1 **Organism activity levels predict marine invertebrate survival during ancient global change**

2 **extinctions**

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4 Running head: Selectivity of global change extinctions

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17 Type of paper: primary research article

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19 **Abstract**

20 Multi-stressor global change, the combined influence of ocean warming, acidification, and

21 deoxygenation, poses a serious threat to marine organisms. Experimental studies imply that

22 organisms with higher levels of activity should be more resilient, but testing this prediction and

23 understanding organism vulnerability at a global scale, over evolutionary timescales, and in

24 natural ecosystems remain challenging. The fossil record, which contains multiple extinctions

25 triggered by multi-stressor global change, is ideally suited for testing hypotheses at broad

26 geographic, taxonomic, and temporal scales. Here, I assess the importance of activity level for

27 survival of well-skeletonized benthic marine invertebrates over a 100 million-year long interval

28 (Permian to Jurassic periods) containing four global change extinctions, including the end-

29 Permian and end-Triassic mass extinctions. More active organisms, based on a semi-quantitative

30 score incorporating feeding and motility, were significantly more likely to survive during three

31 of the four extinction events (Guadalupian, end-Permian, and end-Triassic). In contrast, activity

32 was not an important control on survival during non-extinction intervals. Both the end-Permian

33 and end-Triassic mass extinctions also triggered abrupt shifts to increased dominance by more

34 active organisms. Although mean activity gradually returned toward pre-extinction values, the

35 net result was a permanent ratcheting of ecosystem-wide activity to higher levels. Selectivity

36 patterns during ancient global change extinctions confirm the hypothesis that higher activity, a

37 proxy for respiratory physiology, is a fundamental control on survival, although the roles of

38 specific physiological traits (such as extracellular pCO_2 or aerobic scope) cannot be

39 distinguished. Modern marine ecosystems are dominated by more active organisms, in part

40 because of selectivity ratcheting during these ancient extinctions, so on average may be less

41 vulnerable to global change stressors than ancient counterparts. However, ancient extinctions

42   demonstrate that even active organisms can suffer major extinction when the intensity of

43   environmental disruption is intense.

44

45   **Introduction**

46   Global environmental change subjects marine organisms to the combined stressors of

47   warming ocean temperatures, decreasing pH, and decreasing dissolved oxygen levels (Doney *et*

48   *al.*, 2012). These stresses, if severe enough, could lead to population declines or even extinction.

49   While these environmental shifts will have negative consequences for many organisms, the traits

50   that make an organism vulnerable or resilient are incompletely understood and, as a result,

51   ecosystem-wide outcomes are challenging to predict in the modern ocean (Queirós *et al.*, 2015).

52   Experimental manipulations are instrumental for understanding the physiological mechanisms,

53   but the rates of change are much greater than expected in nature (Peck *et al.*, 2009), the short

54   timescales often preclude population-level responses or evolutionary change, and the organisms

55   may be removed from ecosystem interactions that also affect their survival (Kroeker *et al.*,

56   2013). Likewise, natural low-pH vents provide valuable snapshots of communities under stress

57   (Hall-Spencer *et al.*, 2008), but the long-term evolutionary response under ocean-wide

58   acidification remains difficult to assess. The fossil record provides an additional approach to

59   complement the detailed studies of extant organisms, and is ideally suited for examining large-

60   scale or global patterns over evolutionary timescales – spatial and temporal scales that are

61   difficult to assess in the modern ocean (Queirós *et al.*, 2015).

62   Global change events in Earth's deep time past provide natural experiments during which

63   marine organisms responded to ocean warming, pH decrease, and other stressors. These events,

64   associated with large-magnitude release of volcanic and volcanic-associated carbon dioxide

65   (CO_2) from voluminous flood basalt eruptions, often triggered extinctions in the marine realm

66   (Wignall, 2001). In particular, the Permian, Triassic, and Jurassic periods (called "mid-

67   Phanerozoic" here) contained two smaller crises, the Guadalupian and the Toarcian extinctions,

68   as well as the much larger end-Permian and end-Triassic mass extinctions (Fig. 1). Although the

