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1 Extinction selectivity among marine fishes during multi-stressor global change in the end-
2 Permian and end-Triassic crises

3

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7

8 **ABSTRACT**

9 Ancient mass extinction events such as the end-Permian and end-Triassic crises provide
10 analogues for multi-stressor global change of ocean warming, pH reduction, and
11 deoxygenation. Organism physiology is hypothesized to be a key trait influencing
12 vulnerability to these stressors, but it is not certain how physiology predicts survival over
13 evolutionary timescales and when organisms are faced with opposing or synergistic
14 stressors. Fishes (bony fishes and chondrichthyan fishes) are active organisms with high
15 aerobic scope for thermal tolerance and well-developed acid-base regulation, traits that
16 should confer resilience to global change. To test this, we compiled a database of fossil
17 marine fish occurrences to quantify extinction rates during background and mass
18 extinctions from the Permian through Early Jurassic, using maximum likelihood estimation
19 to compare extinction trajectories with marine invertebrates. Our results show that
20 chondrichthyan fishes suffered less extinction than marine invertebrates during the end-
21 Permian crisis. End-Triassic chondrichthyan extinction rates also were not elevated above
22 background levels. In contrast, bony fishes suffered an end-Triassic extinction comparable
23 to that of marine invertebrates. The differing responses of these two groups imply that a

24 more active physiology can be advantageous during global change, although not uniformly.
25 Permo-Triassic chondrichthyan fishes may have had broader environmental tolerances,
26 facilitating survival. Alternatively, the larger offspring size of chondrichthyan fishes may
27 provide greater energy reserves to offset the demands of warming and acidification.
28 Although more active organisms have adult adaptations for thermal tolerance and pH
29 regulation, some may nevertheless be susceptible to global change during early life stages.

30

31 **INTRODUCTION**

32 Rapid emission of carbon dioxide (CO₂) to the atmosphere triggers a chain of
33 perturbations leading to ocean warming, pH reduction, and deoxygenation. These stressors
34 threaten many marine organisms, with consequences for growth, reproduction,
35 calcification, and ultimately survival (Doney et al., 2012; Kroeker et al., 2013). Although
36 the negative consequences of multi-stressor global change span the tree of life, some
37 organisms will be more vulnerable than others. Organism physiology is likely to play a
38 critical role in resisting or adapting to stresses from warming, hypercapnia (increased
39 *p*CO₂), and hypoxia (Melzner et al., 2009; Pörtner, 2010; Deutsch et al., 2015); however,
40 the degree to which physiology can predict survival at the ecosystem scale and over
41 evolutionary timescales is not as well understood (Queirós et al., 2015).

42 Physiological differences between fishes and invertebrates predict that fishes
43 (including both bony fishes and chondrichthyan sharks and rays) should be more resistant
44 to many global change stresses. While invertebrates may suffer acidosis (decreased pH of
45 body fluids) under elevated *p*CO₂, fishes are typically better able to compensate via active
46 ion exchange and buffering (Claiborne et al., 2002). Although active acid-base
47 compensation incurs energetic costs and may force trade-offs, fishes also tend to have

48 higher internal $p\text{CO}_2$ that can maintain diffusive CO_2 excretion under ocean hypercapnia
49 (Melzner et al., 2009). Fishes may similarly be less vulnerable to thermal stresses, due to
50 their higher activity levels (Peck et al., 2009). The need for short bursts of elevated
51 swimming performance should lead to greater aerobic scope (the excess energy available
52 beyond metabolic maintenance for activities such as growth, reproduction, and
53 locomotion), which may confer greater thermal tolerance (Pörtner, 2010). In contrast,
54 fishes are likely more vulnerable than invertebrates, on average, to stress from hypoxia
55 (Vaquer-Sunyer and Duarte, 2008). Although hypoxia tolerance, like other traits, varies
56 among species (Carlson and Parsons, 2001), more active organisms tend to have higher
57 metabolic oxygen demand (Killen et al., 2010) and higher sublethal or lethal oxygen limits
58 (Vaquer-Sunyer and Duarte, 2008). The synergistic effects of temperature, pH, and
59 dissolved oxygen further complicate predictions of extinction susceptibility during global
60 change (McBryan et al., 2013; Vaquer-Sunyer and Duarte, 2011; Pörtner et al., 2005), so
61 the effects of multi-stressor global change on active organisms such as fishes remain
62 poorly understood.

