Acidification, anoxia, and extinction: A multiple logistic regression analysis of extinction selectivity during the Middle and Late Permian

Matthew E. Clapham[1]* and Jonathan L. Payne[2]*
[1]Department of Earth and Planetary Sciences, University of California–Santa Cruz, 1156 High Street, Santa Cruz, California 95064, USA
[2]Department of Geological and Environmental Sciences, Stanford University, 450 Serra Mall, Building 320, Stanford, California 94305, USA

ABSTRACT

Patterns of taxonomic and ecologic selectivity are the most direct record of processes influencing survival during background and mass extinctions. The Guadalupian (Capitanian) and end-Permian (Changhsingian) extinctions have both been linked to environmental degradation from eruption of large flood basalts; however, the extent to which taxonomic selectivity conforms to the expected stresses remains incompletely understood because many of the relevant biological traits are mutually correlated. Here we use a large occurrence-based database to quantify extinction selectivity during background and mass extinction intervals from the Kungurian (latest Early Permian) to Changhsingian. Our multiple logistic regression analysis confirms that the end-Permian extinction was a physiological crisis, selecting against genera with poorly buffered respiratory physiology and calcareous shells. Genera with unbuffered physiology also fared poorly in the Guadalupian extinction, consistent with recognition of a pronounced crisis only among protists and reef-builders and implying similar respiratory physiological stresses. Despite sharing a similar trigger, the end-Permian extinction was considerably more severe than the Guadalupian or other Phanerozoic physiological crises. Its magnitude may have resulted from a larger environmental perturbation, although the combination of warming, hypercapnia, ocean acidification, and hypoxia during the end-Permian extinction likely exacerbated the crisis because of the multiplicative effects of those stresses. Although ocean carbon cycle and evolutionary changes have reduced the sensitivity of modern ecosystems to physiological stresses, extant marine invertebrates face the same synergistic effects of multiple stressors that were so severe during the end-Permian extinction.

INTRODUCTION

Extinction selectivity is a powerful control on macroevolutionary pattern and can often serve as a fingerprint for underlying causes. The end-Permian mass extinction was the most severe extinction event of the Phanerozoic (Raup and Sepkoski, 1982), causing dramatic and permanent shifts in the taxonomic and ecological structure of marine ecosystems (Bambach et al., 2002; Wagner et al., 2006). The differential impact of the end-Permian extinction on brachiopods relative to bivalves has long been known (e.g., Gould and Calloway, 1980; Sepkoski, 1981). Knoll et al. (1996, 2007; see also Kiessling and Simpson, 2011) have since shown that end-Permian extinction risk varied substantially across major marine animal clades as a function of respiratory and skeletal physiology. From these findings, Knoll et al. (2007) proposed that end-Permian extinction was primarily physiological in nature, resulting from the combined stresses of increased pCO_2 and temperature and reduced pO_2 and carbonate saturation.

Despite the strong association between physiology and extinction risk, the extent to which the end-Permian extinction resulted from direct physiological stress remains incompletely understood for two reasons. First, ecological and physiological variables are often mutually correlated, leading many variables to correlate with extinction risk when considered independently. Second, recent improvements to correlation of the Permian time scale and improved sampling of the Late Permian fossil record have vastly expanded the number of genera known from the Changhsingian, from 443 including all range-through taxa (Knoll et al., 2007) to 701 sampled-in-bin genera here, including many that were previously considered victims of a Guadalupian extinction event (Clapham et al., 2009). Consequently, reanalysis is required to determine the extent to which end-Permian selectivity deviates from preceding stages.

Understanding the role of physiological stresses in marine extinctions is particularly important because a number of major and minor biotic crises were caused by physiologically linked environmental perturbations similar to those faced by the modern marine fauna (Kiessling and Simpson, 2011). Hypoxic conditions, one potential contributor to the end-Permian mass extinction (Wignall and Twitchett, 1996; Grice et al., 2005), are expanding in modern ocean "dead zones" (Diaz and Rosenberg, 2008). At the same time, rapidly increasing pCO_2, also associated with numerous biotic crises (Wignall, 2001; Payne et al., 2010; Kiessling and Simpson, 2011), is exacerbating respiratory stress in those hypoxic settings (Pörtner et al., 2005; Brewer and Peltzer, 2009) and negatively impacting shell production in many calcifying groups via ocean acidification (Caldeira and Wickett, 2003).