69   rates of environmental change are difficult to constrain (Kemp *et al.*, 2015) and the relative

70   contribution of multiple stressors likely differed among the crises, these mid-Phanerozoic events

71   likely featured ocean warming (Gómez & Goy, 2011; Sun *et al.*, 2012; Schobben *et al.*, 2014),

72   pH decrease (inferred from carbon isotope evidence for ocean-atmosphere pCO_2 increase

73   (Hesselbo *et al.*, 2002, 2007; Payne & Clapham, 2012)), and reduced dissolved oxygen levels

74   (Jenkyns, 1988; Cao *et al.*, 2009; Bond & Wignall, 2010). No single event is a perfect analog for

75   21st century global change, but consistent patterns of taxonomic or ecological selectivity across

76   multiple extinctions can test whether traits fundamentally influence survival of marine organisms

77   during global change.

78   Extinction selectivity during ancient global change events has often been interpreted in

79   terms of physiological buffering against CO_2 changes, amount of calcification, or the degree of

80   biological control over calcification (Knoll *et al.*, 2007; Clapham & Payne, 2011; Kiessling &

81   Simpson, 2011; Bush & Pruss, 2013), although earlier studies also considered a wider range of

82   physiological traits (Steele-Petrović, 1979; Knoll *et al.*, 1996). The categorization used in these

83   paleontological studies is only approximate because traits such as extracellular acid-base

84   buffering cannot easily be generalized at higher taxonomic levels and can vary widely within

85   groups (Collard *et al.*, 2014). The capacity for acid-base regulation is also unknown in many

86   important fossil groups, including brachiopods, bryozoans, and crinoids, and has been assumed

87   in previous studies to be negligible (Knoll *et al.*, 2007; Clapham & Payne, 2011; Kiessling &

88   Simpson, 2011). Of groups with known pH buffering capabilities, the categorization used in the

89   previous paleontological studies does not necessarily align with experimental evidence. For

90   example, bivalve molluscs have typically been placed in a category including groups with

91   physiological buffering against CO_2 changes (Knoll *et al.*, 2007; Clapham & Payne, 2011;

92   Kiessling & Simpson, 2011), yet experimental studies suggest that bivalves have only limited

93   ability to compensate for extracellular acid-base changes (Lannig *et al.*, 2010; Heinemann *et al.*,

94   2012; Parker *et al.*, 2013).

95   Furthermore, acid-base compensation requires energetically-costly ion transport

96   mechanisms and may incur trade-offs in other aspects of the organism's biology, such as growth

97   or reproduction (Wood *et al.*, 2008; Collard *et al.*, 2014). Other traits, such as inherently high

98   extracellular pCO_2 (or low extracellular pH) may also confer resilience in the face of ocean

99   acidification without imposing additional costs (Collard *et al.*, 2014). Melzner *et al.* (2009)

100   proposed that more active organisms should be less vulnerable during high CO_2 events because

101   of their inherently higher extracellular pCO_2, which would maintain the diffusive gradient

102   between body fluids and seawater even as seawater pCO_2 rises. In addition, active organisms

103   may have better-developed physiological mechanisms for adjusting to exercise-induced acidosis,

104   which may prove advantageous during seawater-driven acidification (Melzner *et al.*, 2009).

105   Activity level is also proposed to influence survival during rapid warming events.

106   Metabolic oxygen demand increases with increasing temperature in marine invertebrates; as a

107   result, ocean warming can exert stress on marine organisms once oxygen demand exceeds the

108   organism's aerobic scope (Pörtner, 2010). Active organisms, which have the capacity to elevate

109   their metabolic rate during bursts of activity, should on average have higher aerobic scope (the

110   difference between maximum metabolic rate and standard metabolic rate) than sessile organisms

111 (Pörtner, 2010). Peck *et al.* (2009) developed a semi-quantitative activity quotient and found that

112 more active Antarctic organisms had significantly higher maximum thermal tolerance limits in

113 experimental trials.