63 The fossil record provides opportunities to assess the response of marine fishes to
64 multi-stressor global change over evolutionary timescales. In particular, the end-Permian
65 and end-Triassic mass extinctions were triggered by rapid CO_2 release from gigantic flood
66 basalt eruptions, leading to ocean warming and reductions in pH and dissolved oxygen
67 (Payne and Clapham, 2012; Greene et al., 2012; Richoz et al., 2012). Ancient CO_2 -driven
68 extinctions exhibited characteristic selectivity against less active invertebrate clades with
69 weakly buffered respiratory and skeletal physiology (Knoll et al., 2007; Clapham and
70 Payne, 2011; Kiessling and Simpson, 2011). However, there has been little detailed work
71 on extinction selectivity among active marine vertebrate groups during ancient global

72 change events (Friedman and Sallan, 2012). Previous studies of the end-Permian extinction
73 found little loss in richness among bony fishes (Schaeffer, 1973), although they may have
74 undergone elevated turnover following the extinction (Romano et al., 2016). In contrast,
75 multiple Paleozoic chondrichthyan lineages passed through the Permian-Triassic boundary
76 (Mutter and Neuman, 2008; Mutter et al., 2007; Guinot et al., 2013). Chondrichthyan
77 fishes (sharks, rays, and chimaeras) may have had somewhat elevated extinction at the end-
78 Triassic extinction (Guinot and Cavin, 2015; Guinot et al., 2012), but the effect of the
79 extinction on other fishes also remains unclear (Friedman and Sallan, 2012). As a result, it
80 is not certain whether chondrichthyan or bony fishes were more resistant than marine
81 invertebrates, as predicted by physiological differences among the groups, during the end-
82 Permian and end-Triassic mass extinctions.

83 To test the hypothesis that active fishes are less vulnerable to global change
84 stressors, we compare the extinction rates of marine bony fishes and chondrichthyan fishes
85 to that of marine invertebrates through CO₂-driven mass extinctions from the Permian to
86 the Early Jurassic, using occurrences of fossil taxa from the Paleobiology Database. These
87 results will enable us to reconstruct the fate of marine fishes during multi-stressor global
88 change, and will test the importance of physiological adaptations on survival.

89

90 **METHODS**

91 We compiled a comprehensive record of Permian through Middle Jurassic marine
92 fishes from the primary literature using the Paleobiology Database (www.paleobiodb.org).
93 The Paleobiology Database is structured around occurrences, which are records of a taxa in
94 a collection (fossils obtained from a single bed or group of beds at a particular location).
95 The database also holds taxonomic opinions, entered from the primary literature, that are

96 used to update the placement of species and higher taxa to reflect the most current
97 information (even if the higher-level taxonomic placement of isolated chondrichthyan teeth
98 can be debated).

99 We downloaded occurrences for marine sharks, rays, and chimaeras
100 (Chondrichthyes, excluding the clade Xenacanthomorpha) and for marine bony fishes
101 (Actinopterygii and Actinistia, but not lungfishes). We excluded xenacanthomorph sharks
102 (the orders Xenacanthiformes and Bransonelliformes) and lungfishes (Dipnoi) because
103 they are occasionally found washed into marine sediments, despite being freshwater clades.
104 For comparison, we also downloaded occurrences of well-skeletonized, benthic marine
105 invertebrates (Brachiopoda, Bivalvia, Gastropoda, Porifera, Cnidaria, Echinodermata,
106 Bryozoa, Trilobita, Malacostraca, and Ostracoda). These groups represent organisms with
107 lower activity level relative to fishes, in order to assess the potential effect of activity on
108 survival. For all groups, we analyzed the earliest Permian (Asselian stage) to Middle
109 Jurassic (Bathonian stage), only including occurrences from marine environments,
110 constrained to a single geological stage, identified at the genus level or lower, and
111 excluding form taxa (e.g., chondrichthyan dermal denticles). The resulting datasets contain
112 1337 shark, 1817 bony fish, and 120935 marine invertebrate occurrences.

