RESEARCH ARTICLE SUMMARY

CLIMATE IMPACTS

Temperature-dependent hypoxia explains biogeography and severity of end-Permian marine mass extinction

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INTRODUCTION: Climate change triggered by volcanic greenhouse gases is hypothesized to have caused the largest mass extinction in Earth's history at the end of the Permian Period (~252 million years ago). Geochemical evidence provides strong support for rapid global warming and accompanying ocean oxygen (O_2) loss, but a quantitative link among climate, species' traits, and extinction is lacking. To test whether warming and O_2 loss can mechanistically account for the marine mass extinction, we combined climate model simulations with an established ecophysiological framework to predict the biogeographic patterns and severity of extinction. Those predictions were confirmed by a spatially explicit analysis of the marine fossil record.

RATIONALE: The impact of climate change on marine biodiversity depends on both its magnitude and on species' diverse biological sensitivities. Tolerances of marine animals to warming and O_2 loss are physiologically related and can be represented in a single metric: the ratio of temperature-dependent O_2 supply and demand rates. This ratio, termed the Metabolic Index (Φ), measures the environmental scope for aerobic activity and is governed by ocean conditions as well as thermal and hypoxia sensitivity traits that vary across species. If climate warming and O_2 loss reduce Φ below the species-specific minimum requirement for sustained ecological activity (Φ^{crit}), the ocean would no longer support active aerobic metabolism and, by extension, long-term population persistence.

RESULTS: We simulated the greenhouse gas–driven global warming at the end of the Permian using a model of Earth's climate and coupled biogeochemical cycles that matches geochemical proxy data. The imposed increase in atmospheric greenhouse gas levels raises near-surface ocean temperatures by more than ~10°C and depletes global marine O_2 levels by almost 80%.

To predict the impact of these changes on animal habitat and survival, we measured the frequencies of Metabolic Index traits in diverse living species and used them to define a set of model ecophysiotypes. We populated the model Permian ocean with each ecophysiotype wherever conditions provide viable habitat ($\Phi \geq \Phi^{crit}$), yielding an ocean with diverse, locally adapted ecophysiotypes throughout all regions. Across the climate transition, however, ocean warming increases the metabolic O_2 demand amid declining supply; this removes large fractions of global aerobic habitat for the vast majority of ecophysiotypes and implies a high likelihood of extinction. We simulated the resulting mass extinction of ecophysiotypes and found a robust geographic pattern: Extinction intensity should have been lower in the tropics than at high latitudes. The cause of lower tropical extinction is that organisms initially inhabiting these warm, low-O_2 environments can better exploit those conditions when they arise globally, whereas the habitats of more polar species disappear completely.

To test the geographic selectivity of the model extinction, we compared model predictions to spatially explicit reconstructions of genus extinction from the marine fossil record. We found that across diverse taxonomic groups, the observed extinction intensity indeed increases with latitude, consistent with the predicted signature of aerobic habitat loss. Comparison of the model to the fossil record implies that temperature-dependent hypoxia can account for more than half of the observed magnitude of regional extinction (i.e., extirpation).

CONCLUSION: Ocean warming and O_2 loss simulated in an Earth System Model of end-Permian climate change imply widespread loss of aerobic habitat among animal types with diverse thermal and hypoxia tolerances. The resulting extinctions are predicted to select most strongly against higher-latitude species, whose biogeographic niche disappears globally. The combined physiological stresses of ocean warming and O_2 loss largely account for the spatial pattern and magnitude of extinction observed in the fossil record of the "Great Dying." These results highlight the future extinction risk arising from a depletion of the ocean's aerobic capacity that is already under way. ■

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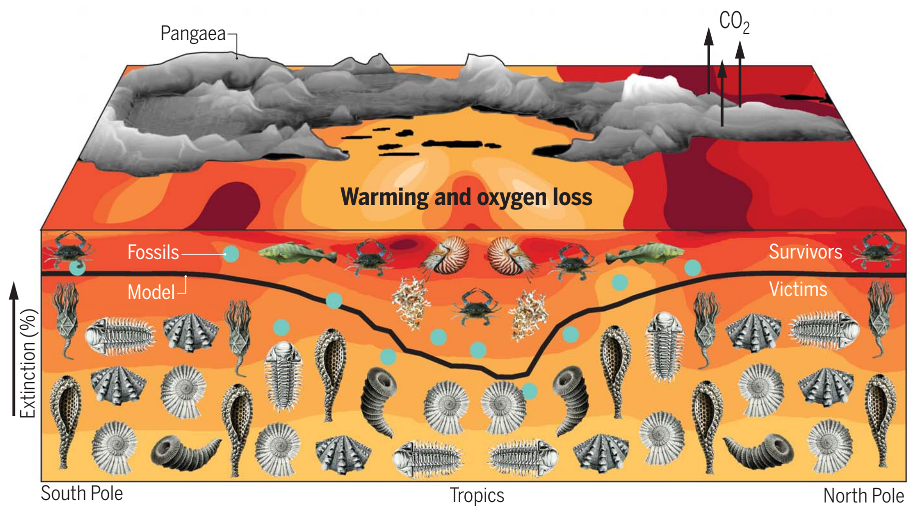

Schematic illustration of temperature-dependent hypoxia as a driver of the end-Permian marine mass extinction. Greenhouse gas forcing in a model of Earth's climate at the end of the Permian drives ocean warming (contours) and oxygen loss that match geochemical proxy data. Ocean warming raises the organismal O_2 demand amid declining supply. The resulting loss of aerobic habitat for diverse physiologies induces a mass extinction in model animal types (line) whose geographic signature—increased severity outside of the tropics—is consistent with reconstructions from the marine fossil record (circles).

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