114   Metabolic rates and extracellular pCO_2 levels cannot be assessed directly in fossil

115 species, but the activity quotient of Peck *et al.* (2009) is based on ecological attributes (feeding

116 mode, movement type, movement speed, and movement frequency) that can be applied to extinct

117 organisms. This is an indirect measure of more directly-relevant physiological parameters, but it

118 is an approach that can harness the vast scope of the fossil record to examine ecosystem-wide

119 outcomes among hundreds of calcified taxa at multiple ancient global change events. I used the

120 fossil records of 3986 benthic marine invertebrate genera from the Paleobiology Database

121 (www.paleobiodb.org) to test the hypothesis that more active organisms are also more likely to

122 survive global change stresses, using mid-Phanerozoic extinctions (Guadalupian, end-Permian,

123 end-Triassic, and Toarcian) as test cases.

124 **Materials and Methods**

125   The Paleobiology Database compiles published fossil records into collections that

126 represent fossils obtained from a discrete stratigraphic interval (generally a bed or a few beds

127 representing a short period of sediment deposition) at a single geographic location. The record of

128 a taxon in that collection, which may be resolved to species, genus, or some higher taxonomic

129 level, is termed an occurrence. Using the database API (http://paleobiodb.org/data1.2), I

130 downloaded occurrences of mostly well-skeletonized benthic marine invertebrate groups

131 (brachiopods, bivalves, gastropods, echinoderms, bryozoans, sponges, cnidarians, trilobites,

132 ostracods, and malacostracan crustaceans) spanning the Artinskian (Early Permian, c. 280 Ma) to

133 Bathonian (Middle Jurassic, c. 167 Ma) stages. Only occurrences from marine environments

134   were downloaded, and they were then filtered to select records identified at the genus level or

135   lower, and to exclude occurrences where the genus identification was uncertain (marked with cf.,

136   aff., ?, or quotation marks in the database). Occurrences were grouped into geological stages and

137   only those restricted to a single stage were included. The resulting dataset contained nearly

138   111,000 genus-level occurrences.

139   Activity quotient is coded at higher taxonomic levels (mostly order and class level),

140   following the scheme used by Peck *et al.* (2009) and using ecology data from the Paleobiology

141   Database, inference from functional morphology, and information about extant members of the

142   group (Table S1). Each attribute (feeding mode, movement type, movement speed, and

143   movement frequency) is scored on an ordinal scale; the quotient is the fourth root of the product

144   of those scores (Peck *et al.*, 2009). Because it is generally not feasible to assess the activity of

145   extinct organisms at finer taxonomic levels, all genera within a higher group are assigned the

146   same activity quotient. As a result, more than 99.5% of occurrences have a recorded activity

147   quotient. This approach undoubtedly overlooks interspecific variability in activity, but

148   differences among groups are likely larger than within-group variability. Furthermore, the

149   activity quotient itself is a broad categorization and is only an approximation of more relevant

150   physiological traits.

151   I used logistic regression to test whether activity quotient was an important predictor of

152   extinction risk, both during global change extinctions and during background intervals of lower

153   extinction intensity. Extinction can be measured in several ways from stage-level binned data; I

154   used the boundary-crosser method (Foote, 2000) and a variation of the three-timer method

155   (Alroy, 2014). For the boundary-crosser method, I examine only the cohort of genera that cross

156   the bottom boundary of a time interval (i.e., are found both within the interval and in any

157   preceding interval). A boundary-crossing genus is coded as "surviving" if it is present in any

158   succeeding interval and "extinct" if it is not. The three-timer method also considers a cohort of

159   genera that cross the bottom boundary of a time interval, but only those that are present in at

160   least two consecutive intervals (i.e., both within the interval in question and in the immediately

161   preceding interval). A genus from that cohort is coded as "surviving" if it is present in the

162   interval immediately following (it is a "three-timer" sensu Alroy (2014)) and as "extinct" if it is

163   not present in that interval, regardless of its occurrence in subsequent times. Alroy (2014)

164   applied a correction for variable sampling when calculating extinction rates, but this cannot

165   easily be used when coding particular genera as surviving/extinct. Variable sampling

166   probabilities may cause apparent losses that can change estimates of extinction rate, but that

167   effect is unlikely to substantially alter activity-based selectivity patterns.