113 Because both bony fish and chondrichthyan records exhibit considerable volatility
114 in sample size, we subsampled the data prior to calculating and comparing extinction rates.
115 Subsampling was performed by randomly selecting 20 occurrences from each stage; stages
116 with fewer than 20 occurrences were retained for assessing the ranges of genera, but we did
117 not calculate extinction rates for those intervals. The marine invertebrate record was
118 subsampled at 1000 occurrences per stage, using the same procedure. All subsampling was
119 performed 100 times. We then calculated the mean boundary-crosser extinction rate

120 (Foote, 2000) and mean counts (N_{bt} , N_b , and N_{bL}) in each stage. The boundary crosser
121 method considers only the cohort of genera that cross the bottom boundary of an interval
122 (N_b); extinct genera have their last appearance within the interval (N_{bL}) and surviving
123 genera cross both bottom and top boundaries (N_{bt}).

124 We used maximum likelihood estimation to compare models that calculated
125 separate extinction rates for vertebrates (chondrichthyan or bony fishes) and invertebrates
126 (“two-rate model”) to models that applied one extinction rate to both groups (“single-rate
127 model”). This approach has been used previously to compare models of extinction
128 selectivity in marine invertebrates (Kiessling and Simpson, 2011), and uses a binomial log-
129 likelihood function:

$$130 \quad N_{bt} \left(\ln \frac{N_{bt}}{N_b} \right) + N_{bL} \left(\ln \frac{N_{bL}}{N_b} \right)$$

131 The single-rate model fits one extinction rate to the pooled counts of both groups. The two-
132 rate model maximizes two separate log-likelihood functions, one for the vertebrate group
133 (sharks or bony fishes) and one for invertebrates, and the resulting log-likelihood values
134 are summed. Following the methods of Kiessling & Simpson (2011), we then used
135 Akaike’s information criterion with small-sample correction (AICc) to measure the relative
136 support for the single-rate and two-rate models given the data in each geological stage.
137 Relative support is expressed as Akaike weights, which summarize the probability of a
138 particular model being the best candidate, given the observed data.

139

140 **RESULTS**

141 Chondrichthyan fishes and marine invertebrates exhibited similar extinction rates
142 during most background intervals, but chondrichthyan extinction rates remained low

143 during the end-Permian and end-Triassic extinctions while marine invertebrates suffered
144 more severely (Fig. 1a). The single-rate model receives stronger support in most
145 background intervals where the log-likelihood can be calculated (we did not estimate
146 extinction rates in the Capitanian or Hettangian, as they contain fewer than 20
147 occurrences). In contrast, maximum likelihood estimation supports a two-rate model
148 (Akaike weight 0.77) during the Changhsingian stage (end-Permian extinction), in which
149 extinction rates were lower among Chondrichthyes than among invertebrates.
150 Chondrichthyan fishes were not unscathed during the Permian-Triassic crisis, however; the
151 order Petalodontiformes has its last appearance in upper Permian strata and
152 Eugeneodontiform sharks disappear within the Olenekian stage (Lower Triassic). Although
153 marine Chondrichthyes do not show an end-Triassic extinction peak, a single-rate model
154 received more support, although very weakly (Akaike weight 0.57). However, the support
155 for a one-rate model in the Rhaetian stage is lower than in most background intervals.

156 The rarity of marine bony fish fossils through much of the Permian (whether
157 taphonomic or a real rarity of fishes in Permian oceans) prevents subsampling or reliable
158 estimation of extinction rates, but both bony fishes and invertebrates exhibit similar
159 extinction trajectories through most stages of the Middle and Late Triassic and Early
160 Jurassic. The boundary-crosser extinction rate is zero at the Permian-Triassic boundary
161 (Fig. 1b), so the maximum likelihood method cannot be applied. Despite that, apparently
162 low bony fish extinction contrasts markedly with the extinction spike observed among
163 invertebrates. However, this low extinction is based on a boundary-crossing cohort of only
164 five genera (in the raw data). Furthermore, it seems likely that many Wuchiapingian
165 genera, primarily from the exceptionally-preserved Marl Slate of England and
166 Kupferschiefer of Germany, actually had longer but not recorded ranges, perhaps surviving

167 to the end-Permian. As a result, intense extinction among bony fishes in the
168 Wuchiapingian, although supporting a two-rate extinction model (Akaike weight 0.77), is
169 possibly an overestimate. Assessment of bony fish extinctions in the Permian will require
170 additional fossil material.

