

Extinction selectivity among marine fishes during multistressor global change in the end-Permian and end-Triassic crises

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ABSTRACT

Ancient mass extinction events such as the end-Permian and end-Triassic crises provide analogues for multistressor global change of ocean warming, pH reduction, and deoxygenation. Organism physiology is hypothesized to be a key trait influencing vulnerability to these stressors, but it is not certain how physiology predicts survival over evolutionary time scales and when organisms are faced with opposing or synergistic stressors. Fishes (bony fishes and chondrichthyan fishes) are active organisms with high aerobic scope for thermal tolerance and well-developed acid-base regulation, traits that should confer resilience to global change. To test this, we compiled a database of fossil marine fish occurrences to quantify extinction rates during background and mass extinctions from the Permian through Early Jurassic, using maximum likelihood estimation to compare extinction trajectories with marine invertebrates. Our results show that fewer chondrichthyan fishes underwent extinction than marine invertebrates during the end-Permian crisis. End-Triassic chondrichthyan extinction rates also were not elevated above background levels. In contrast, bony fishes underwent an end-Triassic extinction comparable 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. Permian–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 multistressor global change span the tree of life, some organisms are more vulnerable than others. Organism physiology is likely to play a critical role in resisting or adapting to stresses from warming, reduced pH, 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 time scales is not as well understood (Queirós et al., 2015).

Physiological differences between fishes and invertebrates predict that marine fishes should be more resistant to many global change stresses. While invertebrates may undergo acidosis (decreased pH of body fluids) under elevated pCO₂, 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 pCO₂ that can maintain diffusive

CO₂ excretion under reduced ocean pH (Melzner et al., 2009). Fishes may similarly be less vulnerable to thermal stresses if more active organisms have greater thermal tolerance (Peck et al., 2009). The need for short bursts of elevated performance should lead to greater aerobic scope (the excess energy available beyond metabolic maintenance for growth, reproduction, and locomotion), which may confer greater thermal tolerance (Pörtner, 2010). In contrast, fishes are probably more vulnerable than invertebrates, on average, to hypoxia (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 multistressor global change on active organisms such as fishes remain poorly understood.

The fossil record provides opportunities to assess the response of marine fishes to multistressor global change over evolutionary time scales. In particular, the end-Permian and end-Triassic mass extinctions were triggered by rapid CO₂ release from 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 CO₂-driven extinctions exhibited characteristic selectivity against less active invertebrate clades (Knoll et al., 2007; Clapham and Payne, 2011; Kiessling and Simpson, 2011; Clapham, 2017). 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 (sharks, rays, and chimaeras) passed through the Permian–Triassic boundary (Mutter and Neuman, 2008; Mutter et al., 2007; Guinot et al., 2013). Chondrichthyan fishes may have had somewhat elevated extinction at the end-Triassic crisis (Guinot and Cavin, 2015; Guinot et al., 2012), but its effect on other fishes 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 those of marine invertebrates from the Permian to the Early Jurassic. These results will enable us to reconstruct the fate of marine fishes during multistressor 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). We entered occurrences for marine sharks, rays, and chimaeras (Chondrichthyes, excluding the clade Xenacanthomorpha) and for marine bony fishes (Actinopterygii and Actinistia, but not lungfishes). We excluded xenacanthiform sharks (the orders Xenacanthiformes and Bransonelliformes) and lungfishes (Dipnoi) because they are

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occasionally found washed into marine sediments, despite being freshwater clades. For comparison to groups with lower activity levels relative to fishes, we also downloaded occurrences of benthic marine invertebrates (Brachiopoda, Bivalvia, Gastropoda, Porifera, Cnidaria, Echinodermata, Bryozoa, Trilobita, Malacostraca, and Ostracoda). For all groups, we analyzed the Asselian to Bathonian stages, 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 data sets contain 1337 chondrichthyan, 1817 bony fish, and 120,935 marine invertebrate occurrences.

Because both bony fish and chondrichthyan records exhibit considerable volatility in sample size, we subsampled the data prior to calculating extinction rates. Subsampling randomly selected 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. We subsampled the marine invertebrate record at 1000 occurrences per stage. All subsampling was performed 100 times. We then calculated the mean boundary-crosser extinction rate (Foote, 2000) and mean counts (N_{bt} , number that crosses both boundaries; N_b , bottom boundary crossers; N_{bl} , number that crosses bottom boundary only) in each stage.