168   I also quantified the effects that these crises had on global average activity levels to see if

169   selectivity drove long-term shifts towards communities dominated by more active organisms

170   (Gould & Calloway, 1980; Sepkoski, 1981). I calculated mean activity level of organisms in

171   each time interval in two ways. First, I calculated mean activity on a per-occurrence basis

172   (including an activity value for each occurrence of a genus); this approximates the commonness

173   of each genus and weights common genera more heavily. For ostracods, which are microfossils

174   and are sampled with different protocols from the other macrofossils, variations in the number of

175   occurrences can reflect researcher interest more than true variations in commonness. To account

176   for that, I also calculated mean activity on a per-genus basis, by including one activity value per

177   genus regardless of its number of occurrences.

178

179   **Results**

180   *Extinction selectivity*

181   The Guadalupian (Capitanian stage), end-Permian (Changhsingian and Induan stages),

182   and end-Triassic (Rhaetian stage) extinctions exhibited significant selectivity against less-active

183   genera, regardless of the choice of extinction metric (Fig. 2). Most genus extinctions in the

184   Induan stage occurred in the first 50-100 ka, reflecting the final losses during the end-Permian

185   mass extinction (Shen *et al.*, 2011). Activity level was not a significant predictor of survival

186   during the Pliensbachian or Toarcian stages (the Toarcian extinction occurred within the early

187   part of the Toarcian stage, so . Logistic regression results indicate that the odds of survival

188   increased by approximately 10% for every unit increase in the activity quotient. One unit

189   corresponds to the difference between rhynchonelliform brachiopods and infaunal suspension-

190   feeding bivalves, for example, although it should be noted that the activity quotient is a semi-

191   quantitative score, not a linear scale. In contrast, background extinction, in stages other than the

192   four global change crises, was typically independent of activity quotient or may have

193   preferentially affected more active genera. The Roadian stage of the Permian and Sinemurian

194   stage of the Jurassic are significant with the three-timer method, but it should be noted that the

195   risk of false positive results is elevated when conducting multiple tests (significance in both

196   boundary-crosser and three-timer analyses is more robust). Although active genera were also

197   more likely to survive during the Norian stage (with the boundary-crosser method only; fig. 2b),

198   this may reflect backwards smearing of the end-Triassic extinction in boundary-crosser data

199   (Alroy, 2014) due to incomplete Rhaetian sampling.

200

201   *Trends in activity level*

202   Due to the numerical dominance of brachiopods, mean activity level was consistently low

203   during the Permian, both when assemblage-wide mean activity is weighted by occurrence counts

204   (Fig. 3a) or only using a single value per genus regardless of its number of occurrences (Fig. 3b).

205   Although the Guadalupian extinction exhibited significant selectivity against less active

206   organisms, there is no noticeable shift in mean occurrence-weighted activity level across the

207   event. Genus-weighted activity may have increased in the late Permian, consistent with

208   extinction selectivity, but any shift is small if present, likely the result of the small magnitude of

209   extinction among marine invertebrates overall (Clapham *et al.*, 2009). Activity levels increased

210   markedly in the Changhsingian, but that shift is an artifact of intensive sampling of ostracods in

211   the latest Permian (there is nearly a fourfold increase in the number of ostracod occurrences from

212   the preceding Wuchiapingian stage). After excluding ostracods, occurrence-weighted activity

213   levels in both the Wuchiapingian and Changhsingian are consistent with earlier Permian values

214   and there is no significant trend over time (a non-significant decrease of 0.0009 activity units per

215   Myr, $R^2 = 0.01$, p = 0.81). In contrast, there was a small increase in mean activity level from the

216   middle Permian to the late Permian when assemblage-wide mean activity is weighted by genus

217   rather than by occurrence (Fig. 3b). Mean activity increased from 1.78-1.87 in the late early and

218   middle Permian (1.95 in the Kungurian) to 2.07 in the Wuchiapingian and 2.08 in the

219   Changhsingian.

220   The end-Permian mass extinction, approximately 252 Ma, triggered a large increase in

221   the mean activity of benthic macroinvertebrates as measured by occurrence-weighted mean