METHODS

We use a database of nearly 50,000 marine invertebrate fossil occurrences from 8900 collections to examine physiological, mineralogical, and ecological influences on genus-level extinction risk during the end-Permian (Changhsingian) and Guadalupian (Capitanian) extinctions. Extinction during the Changhsingian is assessed from occurrences in nearly 1900 Triassic collections, supplemented by data from the Paleobiology Database (http://www.paleodb.org). We further examine extinction selectivity during the other latest Early to Late Permian stages (Kungurian, Roadian, Wordian, and Wuchiapingian) to compare extinction patterns against a historical baseline. Species richness per genus (excluding occurrences in open nomenclature), abundance (number of occurrences), and geographic range (number of equal-area geographic bins occupied) were determined separately in each stage. Species richness was included in our analyses because genus-level traits such as abundance and geographic range are confounded by the number of species per genus. Physiology, skeletal mineralogy, and life habit were assumed to be constant over the lifetime of a genus. Although an organism's ability to buffer intracellular conditions and shell calcification against changes in ambient water chemistry is highly variable within clades, even at the species or genus level (Widdicombe and Spicer, 2008; Kroeker et al., 2010), we followed Kiessling and Simpson (2011) and Knoll et al. (1996, 2007) in classifying genera broadly as having well-buffered (active) or poorly buffered (passive) physiology. Well-buffered groups include bivalves, gastropods, cephalopods, ostracods, and trilobites, whereas corals, sponges, brachiopods, bryozoans, and crinoids were considered to have a poorly buffered physiology. Skeletal mineralogy was coded as aragonite, calcite (including bimineralic shells), or noncarbonate (chitin, phosphate, silica). Because infaunal taxa may experience and thus have adaptations for physiological stresses such as hypoxia or hypercapnia, each genus was classified as infaunal or

---

*E-mails: mclapham@ucsc.edu; jlpayne@stanford.edu.

Geology, November 2011; v. 39; no. 11; p. 1059–1062; doi:10.1130/G32230.1; 1 figure; Data Repository item 2011310.

noninfaunal (combining epifaunal and swimming taxa). We used multiple logistic regression (e.g., Payne and Finnegan, 2007) to assess the independent associations of the ecological and physiological predictors with extinction risk (see the GSA Data Repository[1]). The multiple regression analysis simultaneously considered species richness, abundance, geographic range, life position, mineralogy (aragonite versus calcite), mineralogy (carbonate versus noncarbonate), and physiology as predictors, but did not include interaction terms between them.

RESULTS

Taxa with poorly buffered physiology were at significantly greater risk of extinction only during the Capitanian and Changhsingian stages, representing the Guadalupian and end-Permian extinctions, but not during other stages (Fig. 1A). We also observe selectivity with respect to skeletal mineralogy during the Changhsingian only, at which time having a skeleton made of a compound other than calcium carbonate was highly beneficial (Fig. 1C). Although the sample sizes are small, taxa with phosphatic or siliceous skeletons (linguliform brachiopods, conulariids, and hexactinellid and nonhypercalcified demosponges) were significantly more likely to survive the end-Permian extinction, even when accounting for differences in physiology, geographic range, and other traits. Noncarbonate mineralogy did not confer any advantages during background extinction or during the Guadalupian crisis. We observe no significant differences between taxa with aragonite and calcite (including bimineralic) shells.

Even though infaunal taxa are typically regarded as having broader physiological tolerances than closely related epifaunal genera due to more frequent exposure to hypoxic and hypercapnic conditions in their burrows (Knoll et al., 1996, 2007; Widdicombe and Spicer, 2008), life position did not predict survival during the two crisis intervals. Infaunal taxa were more likely to survive only in the Kungurian and Wordian stages, a pattern likely driven by high extinction intensity among ammonoids. When ammonoids are excluded from the analysis, life position is only a significant predictor of extinction risk for the Changhsingian. In contrast to previous findings, however, we observed that infaunal genera were more likely to go extinct than epifaunal genera during the Changhsingian ($p = 0.01$), likely the result of the more complete record of Changhsingian taxa (particularly bivalves, the main infaunal group) used here.