We used maximum likelihood estimation to compare models of extinction selectivity, following the approach of Kiessling and Simpson (2011), using a binomial log-likelihood function:

$$N_{bt} \left(\ln \frac{N_{bt}}{N_b} \right) + N_{bl} \left(\ln \frac{N_{bl}}{N_b} \right). \quad (1)$$

The single-rate model fits one extinction rate to the pooled counts of both groups (Chondrichthyes + invertebrates or bony fishes + invertebrates). The two-rate model maximizes two separate log-likelihood functions, one for the vertebrate group and one for invertebrates, and the resulting log-likelihood values are summed. We then used the Akaike information criterion with small-sample correction (AICc) expressed as Akaike weights to 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. In contrast, maximum likelihood estimation supports a two-rate model during the Changhsingian stage (end-Permian extinction), with lower extinction rates among Chondrichthyes (Akaike weight 0.77). Chondrichthyan fishes were not unscathed during the crisis, however; the order Petalodontiformes had its last appearance in upper Permian strata and eugeneodontiform sharks disappeared within the Olenekian stage (Early Triassic). Although marine Chondrichthyes do not show an end-Triassic extinction peak, a single-rate model received more support, although very weakly compared to background intervals (Akaike weight 0.57).

The rarity of marine bony fish fossils through much of the Permian (whether taphonomic or a real rarity of fishes in Permian oceans) prevents