222   activity (Fig. 3a, excluding ostracods) or by genus-weighted mean activity (Fig. 3b). If ostracods

223   are included, occurrence-weighted mean activity reached Triassic levels by the Changhsingian

224   but, as discussed earlier, that increase is an artifact of publication quantity; the increase does not

225 occur in genus-weighted results or when ostracods are excluded from occurrence-weighted

226 values. Increased mean activity values primarily resulted from a shift from brachiopod to

227 mollusk dominance (Gould & Calloway, 1980; Fraiser & Bottjer, 2007), as well as the intense

228 and selective extinction of other predominantly sessile groups like crinoids, bryozoans, and

229 corals (Payne & Clapham, 2012).

230 Mean activity may have trended to lower values during the Triassic as part of post-

231 extinction biotic recovery. Although the slope of the occurrence-weighted trend, excluding

232 ostracods, does not differ significantly from zero (a decrease of 0.003 activity units per Myr, R^2

233 $= 0.14$, p $= 0.41$), the data are noisy and the statistical power with only seven data points is low.

234 However, the decrease as measured by genus-weighted mean activity is stronger (a decrease of

235 0.007 activity units per Myr, $R^2 = 0.52$, p $= 0.07$). Furthermore, independent evidence indicates

236 that less active groups, such as brachiopods, crinoids, and corals, became more abundant

237 (Stanley, 2003; Clapham & Bottjer, 2007; Greene *et al.*, 2011), suggesting that the trend toward

238 lower mean activity is likely real.

239 Mean activity level also increased following the end-Triassic mass extinction as a result

240 of the selective losses during the crisis. The magnitude of the increase was smaller than at the

241 end-Permian event, likely because the end-Triassic extinction was less intense and because latest

242 Triassic communities already contained a higher proportion of active organisms. Mean activity

243 levels may have decreased slightly through the Early and Middle Jurassic, although the slope is

244 shallower than the Triassic decrease. The trend in occurrence-weighted data, excluding

245 ostracods, does not differ significantly from zero (a decrease of 0.001 activity units per Myr, R^2

246 $= 0.03$, p $= 0.72$). The trend in genus-weighted data is slightly stronger (a decrease of 0.003

247 activity units per Myr, $R^2 = 0.45$, p $= 0.1$). Despite changes like the increased prominence of

248   low-activity corals after an Early Jurassic low in reef-building (Stanley, 2003), the overall trend

249   towards lower mean activity is weak.

250   Consistent with the lack of observed selectivity, there is only weak evidence for a long-

251   term shift in mean activity associated with the Toarcian extinction. Activity increased in

252   occurrence-weighted data (Fig. 3a, although actual values are comparable to earlier Jurassic

253   stages), but decreased in genus-weighted data (Fig. 3b). The timing of the extinction, within the

254   early Toarcian rather than at a stage boundary, also complicates analysis because some Toarcian

255   occurrences are derived from pre-extinction strata. The Pliensbachian-Toarcian boundary does

256   not exhibit any clearer of a shift, however. Mean activity instead decreased from the

257   Pliensbachian to Toarcian when ostracods are excluded from occurrence-weighted data,

258   increased slightly when ostracods are included (Fig. 3a), and exhibited a more pronounced

259   increase in the genus-weighted data (Fig. 3b). Middle Jurassic activity values are also consistent

260   with a single Jurassic trend to lower mean activity. Although a transient shift following the

261   extinction cannot be ruled out, especially because the Toarcian data point mixes pre- and post-

262   extinction occurrences, the small magnitude of extinction suggests that long-term global effects

263   may have been minimal.

264

265   **Discussion**

266   *Biotic selectivity of global change*

267   The pattern of extinction from the Permian through Jurassic supports the hypothesis of

268   Peck *et al.* (2009) that an organism's activity quotient is an important predictor of survival

269   during global change events. Active organisms were preferentially likely to survive the

270   Guadalupian, end-Permian, and end-Triassic extinctions, despite activity levels being largely

271   unimportant during background intervals (Fig. 2).

