant during background intervals (Fig. 2).

Although survival was significantly influenced by the activity quotient during global change mass extinctions, the magnitude of the effect was small (only a 10% increase in the odds of survival per unit increase in activity quotient). There are several possible explanations, which are not mutually exclusive. First, the extinction events were precipitated by multiple stressors that may have had different effects on marine organisms in combination than alone (Kroeker *et al.*, 2013; Deutsch *et al.*, 2015). For example, warming temperature and increasing pCO_2 were important during the end-Permian mass extinction (Payne *et al.*, 2004; Sun *et al.*, 2012; Schobben *et al.*, 2014), driving the selectivity that favored survival of active organisms (Knoll *et al.*, 2007; Clapham & Payne, 2011). However, expanded oxygen minimum zones (Brennecka *et al.*, 2011) may have imposed additional or synergistic selective pressures (Deutsch *et al.*, 2015), while local areas of shallow-marine hydrogen sulfide accumulation (Cao *et al.*, 2009) likely had unpredictable biotic consequences. The relative importance of warming, ocean pH changes, and anoxia also differed among the extinctions and likely also varied geographically within each extinction. The precise contributions of each stressor (water temperature, pH, or oxygenation) to extinction cannot be disentangled, but that is largely unimportant because all are fundamentally interlinked during global change events and forced by a common underlying driver (Algeo *et al.*, 2011).

Second, the activity quotient is coded at high taxonomic levels (nearly all gastropods receive the same score, for example) and is not an exact measure of the physiological attributes important for survival. Feeding type and movement speed, duration, or frequency are unlikely to be directly responsible for survival, but the activity quotient should correlate broadly with relevant physiological traits such as aerobic scope, acid-base regulation, or extracellular pCO_2 (Melzner *et al.*, 2009; Peck *et al.*, 2009; Pörtner, 2010). Applying the activity quotient at high taxonomic levels is also an oversimplification and reduces its predictive power, as physiological traits like acid-base regulation can differ even among species within a clade (Collard *et al.*, 2014). Global change stressors also act on larval life stages (Byrne & Przeslawski, 2013), in which case adult traits such as activity may be less important.

Third, survival during mass extinctions is influenced by numerous factors, potentially including population size or geographic range (Orzechowski *et al.*, 2015), habitat or habitat breadth (Nürnberg & Aberhan, 2013), body size (Schaal *et al.*, 2016), shell mineralogy (Clapham & Payne, 2011), or other individual- or population-level traits, diluting the effect of physiology. Stochastic effects may further obscure deterministic, trait-mediated outcomes during extinctions.

Although activity level is one of many traits that influence survival during complex environmental perturbations, its consistent significance during extinctions (but not background intervals) supports hypotheses that physiological traits are a fundamental constraint on extinction risk during global change. Despite the importance of respiratory physiology on broad taxonomic patterns of extinction at a global scale, survival of particular species will be strongly modulated by species-specific traits and local conditions. Nevertheless, activity level emerges as a robust predictor of survival despite the complex suite of environmental perturbations (ocean warming, anoxia, and likely pH decrease) during each event and despite likely differences in the magnitude of stressors among the extinctions.

Role of global change in long-term ecosystem shifts

The well-skeletonized component of benthic marine ecosystems was once dominated by sessile, low-activity organisms like brachiopods, bryozoans, and crinoids but is now composed primarily of more active bivalves, gastropods, crustaceans, and echinoids (Sepkoski, 1981). Mass extinctions like the end-Permian extinction have long been invoked as a major contributor to this ecological transition (Gould & Calloway, 1980), driving a shift to more motile organisms (Bambach *et al.*, 2002), in addition to the roles of longer-term biotic interactions and environmental changes (Aberhan *et al.*, 2006; Finnegan *et al.*, 2011). Permian-Jurassic trends in assemblage-wide mean activity levels demonstrate the importance not only of the end-Permian mass extinction, but also the end-Triassic extinction, as abrupt and major shifts from less active to more active organisms. Although ecosystem-wide mean activity levels gradually declined during the post-extinction recovery of groups like brachiopods and corals, the net result was an episodic ratcheting of marine ecosystems into new states each with increased dominance by more active organisms.

This stepwise trend toward increasing dominance by more active organisms likely even underestimates the increase in energetics within the marine ecosystem. The use of the same activity level across higher taxonomic groups obscures any signal of energetic increases within groups or of increases in overall biomass (Bambach, 1993). The fossil record contains evidence for substantial long-term body size increases, both within groups and because of replacement of smaller-bodied groups with larger ones (Finnegan *et al.*, 2011; Heim *et al.*, 2015). In addition to body size increases, many Cenozoic groups contain more numerous predatory or otherwise more active members than occurred during the Paleozoic or early Mesozoic (Bush *et al.*, 2007; Finnegan *et al.*, 2011). The combination of these longer-term body-size and energetic trends with the activity ratcheting during mid-Phanerozoic global change extinctions ultimately led to modern shelly communities dominated by more active taxonomic groups.