Background extinction selectivity was more consistently significant with respect to geographic range than with respect to other measures of rarity or commonness. Narrowly distributed genera were at significantly greater risk of extinction during background intervals in the Permian (Kungurian–Wuchiapingian), but the relationship weakened considerably in the Changhsingian, although it was still marginally significant ($p = 0.049$) (Fig. 1F). Abundance was not a significant predictor of extinction risk in the Changhsingian or most background intervals (Fig. 1E).

DISCUSSION

Our multiple regression analysis generally confirms previous findings of physiological selectivity during the Changhsingian and Capitanian extinctions (Knoll et al., 2007; Kiessling and Simpson, 2011). Kiessling and Simpson (2011) also identified the Wuchiapingian as a stage in which extinction rates were higher among unbuffered groups. Our results do not agree with this previous finding, but the discrepancy is most likely the result of differences in analytical methods or taxonomic breadth among the data sets. Kiessling and Simpson (2011) used a maximum-likelihood model comparison of extinction rates, excluded single-bin genera from the calculation of extinction intensity, and included calcareous algae and

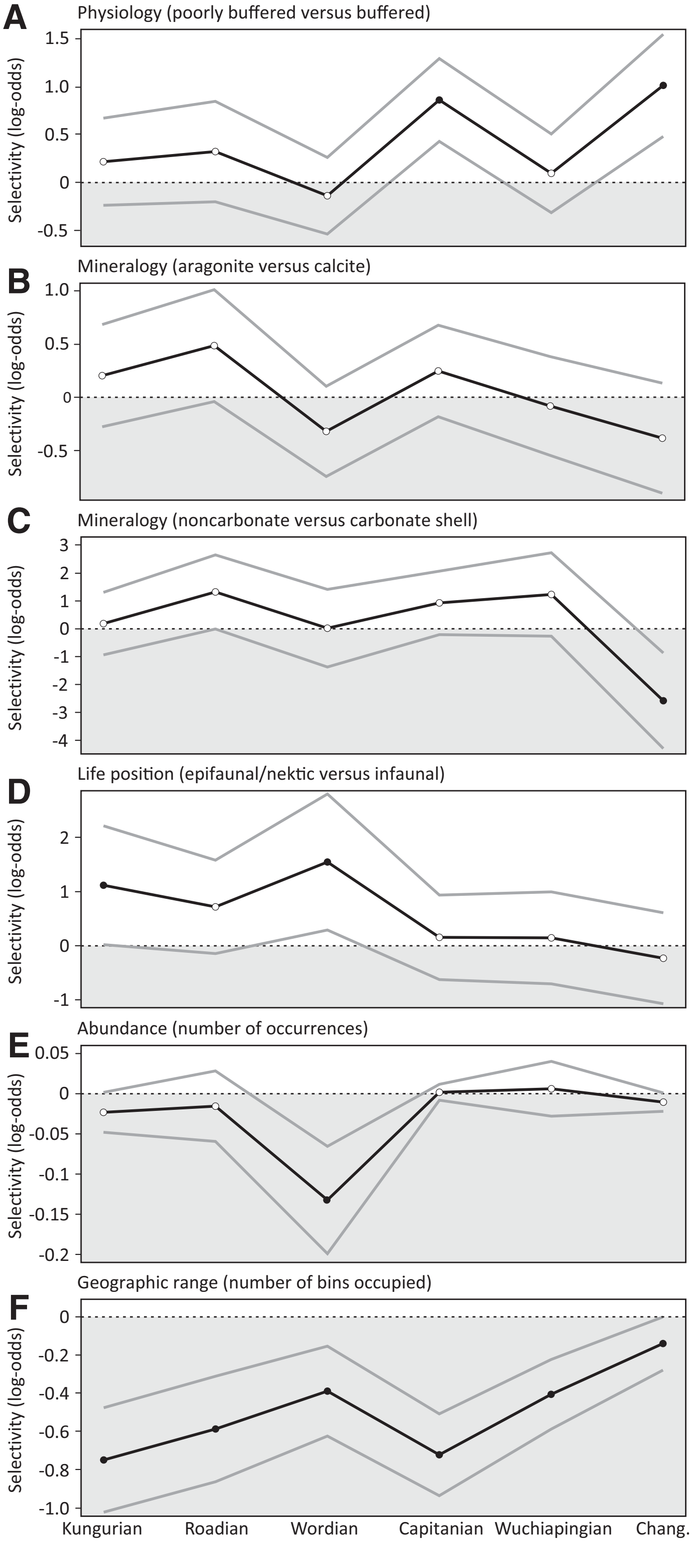

Figure 1. Kungurian–Changhsingian trends in biological and ecological selectivity of genus survivorship. In all plots, log-odds of zero indicate no association between the trait and survival; significant associations ($p < 0.05$) are indicated by solid symbols. Shaded gray areas indicate preferential survival of taxa with poorly buffered physiology (A), aragonite shell mineralogy (B), noncarbonate shell mineralogy (C), noninfaunal (epifaunal and nektic combined) life position (D), high abundance (E), and broad geographic range (F).

---

[1] GSA Data Repository item 2011310, Table DR1 (data matrix used in multiple logistic regression analyses), is available online at www.geosociety.org/pubs/ft2011.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

foraminifera in addition to marine invertebrates, whereas we used logistic regression, proportional extinction, included single-bin genera, and restricted analysis to invertebrate groups.

Preferential extinction of taxa with a poorly buffered physiology, independent of the influence of other ecological and mineralogical traits, implies that end-Permian extinction kill mechanisms were primarily physiological in nature. Several different physiological kill mechanisms are possible, including hypoxia (e.g., Wignall and Twitchett, 1996; Grice et al., 2005), hypercapnia, and/or reduced carbonate saturation (e.g., Knoll et al., 2007; Payne et al., 2010; Kiessling and