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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

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

INTRODUCTION

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

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

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

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

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

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

METHODS

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

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

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

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

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

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

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

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

RESULTS

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

CONCLUSIONS

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

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

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FIGURE CAPTIONS

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