The composition of modern marine ecosystems has therefore been shaped by ancient global change extinctions and the physiological stresses from warming, acidification, and anoxia. As a result, dominant marine groups today tend to have higher activity levels than dominant groups in the Permian and should, on average, be less vulnerable to global change stresses. However, extreme crises like the end-Permian extinction severely impacted nearly all groups, even organisms with higher activity levels, implying that survival of prior events does not entirely eliminate the threat from global change.

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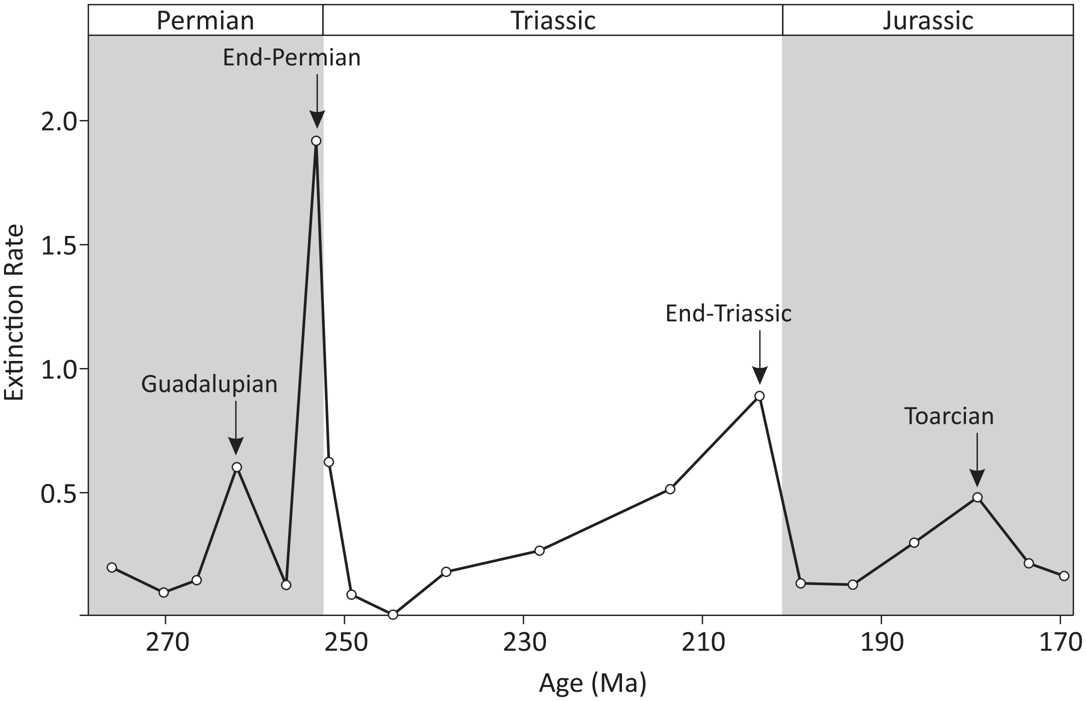
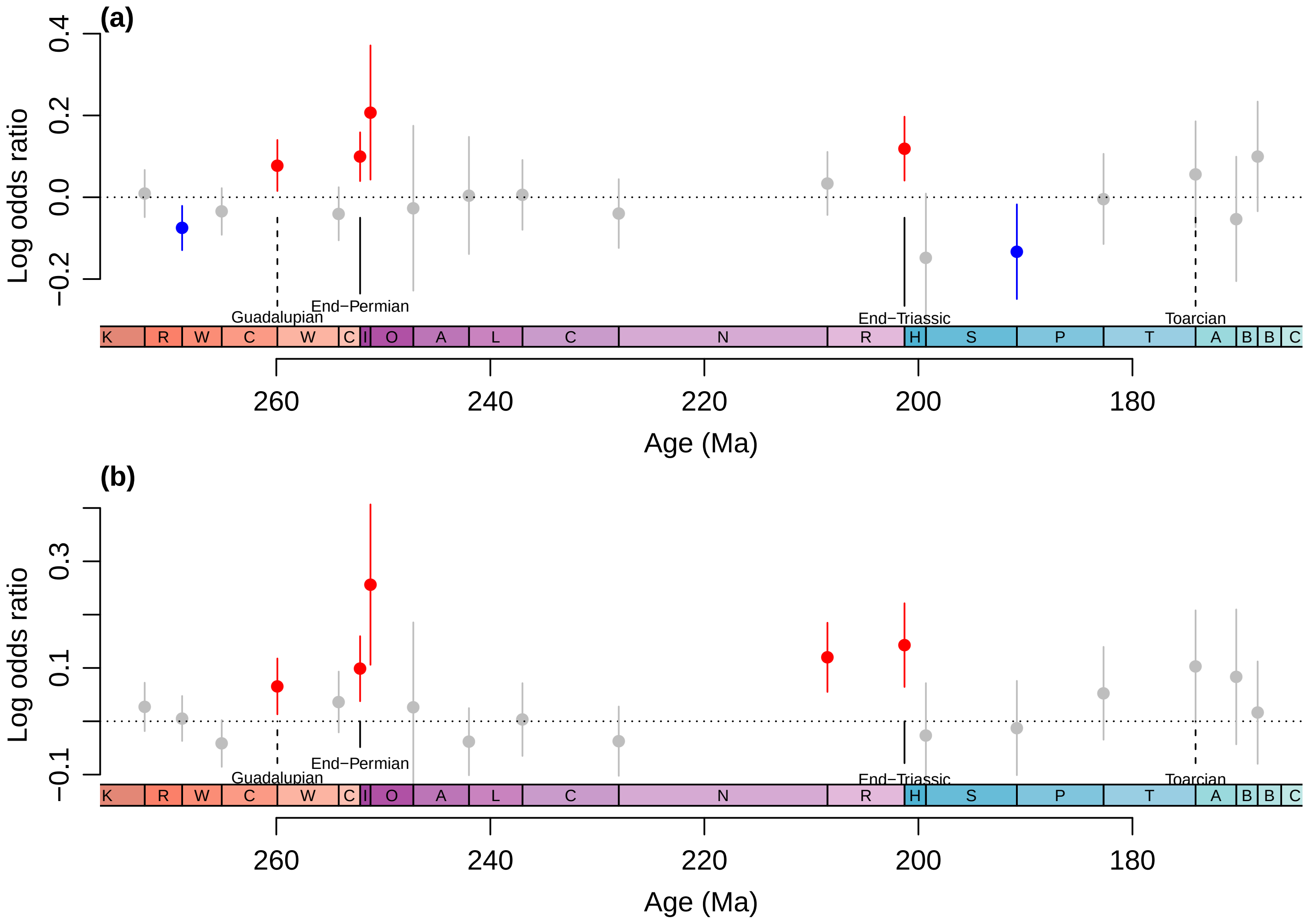
Figure 1. Extinction rate (three-timer method, calculated at www.fossilworks.org using SQS subsampling at a quorum of 0.8) of well-skeletonized marine invertebrate groups from the Early Permian to Middle Jurassic. Labels indicate the position of major mass extinctions (end-Permian and end-Triassic) and smaller extinctions (Guadalupian and Toarcian).