Simpson, 2011). Because taxa with weakly buffered respiratory physiology are less adept at controlling intracellular pH and maintaining respiratory efficiency under elevated CO_2 levels, they are likely more susceptible at a population level to extinction from hypercapnia or ocean acidification (Knoll et al., 2007; Kiessling and Simpson, 2011). The importance of shell mineralogy, indicated by preferential survival of genera with noncarbonate skeletons independent of the preferential survival of genera with buffered physiology, further suggests that ocean acidification was a major stress. Although selectivity patterns are best interpreted to reflect physiological stresses related to CO_2 concentrations and ocean carbonate chemistry, hypoxia likely also contributed to the severity of end-Permian extinctions. The physiological effects of hypoxia and hypercapnia are not independent; instead, hypoxic stress interacts with stress from hypercapnia and high temperature to reduce respiratory efficiency and growth rates (Pörtner et al., 2005). As the effects are multiplicative, pre-existing widespread hypoxia may have been an important precondition for the end-Permian mass extinction, exacerbating the effects of volcanic CO_2 release and warming.

The Capitanian is the only studied stage other than the Changhsingian to include physiology as a significant predictor of survivorship, suggesting that the two crises may be rooted in similar environmental perturbations. The Capitanian extinction has been linked to a large flood basalt eruption, the Emeishan igneous province (Zhou et al., 2002; Wignall et al., 2009; Bond et al., 2010), and although shell mineralogy was not an important control on extinction in the Capitanian, the overall selectivity is consistent with physiological extinction stresses from Emeishan CO_2 release.

A physiological cause for the Guadalupian event also explains the variation in extinction intensity across protist and invertebrate groups. The extinction was extremely severe for larger fusulinid foraminifera (Stanley and Yang, 1994; Bond and Wignall, 2009) and reduced the number and volume of hypercalcified sponge reefs (Weidlich, 2002; Kiessling and Simpson, 2011), two groups with very minimal physiological control over respiration and calcification. In contrast, extinction rates were only minimally elevated among brachiopods, bivalves, and gastropods (Clapham et al., 2009). Although there was not a major invertebrate extinction, physiological stresses during the Guadalupian crisis can explain ecological changes such as species-level turnover and a shift in dominant brachiopod genera in South China (Shen and Zhang, 2008) and a shift toward greater molluscan abundance in shelf communities (Clapham and Bottjer, 2007).