171 Most Triassic stages are best fit by a single-rate model, when bony fishes and
172 invertebrates exhibited strikingly similar extinction peaks, including during the end-
173 Triassic extinction (Rhaetian stage) (Fig. 1b). A two-rate extinction model, with higher
174 extinction rates among bony fishes, is instead moderately better supported in the Olenekian
175 stage (Akaike weight 0.68). Higher extinction rates during the Olenekian are consistent
176 with turnover in pelagic ecosystems, especially at higher trophic levels, during the late
177 Smithian substage (Scheyer et al., 2014). Rhaetian data (the end-Triassic extinction)
178 strongly support a single-rate model (Akaike weight 0.73, but note that this is close to the
179 strongest AIC support possible for two models with the same total likelihood and differing
180 by one parameter). The Pliensbachian stage of the Early Jurassic lacks sufficient
181 occurrences for subsampling, but other Jurassic intervals provide most support for a single-
182 rate extinction or equivocal support for either model (two-rate model support in the
183 Sinemurian stage is 0.57, but extinction is likely artificially high due to the exceptionally-
184 preserved Lyme Regis fish fauna).

185

186 **DISCUSSION**

187 The striking divergence between chondrichthyan and invertebrate extinction
188 trajectories during the two mass extinction events supports the hypothesis that active
189 Chondrichthyes are on average less vulnerable to multi-stressor global change. A model
190 with separate extinction rates for Chondrichthyes and invertebrates during the end-Permian

191 mass extinction receives strong support (although some chondrichthyan clades nevertheless
192 suffered extinction), but the end-Triassic mass extinction is more equivocal in the
193 maximum likelihood analysis. Nevertheless, the lack of an end-Triassic extinction peak in
194 the chondrichthyan record is also consistent with the group being on average more resistant
195 to stresses from the combination of warming, reduced pH, or hypoxia. The equivocal AIC
196 support for a two-rate extinction model in the Rhaetian likely results from less severe
197 extinctions among marine invertebrates, in comparison to the end-Permian extinction,
198 rather than from differences in the response of sharks.

199 However, it is also possible that different chondrichthyan groups varied in their
200 sensitivity to extinction stresses, whether physiological or dietary (e.g., durophagous
201 groups may have suffered more; Friedman and Sallan, 2012). Although there is uncertainty
202 in the taxonomic affinity of isolated teeth, neoselachian sharks (the clade including all
203 extant sharks and rays) were likely present in the Permian (e.g., Koot et al., 2013).
204 However, the group became more diverse by the Late Triassic (Cuny and Benton, 1999).
205 Two of three extinct genera in the Rhaetian belonged to the Neoselachii, whereas six of
206 eight survivors were hybodontiform sharks (an extinct order that dominated Triassic
207 faunas). The sample size is too small to draw confident conclusions (there is no significant
208 difference in outcome between the two groups, according to a Fisher's exact test; $p=0.56$),
209 but these results raise the hypothesis that hybodontiform sharks may have been particularly
210 resistant to warming, reduced pH, and/or hypoxia. Although testing this hypothesis will
211 require a richer Late Triassic shark record, Paleozoic and Mesozoic stem-group
212 Chondrichthyes, such as ctenacanthiform and hybodontiform sharks, were commonly
213 euryhaline, with genera occurring in marine, brackish, and freshwater environments (e.g.,
214 Fischer et al., 2012). This wide distribution potentially allowed them to occupy refugia

215 where extinction-related stresses were not as intense. These taxa presumably also had well-
216 developed osmoregulatory capacity, similar to modern euryhaline sharks (Reilly et al.,
217 2011). Because osmoregulation and acid-base regulation involve related ion transport
218 mechanisms (Hammerschlag, 2006), some Paleozoic and early Mesozoic stem-group
219 Chondrichthyes may also have been more able to maintain acid-base balance during
220 reductions in ocean pH.

221 In contrast to the chondrichthyan record, marine bony fishes suffered elevated
222 losses comparable to marine invertebrate extinctions during the end-Triassic mass
223 extinction, implying that active organisms may not have uniformly been more resistant to
224 multi-stressor global change. Permian and Triassic bony fishes, which were dominantly
225 lower actinopterygians rather than teleosts (Romano et al., 2016), likely nevertheless
226 possessed active pH regulation or buffering, as those traits can be found in modern
227 members of basal fish clades (hagfish and sturgeon; Baker et al., 2009; Baker et al., 2015).
228 Permian and Triassic bony fishes would also have been more active than benthic
229 invertebrates, with higher aerobic scope. However, global change integrates multiple
230 stressors, and the end-Permian and end-Triassic extinctions were triggered by the
231 combination of not only warming and reduced pH, but also hypoxia (e.g., Algeo et al.,
232 2011), which may have been a more important stressor on active marine fishes (Vaquer-
233 Sunyer and Duarte, 2008). As most Permian and Triassic bony fishes belonged to non-
234 teleost actinopterygian groups, they likely possessed the capability to breathe air as well as
235 ventilating through gills, similar to modern representatives of those groups (Perry et al.,
236 2001). However, this trait should have made Permo-Triassic bony fishes less vulnerable to
237 hypoxia than coeval chondrichthyan fishes, opposite to the trend observed in the data. The
238 different responses of bony fishes and sharks may instead reflect the greater number of