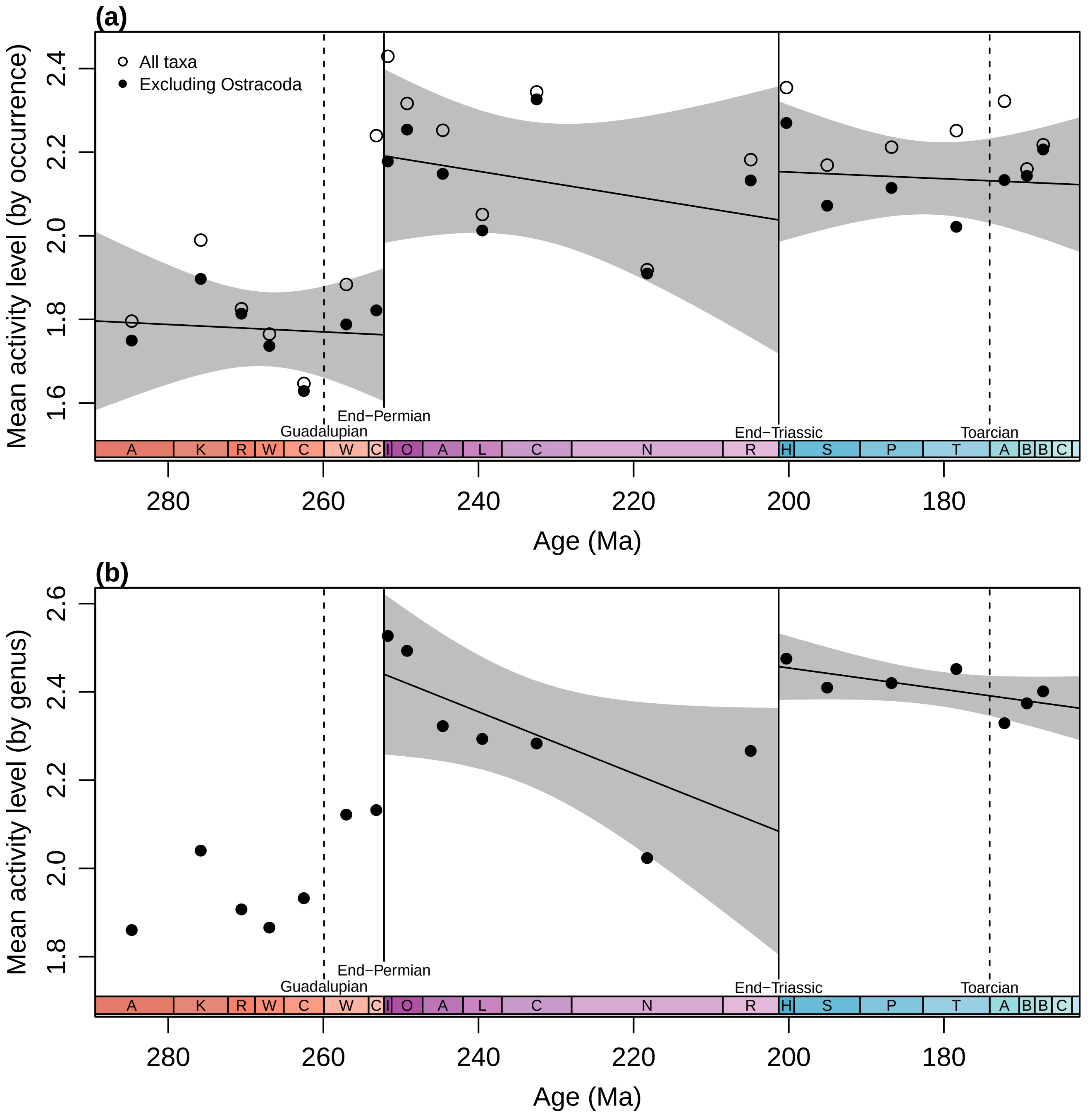
Figure 2. Selectivity of background and mass extinctions, measured by (a) three-timer method or (b) boundary-crosser method. Positive log odds ratio values indicate that more active organisms were more likely to survive during a particular stage (red); negative log odds ratios indicate that higher activity levels increased the risk of extinction (blue). Error bars are 95% confidence intervals. Stages of the geological timescale are Permian: K=Kungurian, R=Roadian, W=Wordian, C=Capitanian (Guadalupian extinction), W=Wuchiapingian, C=Changhsingian