The Guadalupian and end-Permian extinctions were two of multiple physiologically driven extinctions or reef crises in the fossil record, including end-Triassic, Toarcian, and Paleocene–Eocene (PETM) events (Kiessling and Simpson, 2011). These other crises, although much less severe than the end-Permian extinction, were also associated with large-magnitude perturbations to the carbon cycle likely caused by flood basalts (Courtillot, 1994; Wignall, 2001) or methane clathrate release (PETM; Zachos et al., 2008), suggesting similar stresses from warming, hypercapnia, and ocean acidification.

Given likely similarities in geological triggers, why was the end-Permian event more severe than those of other physiological crises? First, Permian oceans were likely more sensitive to acidification than their younger counterparts because the deep sea lacked a substantial reservoir of fine-grained biogenic carbonate sediment, the primary buffer today against acidification on timescales of thousands to tens of thousands of years (Archer, 2005). Consequently, rapid unbuffered release of CO_2 would have had larger effects on global ocean pH and calcium carbonate saturation state during the Permian than during the Jurassic to Holocene. Second, the global marine biota was also likely more sensitive to physiological stress at the end of the Permian than at other times. Permian marine ecosystems were dominated by members of the Paleozoic fauna (Sepkoski, 1981), primarily low-metabolism, physiologically unbuffered groups such as brachiopods, bryozoans, and crinoids. Those groups are rare today and have largely been replaced by molluscan clades with more buffered physiology (e.g., Bambach et al., 2002). Third, the comparative magnitudes of the major end-Permian and minor Guadalupian extinctions suggest a potential relationship with the magnitude of the environmental perturbation, as the Siberian Traps were also considerably larger than the Emeishan Basalts (Ali et al., 2005; Reichow et al., 2009). The relationship does not hold for other extinctions, however (Wignall, 2001), and is complicated by volatile release from magma–host rock interactions (e.g., Ganino and Arndt, 2009; Svensen et al., 2009). The confluence of multiple stressors (elevated CO_2, increased temperature, and widespread hypoxia) may also have contributed to the extreme severity of the end-Permian crisis given the synergistic physiological effects of those conditions.

CONCLUSIONS

Our results indicate that the end-Permian mass extinction was a physiologically selective crisis, favoring taxa with well-buffered physiology and noncarbonate shells, consistent with stresses from warming, elevated pCO_2, and anoxia resulting from Siberian Traps volcanism. Despite its much smaller magnitude, the Guadalupian extinction is the only other Permian stage to exhibit similar physiological selectivity. Physiological stresses from the smaller Emeishan flood basalts also explain the pronounced taxonomic differences of the Guadalupian crisis, affecting foraminifera and reef-builders far more severely than most other marine invertebrates. The end-Permian extinction may have been more severe than other Phanerozoic crises because of the lack of deep-sea carbonates, the prevalence of physiologically unbuffered clades, or the extreme magnitude of the environmental perturbation, but the confluence of multiple physiological stressors likely also played a major role.

The Guadalupian, end-Permian, and other physiological extinctions of the Phanerozoic contain lessons for the future of modern marine organisms faced with a warming world, ocean acidification, and spreading hypoxia. On the one hand, many extant marine invertebrates are less susceptible to the kinds of physiological stresses that were so catastrophic in the Permian, perhaps because the composition of marine ecosystems has been tempered by multiple physiological crises during the last 250 million years. On the other hand, the combination of warming, acidification, and hypoxia, as seen in the end-Permian extinction, exacerbates the physiological impact, even in groups with greater buffering capacity. Furthermore, the physiology of many ecologically important groups, such as reef-building corals, is minimally buffered, like their Paleozoic counterparts, and those groups will be at particular risk as anthropogenic stresses grow larger.

ACKNOWLEDGMENTS

We thank D.P.G. Bond and an anonymous reviewer for thoughtful comments, and S.C. Wang for discussions of statistical terminology. This is Paleobiology Database contribution 136.

REFERENCES CITED

Ali, J.R., Thompson, G.M., Zhou, M.F., and Song, X.Y., 2005, Emeishan large igneous province, SW China: Lithos, v. 79, p. 475–489, doi:10.1016/j.lithos.2004.09.013.

Archer, D., 2005, Fate of fossil fuel CO_2 in geologic time: Journal of Geophysical Research, v. 110, C09S05.