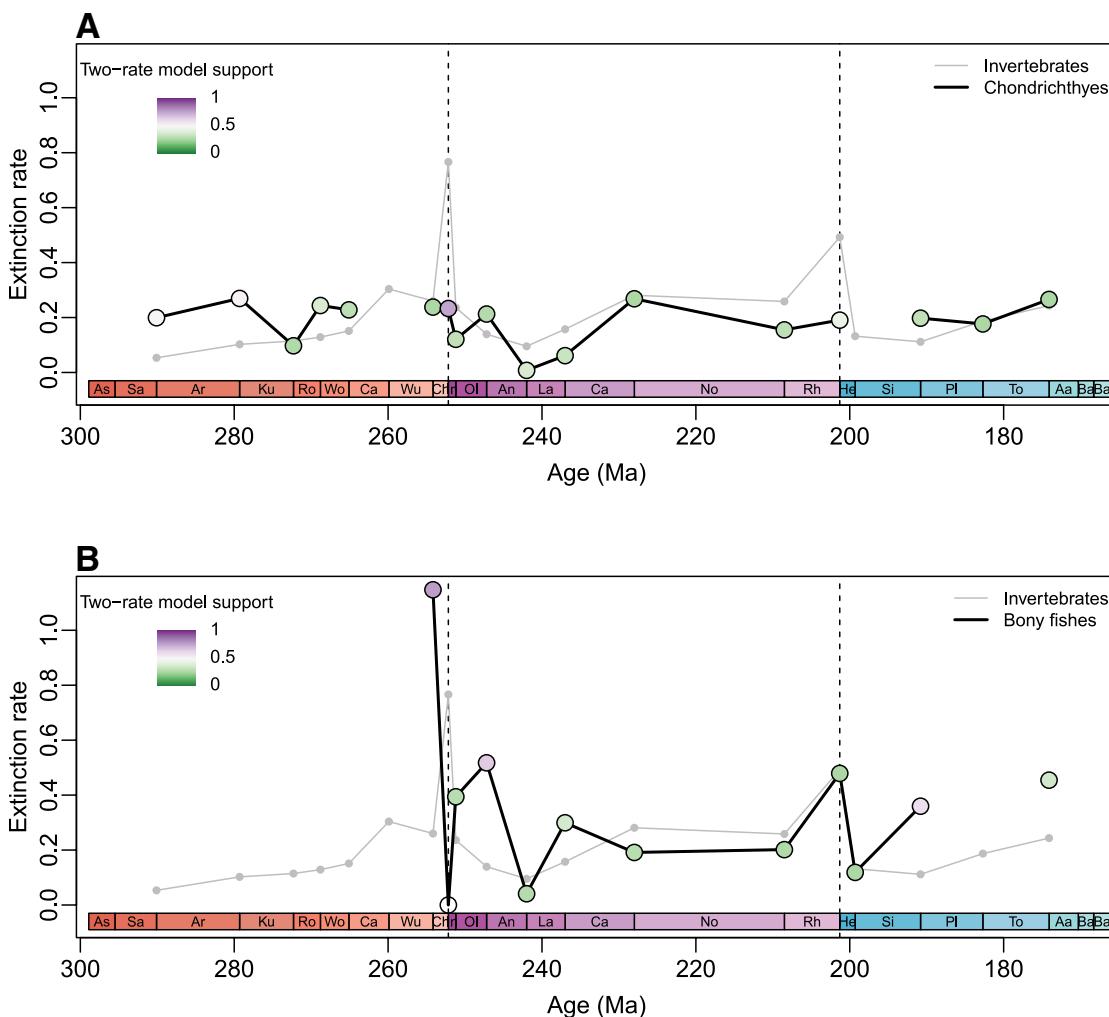


Figure 1. Genus-level boundary-crosser extinction rates for fishes compared to marine invertebrates, from the Permian through Early Jurassic. A: For marine chondrichthyan fishes (sharks, rays, and chimaeras). **B:** For marine bony fishes. The color for each stage is based on the proportional support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

reliable estimation of extinction rates. The boundary-crosser extinction rate is zero at the Permian-Triassic boundary (Fig. 1B), although it seems plausible that some Wuchiapingian genera, nearly exclusively from exceptionally preserved localities in England and Germany, actually survived later in the Permian. As a result, extinction among bony fishes in the Wuchiapingian, despite supporting a two-rate extinction model (Akaike weight 0.77), is possibly an overestimate, while low end-Permian extinction rates may be underestimates. Assessment of bony fish extinctions in the Permian will require additional fossil material.

Most Triassic and Jurassic stages are best fit by a single-rate model, with bony fishes and invertebrates exhibiting similar extinction peaks, including during the end-Triassic extinction (Rhaetian stage) (Fig. 1B). A two-rate extinction model is instead moderately better supported in the Olenekian stage (Akaike weight 0.68), consistent with elevated turnover in pelagic ecosystems, including among fishes, during the 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 the 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, UK, 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 multistressor 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 underwent extinction), but the end-Triassic mass extinction is more equivocal. Nevertheless, the lack of an end-Triassic extinction peak in the chondrichthyan record is also consistent with the group being 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 Chondrichthyes.

However, it is also possible that different chondrichthyan groups varied in their sensitivity to extinction stresses. Although identifications of isolated teeth may be uncertain, neoselachian sharks (the clade including all living species) 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 especially resistant to warming, reduced pH, and/or hypoxia. Although testing this idea will require a richer Late Triassic shark record, Paleozoic and Mesozoic stem-group Chondrichthyes, including hybodontiform sharks, commonly included genera occurring in marine to freshwater environments (e.g., Fischer et al., 2012), possibly allowing 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), euryhaline hybodontiform sharks 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 underwent 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 multistressor 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 (e.g., hagfish and sturgeon; Baker et al., 2009, 2015). Permian and Triassic bony fishes would also have been more active, with higher aerobic scope, than benthic invertebrates. 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). Although active organisms may be more susceptible to hypoxia, non-teleost actinopterygian fishes that dominated the Triassic likely possessed the capability to breathe air as well as ventilate through gills, similar to modern representatives of those groups (Perry et al., 2001). This trait should have made bony fishes less vulnerable to hypoxia than chondrichthyan fishes during the Triassic extinction, opposite to the observed trend. The different responses of bony fishes and sharks may instead reflect the greater number of euryhaline genera among Chondrichthyes (only ~10% of Permian-Triassic bony fishes were euryhaline; Romano et al., 2016), if coastal areas acted as refugia from hypoxic conditions.

Elevated extinction rates occurred among bony fishes despite adult traits that should have been favorable for survival. 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). Among oviparous taxa, 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 undergo elevated extinctions during the end-Permian or end-Triassic crises, but extinction trajectories among bony fishes were comparable to those of marine invertebrates during the Triassic. Although outcomes among Chondrichthyes are consistent with the hypothesis that more active organisms are more resistant to multistressor global change, bony fish extinctions imply that higher activity is not consistently beneficial. Preferential survival of Permian and Triassic chondrichthyans relative to invertebrates or bony fishes 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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