272   Although survival was significantly influenced by the activity quotient during global

273   change mass extinctions, the magnitude of the effect was small (only a 10% increase in the odds

274   of survival per unit increase in activity quotient). There are several possible explanations, which

275   are not mutually exclusive. First, the extinction events were precipitated by multiple stressors

276   that may have had different effects on marine organisms in combination than alone (Kroeker *et*

277   *al.*, 2013; Deutsch *et al.*, 2015). For example, warming temperature and increasing pCO_2 were

278   important during the end-Permian mass extinction (Payne *et al.*, 2004; Sun *et al.*, 2012;

279   Schobben *et al.*, 2014), driving the selectivity that favored survival of active organisms (Knoll *et*

280   *al.*, 2007; Clapham & Payne, 2011). However, expanded oxygen minimum zones (Brennecka *et*

281   *al.*, 2011) may have imposed additional or synergistic selective pressures (Deutsch *et al.*, 2015),

282   while local areas of shallow-marine hydrogen sulfide accumulation (Cao *et al.*, 2009) likely had

283   unpredictable biotic consequences. The relative importance of warming, ocean pH changes, and

284   anoxia also differed among the extinctions and likely also varied geographically within each

285   extinction. The precise contributions of each stressor (water temperature, pH, or oxygenation) to

286   extinction cannot be disentangled, but that is largely unimportant because all are fundamentally

287   interlinked during global change events and forced by a common underlying driver (Algeo *et al.*,

288   2011).

289   Second, the activity quotient is coded at high taxonomic levels (nearly all gastropods

290   receive the same score, for example) and is not an exact measure of the physiological attributes

291   important for survival. Feeding type and movement speed, duration, or frequency are unlikely to

292   be directly responsible for survival, but the activity quotient should correlate broadly with

293   relevant physiological traits such as aerobic scope, acid-base regulation, or extracellular pCO_2

294   (Melzner *et al.*, 2009; Peck *et al.*, 2009; Pörtner, 2010). Applying the activity quotient at high

295   taxonomic levels is also an oversimplification and reduces its predictive power, as physiological

296   traits like acid-base regulation can differ even among species within a clade (Collard *et al.*,

297   2014). Global change stressors also act on larval life stages (Byrne & Przeslawski, 2013), in

298   which case adult traits such as activity may be less important.

299   Third, survival during mass extinctions is influenced by numerous factors, potentially

300   including population size or geographic range (Orzechowski *et al.*, 2015), habitat or habitat

301   breadth (Nürnberg & Aberhan, 2013), body size (Schaal *et al.*, 2016), shell mineralogy (Clapham

302   & Payne, 2011), or other individual- or population-level traits, diluting the effect of physiology.

303   Stochastic effects may further obscure deterministic, trait-mediated outcomes during extinctions.

304   Although activity level is one of many traits that influence survival during complex

305   environmental perturbations, its consistent significance during extinctions (but not background

306   intervals) supports hypotheses that physiological traits are a fundamental constraint on extinction

307   risk during global change. Despite the importance of respiratory physiology on broad taxonomic

308   patterns of extinction at a global scale, survival of particular species will be strongly modulated

309   by species-specific traits and local conditions. Nevertheless, activity level emerges as a robust

310   predictor of survival despite the complex suite of environmental perturbations (ocean warming,

311   anoxia, and likely pH decrease) during each event and despite likely differences in the magnitude

312   of stressors among the extinctions.

313

314   *Role of global change in long-term ecosystem shifts*

315   The well-skeletonized component of benthic marine ecosystems was once dominated by

316   sessile, low-activity organisms like brachiopods, bryozoans, and crinoids but is now composed

317   primarily of more active bivalves, gastropods, crustaceans, and echinoids (Sepkoski, 1981). Mass

318   extinctions like the end-Permian extinction have long been invoked as a major contributor to this

319   ecological transition (Gould & Calloway, 1980), driving a shift to more motile organisms

320   (Bambach *et al.*, 2002), in addition to the roles of longer-term biotic interactions and

321   environmental changes (Aberhan *et al.*, 2006; Finnegan *et al.*, 2011). Permian-Jurassic trends in

322   assemblage-wide mean activity levels demonstrate the importance not only of the end-Permian

323   mass extinction, but also the end-Triassic extinction, as abrupt and major shifts from less active

324   to more active organisms. Although ecosystem-wide mean activity levels gradually declined

325   during the post-extinction recovery of groups like brachiopods and corals, the net result was an

326   episodic ratcheting of marine ecosystems into new states each with increased dominance by

327   more active organisms.