Bambach, R.K., Knoll, A.H., and Sepkoski, J.J., 2002, Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm:

Proceedings of the National Academy of Sciences of the United States of America, v. 99, p. 6854–6859, doi:10.1073/pnas.092150999.

Bond, D.P.G., and Wignall, P.B., 2009, Latitudinal selectivity of foraminifer extinctions during the late Guadalupian crisis: Paleobiology, v. 35, p. 465–483, doi:10.1666/0094-8373-35.4.465.

Bond, D.P.G., Wignall, P.B., Wang, W., Izon, G., Jiang, H.S., Lai, X.L., Sun, Y.D., Newton, R.J., Shao, L.Y., Védrine, S., and Cope, H., 2010, The mid-Capitanian (Middle Permian) mass extinction and carbon isotope record of South China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 292, p. 282–294, doi:10.1016/j.palaeo.2010.03.056.

Brewer, P.G., and Peltzer, E.T., 2009, Limits to marine life: Science, v. 324, p. 347–348, doi:10.1126/science.1170756.

Caldeira, K., and Wickett, M.E., 2003, Anthropogenic carbon and ocean pH: Nature, v. 425, p. 365, doi:10.1038/425365a.

Clapham, M.E., and Bottjer, D.J., 2007, Prolonged Permian–Triassic ecological crisis recorded by molluscan dominance in Late Permian offshore assemblages: Proceedings of the National Academy of Sciences of the United States of America, v. 104, p. 12,971–12,975, doi:10.1073/pnas.0705280104.

Clapham, M.E., Shen, S.Z., and Bottjer, D.J., 2009, The double mass extinction revisited: Reassessing the severity, selectivity, and causes of the end-Guadalupian biotic crisis (Late Permian): Paleobiology, v. 35, p. 32–50, doi:10.1666/08033.1.

Courtillot, V., 1994, Mass extinctions in the last 300 million years: One impact and seven flood basalts: Israel Journal of Earth Sciences, v. 43, p. 255–266.

Diaz, R.J., and Rosenberg, R., 2008, Spreading dead zones and consequences for marine ecosystems: Science, v. 321, p. 926–929, doi:10.1126/science.1156401.

Ganino, C., and Arndt, N.T., 2009, Climate changes caused by degassing of sediments during the emplacement of large igneous provinces: Geology, v. 37, p. 323–326, doi:10.1130/G25325A.1.

Gould, S.J., and Calloway, C.B., 1980, Clams and brachiopods—Ships that pass in the night: Paleobiology, v. 6, p. 383–396.

Grice, K., Cao, C.Q., Love, G.D., Böttcher, M.E., Twitchett, R.J., Grosjean, E., Summons, R.E., Turgeon, S.C., Dunning, W., and Jin, Y.G., 2005, Photic zone euxinia during the Permian–Triassic superanoxic event: Science, v. 307, p. 706–709, doi:10.1126/science.1104323.

Kiessling, W., and Simpson, C., 2011, On the potential for ocean acidification to be a general cause of ancient reef crises: Global Change Biology, v. 17, p. 56–67.

Knoll, A.H., Bambach, R.K., Canfield, D.E., and Grotzinger, J.P., 1996, Comparative Earth history and Late Permian mass extinction: Science, v. 273, p. 452–457, doi:10.1126/science.273.5274.452.

Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S., and Fischer, W.W., 2007, Paleophysiology and end-Permian mass extinction: Earth and Planetary Science Letters, v. 256, p. 295–313, doi:10.1016/j.epsl.2007.02.018.

Kroeker, K.J., Kordas, R.L., Crim, R.N., and Singh, G.G., 2010, Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms: Ecology Letters, v. 13, p. 1419–1434.

Payne, J.L., and Finnegan, S., 2007, The effect of geographic range on extinction during background and mass extinction: Proceedings of the National Academy of Sciences of the United States of America, v. 104, p. 10,506–10,511.

Payne, J.L., Turchyn, A.V., Paytan, A., DePaolo, D.J., Lehrmann, D.J., Yu, M.Y., and Wei, J.Y., 2010, Calcium isotope constraints on the end-Permian mass extinction: Proceedings of the National Academy of Sciences of the United States of America, v. 107, p. 8543–8548.