(end-Permian extinction); Triassic: I=Induan (end-Permian extinction), O=Olenekian, A=Anisian, L=Ladinian, C=Carnian, N=Norian, R=Rhaetian (end-Triassic extinction); Jurassic: H=Hettangian, S=Sinemurian, P=Pliensbachian, T=Toarcian (Toarcian extinction, although note that the extinction occurred within, not at the end of, the stage), A=Aalenian, B=Bajocian, B=Bathonian.

Figure 3. Trends in mean activity level of well-skeletonized benthic invertebrates, averaged by-occurrence (a; one value per occurrence of a taxon) or by-genus (b; only a single value per genus regardless of the number of occurrences). Per-occurrence mean activity is shown for all studied taxa (open circles) and after excluding Ostracoda (solid circles). Separate trends and shaded 95% confidence intervals (data excluding Ostracoda) are shown for the Permian, Triassic, and Jurassic periods (no trend is given for by-genus activity during the Permian because of the potential shift at the Guadalupian extinction). Solid vertical lines mark the end-Permian and end-Triassic mass extinctions; dashed lines mark the Guadalupian and Toarcian extinctions (note that the Toarcian extinction actually occurred within the early Toarcian, not at its end).


Permian
Triassic
Jurassic
End-Permian
Guadalupian
End-Triassic
Toarcian
Extinction Rate
2.0
1.5
1.0
0.5
270
250
230
210
190
170
Age (Ma)


(a)
(b)
Log odds ratio
0.4
0.2
0.0
−0.2
0.3
0.1
−0.1
Guadalupian
End−Permian
End−Triassic
Toarcian
K
R
W
C
W
C
I
O
A
L
C
N
R
H
S
P
T
A
B
B
C
260
240
220
200
180
Age (Ma)

(a)
Mean activity level (by occurrence)
All taxa
Excluding Ostracoda
1.6
1.8
2.0
2.2
2.4
Guadalupian
End−Permian
End−Triassic
Toarcian
A K R W C W C I O A L C N R H S P T A B B C
280
260
240
220
200
180
Age (Ma)
(b)
Mean activity level (by genus)
1.8
2.0
2.2
2.4
2.6
Guadalupian
End−Permian
End−Triassic
Toarcian
A K R W C W C I O A L C N R H S P T A B B C
280
260
240
220
200
180
Age (Ma)