328   This stepwise trend toward increasing dominance by more active organisms likely even

329   underestimates the increase in energetics within the marine ecosystem. The use of the same

330   activity level across higher taxonomic groups obscures any signal of energetic increases within

331   groups or of increases in overall biomass (Bambach, 1993). The fossil record contains evidence

332   for substantial long-term body size increases, both within groups and because of replacement of

333   smaller-bodied groups with larger ones (Finnegan *et al.*, 2011; Heim *et al.*, 2015). In addition to

334   body size increases, many Cenozoic groups contain more numerous predatory or otherwise more

335   active members than occurred during the Paleozoic or early Mesozoic (Bush *et al.*, 2007;

336   Finnegan *et al.*, 2011). The combination of these longer-term body-size and energetic trends with

337 the activity ratcheting during mid-Phanerozoic global change extinctions ultimately led to

338 modern shelly communities dominated by more active taxonomic groups.

339   The composition of modern marine ecosystems has therefore been shaped by ancient

340 global change extinctions and the physiological stresses from warming, acidification, and anoxia.

341 As a result, dominant marine groups today tend to have higher activity levels than dominant

342 groups in the Permian and should, on average, be less vulnerable to global change stresses.

343 However, extreme crises like the end-Permian extinction severely impacted nearly all groups,

344 even organisms with higher activity levels, implying that survival of prior events does not

345 entirely eliminate the threat from global change.

346

352

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488 **Figure 1.** Extinction rate (three-timer method, calculated at www.fossilworks.org using SQS

489 subsampling at a quorum of 0.8) of well-skeletonized marine invertebrate groups from the Early

490 Permian to Middle Jurassic. Labels indicate the position of major mass extinctions (end-Permian

491 and end-Triassic) and smaller extinctions (Guadalupian and Toarcian).

492 **Figure 2.** Selectivity of background and mass extinctions, measured by (a) three-timer method or

493 (b) boundary-crosser method. Positive log odds ratio values indicate that more active organisms

494 were more likely to survive during a particular stage (red); negative log odds ratios indicate that

495 higher activity levels increased the risk of extinction (blue). Error bars are 95% confidence

496 intervals. Stages of the geological timescale are Permian: K=Kungurian, R=Roadian,

497 W=Wordian, C=Capitanian (Guadalupian extinction), W=Wuchiapingian, C=Changhsingian

498   (end-Permian extinction); Triassic: I=Induan (end-Permian extinction), O=Olenekian,

499   A=Anisian, L=Ladinian, C=Carnian, N=Norian, R=Rhaetian (end-Triassic extinction); Jurassic:

500   H=Hettangian, S=Sinemurian, P=Pliensbachian, T=Toarcian (Toarcian extinction, although note

501   that the extinction occurred within, not at the end of, the stage), A=Aalenian, B=Bajocian,

502   B=Bathonian.

503   **Figure 3.** Trends in mean activity level of well-skeletonized benthic invertebrates, averaged by-

504   occurrence (a; one value per occurrence of a taxon) or by-genus (b; only a single value per genus

505   regardless of the number of occurrences). Per-occurrence mean activity is shown for all studied

506   taxa (open circles) and after excluding Ostracoda (solid circles). Separate trends and shaded 95%

507   confidence intervals (data excluding Ostracoda) are shown for the Permian, Triassic, and Jurassic

508   periods (no trend is given for by-genus activity during the Permian because of the potential shift

509   at the Guadalupian extinction). Solid vertical lines mark the end-Permian and end-Triassic mass

510   extinctions; dashed lines mark the Guadalupian and Toarcian extinctions (note that the Toarcian

511   extinction actually occurred within the early Toarcian, not at its end).

(a)

Log odds ratio

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

Age (Ma)

(b)

Log odds ratio

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

Age (Ma)

(a)

(b)