239 euryhaline genera among Chondrichthyes, if coastal areas acted as refugia from hypoxic
240 conditions. Only about 10% of Permo-Triassic bony fishes were euryhaline (Romano et al.,
241 2016), but the limited Permian record prevents rigorous testing of selectivity within bony
242 fishes.

243 Elevated extinction rates occurred among bony fishes despite adult traits that
244 should have been favorable for survival. If adult traits were less important, it is instead
245 possible that early life history stages of bony fishes, which tend to produce more numerous,
246 smaller offspring, compared to chondrichthyan fishes, which typically produce fewer,
247 larger offspring (Hutchings et al., 2012), may have contributed to the differential
248 selectivity. Global change stressors can have serious consequences for early life history
249 stages, largely as an energy budget problem due to increased maintenance costs (e.g.,
250 Sokolova et al., 2012; Jager et al., 2016; Di Santo, 2015). Among oviparous taxa (most
251 were likely oviparous, but some Triassic fishes may have been viviparous; Bürgin, 1990),
252 larger chondrichthyan eggs and embryos would have had greater energy reserves available
253 to offset additional energetic costs imposed by warming or acidification. Elevated
254 extinction among bony fishes during the end-Triassic extinction may then reflect greater
255 vulnerability at early life history stages, due to small embryos with limited energy reserves,
256 rather than differences in adult traits of bony and chondrichthyan fishes.

257

258 **CONCLUSIONS**

259 Marine chondrichthyans did not suffer elevated extinctions during the end-Permian
260 or end-Triassic crises, but extinction trajectories among bony fishes were comparable to
261 marine invertebrates during the Triassic. Although outcomes among Chondrichthyes are
262 consistent with the hypothesis that more active organisms are more resistant to multi-

263 stressor global change, bony fish extinctions imply that higher activity is not consistently
264 beneficial. The complicated role of activity levels may be a consequence of
265 counterbalancing stressors, where warming and reduced pH likely favor survival of more
266 active organisms but hypoxia more severely impacts those groups. Preferential survival of
267 Permian and Triassic chondrichthyans may have occurred because more genera had
268 broader environmental distribution in marine, brackish, and freshwater habitats, or because
269 their reproductive strategies produced larger embryos with greater energy reserves to
270 withstand energetic costs of global change. Because of multiple stressors during global
271 change extinctions, and because those stressors act across multiple stages of life history,
272 the extinction history of Permian and Triassic marine fishes implies that active organisms
273 may still be at risk when faced with warming, reduced pH, and hypoxia.

274

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278 publication #XXX.

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433 **FIGURE CAPTIONS**

434 **Fig. 1.** Genus-level boundary-crosser extinction rates for marine chondrichthyan fishes
435 (sharks, rays, and chimaeras) (A) and bony fishes (B), compared to marine invertebrates,
436 from the Permian through Early Jurassic. The color for each stage is based on the
437 proportional support (Akaike weight) for a two-rate extinction, in which invertebrates and
438 the vertebrate group had different extinction rate, relative to a model fitting a single
439 extinction rate to both groups. Dashed lines show the position of the end-Permian
440 (Changhsingian stage) and end-Triassic (Rhaetian stage) mass extinctions. Stages of the
441 geological timescale are Permian: As=Asselian, Sa=Sakmarian, Ar=Artinskian,
442 Ku=Kungurian, Ro=Roadian, Wo=Wordian, Ca=Capitanian, Wu=Wuchiapingian,
443 Ch=Changhsingian; Triassic: In=Induan, Ol=Olenekian, An=Anisian, La=Ladinian,
444 Ca=Carnian, No=Norian, Rh=Rhaetian; Jurassic: He=Hettangian, Si=Sinemurian,
445 Pl=Pliensbachian, To=Toarcian, Aa=Aalenian, Ba=Bajocian, Ba=Bathonian.