Pörtner, H.O., Langenbuch, M., and Michaelidis, B., 2005, Synergistic effects of temperature extremes, hypoxia, and increases in CO_2 on marine animals: From Earth history to global change: Journal of Geophysical Research, v. 110, C09S10, doi:10.1029/2004JC002561.

Raup, D.M., and Sepkoski, J.J., 1982, Mass extinctions in the marine fossil record: Science, v. 215, p. 1501–1503, doi:10.1126/science.215.4539.1501.

Reichow, M.K., Pringle, M.S., Al'Mukhamedov, A.I., Allen, M.B., Andreichev, V.L., Buslov, M.M., Davies, C.E., Fedoseev, G.S., Fitton, J.G., Inger, S., Medvedev, A.Ya., Mitchell, C., Puchkov, V.N., Safonova, I.Yu., Scott, R.A., and Saunders, A.D., 2009, The timing and extent of the eruption of the Siberian Traps large igneous province: Implications for the end-Permian environmental crisis: Earth and Planetary Science Letters, v. 277, p. 9–20, doi:10.1016/j.epsl.2008.09.030.

Sepkoski, J.J., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36–53.

Shen, S.Z., and Zhang, Y.C., 2008, Earliest Wuchiapingian (Lopingian, Late Permian) brachiopods in southern Hunan, South China: Implications for pre-Lopingian crisis and onset of Lopingian recovery/radiation: Journal of Paleontology, v. 82, p. 924–937, doi:10.1666/07-118.1.

Stanley, S.M., and Yang, X., 1994, A double mass extinction at the end of the Paleozoic era: Science, v. 266, p. 1340–1344, doi:10.1126/science.266.5189.1340.

Svensen, H., Planke, S., Polozov, A.G., Schmidbauer, N., Corfu, F., Podladchikov, Yu., Y., and Jamtveit, B., 2009, Siberian gas venting and the end-Permian environmental crisis: Earth and Planetary Science Letters, v. 277, p. 490–500.

Wagner, P.J., Kosnik, M.A., and Lidgard, S., 2006, Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems: Science, v. 314, p. 1289–1292, doi:10.1126/science.1133795.

Weidlich, O., 2002, Permian reefs re-examined: Extrinsic control mechanisms of gradual and abrupt changes during 40 my of reef evolution: Geobios, v. 35, Supplement 1, p. 287–294, doi:10.1016/S0016-6995(02)00066-9.

Widdicombe, S., and Spicer, J.I., 2008, Predicting the impact of ocean acidification on benthic biodiversity: What can animal physiology tell us?: Journal of Experimental Marine Biology and Ecology, v. 366, p. 187–197, doi:10.1016/j.jembe.2008.07.024.

Wignall, P.B., 2001, Large igneous provinces and mass extinctions: Earth-Science Reviews, v. 53, p. 1–33, doi:10.1016/S0012-8252(00)00037-4.

Wignall, P.B., and Twitchett, R.J., 1996, Ocean anoxia and the end Permian mass extinction: Science, v. 272, p. 1155–1158, doi:10.1126/science.272.5265.1155.

Wignall, P.B., Sun, Y.D., Bond, D.P.G., Izon, G., Newton, R.J., Védrine, S., Widdowson, M., Ali, J.R., Lai, X.L., Jiang, H.S., Cope, H., and Bottrell, S.H., 2009, Volcanism, mass extinction, and carbon isotope fluctuations in the Middle Permian of China: Science, v. 324, p. 1179–1182, doi:10.1126/science.1171956.

Zachos, J.C., Dickens, G.R., and Zeebe, R.E., 2008, An early Cenozoic perspective on greenhouse warming and carbon cycle dynamics: Nature, v. 451, p. 279–283, doi:10.1038/nature06588.

Zhou, M.F., Malpas, J., Song, X.Y., Robinson, P.T., Sun, M., Kennedy, A.K., Lesher, C.M., and Keays, R.R., 2002, A temporal link between the Emeishan large igneous province (SW China) and the end-Guadalupian mass extinction: Earth and Planetary Science Letters, v. 196, p. 113–122.

Manuscript received 6 March 2011
Revised manuscript received 13 June 2011
Manuscript accepted 21 June 2011

Printed in USA