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Anoxia/high temperature double whammy during the Permian-Triassic marine crisis and its aftermath

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The Permian-Triassic mass extinction was the most severe biotic crisis in the past 500 million years. Many hypotheses have been proposed to explain the crisis, but few account for the spectrum of extinction selectivity and subsequent recovery. Here we show that selective losses are best accounted for by a combination of lethally warm, shallow waters and anoxic deep waters that acted to severely restrict the habitable area to a narrow mid-water refuge zone. The relative tolerance of groups to this double whammy provides the first clear explanation for the selective extinction losses during this double-pulsed crisis and also the fitful recovery. Thus, high temperature intolerant shallow-water dwellers, such as corals, large foraminifers and radiolarians were eliminated first whilst high temperature tolerant ostracods thrived except in anoxic deeper-waters. In contrast, hypoxia tolerant but temperature intolerant small foraminifers were driven from shallow-waters but thrived on dysoxic slopes margins. Only those mollusc groups, which are tolerant of both hypoxia and high temperatures, were able to thrive in the immediate aftermath of the extinction. Limited Early Triassic benthic recovery was restricted to mid-water depths and coincided with intervals of cooling and deepening of water column anoxia that expanded the habitable mid-water refuge zone.

The impact of rising ocean temperature and declining oxygen concentration is of major concern for 21st century marine life[1,2]. Recent analyses reveal that such trends were operational in marine environments during the greatest of all biotic disasters: the mass extinction straddling the Permian-Triassic boundary (PTB) 252 million years ago[3–5]. Both the nature of global palaeogeography (a single Pangeana supercontinent) and biota (e.g. no pelagic carbonate production) were fundamentally different to today, negating any direct analogue potential but the dramatic scale of temperature rise and spread of marine anoxia 252 Myrs ago illustrates an extreme development of these environmental factors and their consequences[3–5]. The Permian-Triassic mass extinction wiped out over 90% of marine species[6], leaving a depauperate ocean and protracted recovery process[3,7,8]. Many hypotheses have been proposed to explain this extinction, but they do not explain the spectrum of extinction selectivity and subsequent fitful recovery. Here we show that the known effects of rising ocean temperature and declining oxygen concentration on modern marine groups best explains the major but selective extinction losses during the PTB crisis.

Hypoxia is encountered in the oxygen minimum zone (OMZ) of modern oceans and occurs perennially in anoxic basins such as the Black Sea and Cariaco Basin. Consequently, many laboratory experiments and oceanographic surveys have studied the biological responses to hypoxia (ref. 9, Table S1). Hypoxia changes the behaviour, feeding rate and growth of organisms, affects species interactions including predation, leads to mortality and decreased biomass and diversity[10,11]. Temperature also has a key influence on marine organisms and its biological effects are complex and wide-ranging[12]. Experiments show that elevated temperature can affect the development, growth, and settlement of biota, and lead to mortality when it reaches upper thermal limits, which vary amongst groups (Table S2). Here, we take experimental studies and physical, chemical, and biological records in modern oceans and use them as a standpoint to evaluate the causation of the Permian-Triassic event.

Results

Experimental studies show that marine organisms are adversely affected by dissolved oxygen concentration below 10% of air saturation and they die below 4% (Fig. 1a). Hypoxia tolerance varies considerably among phyla and
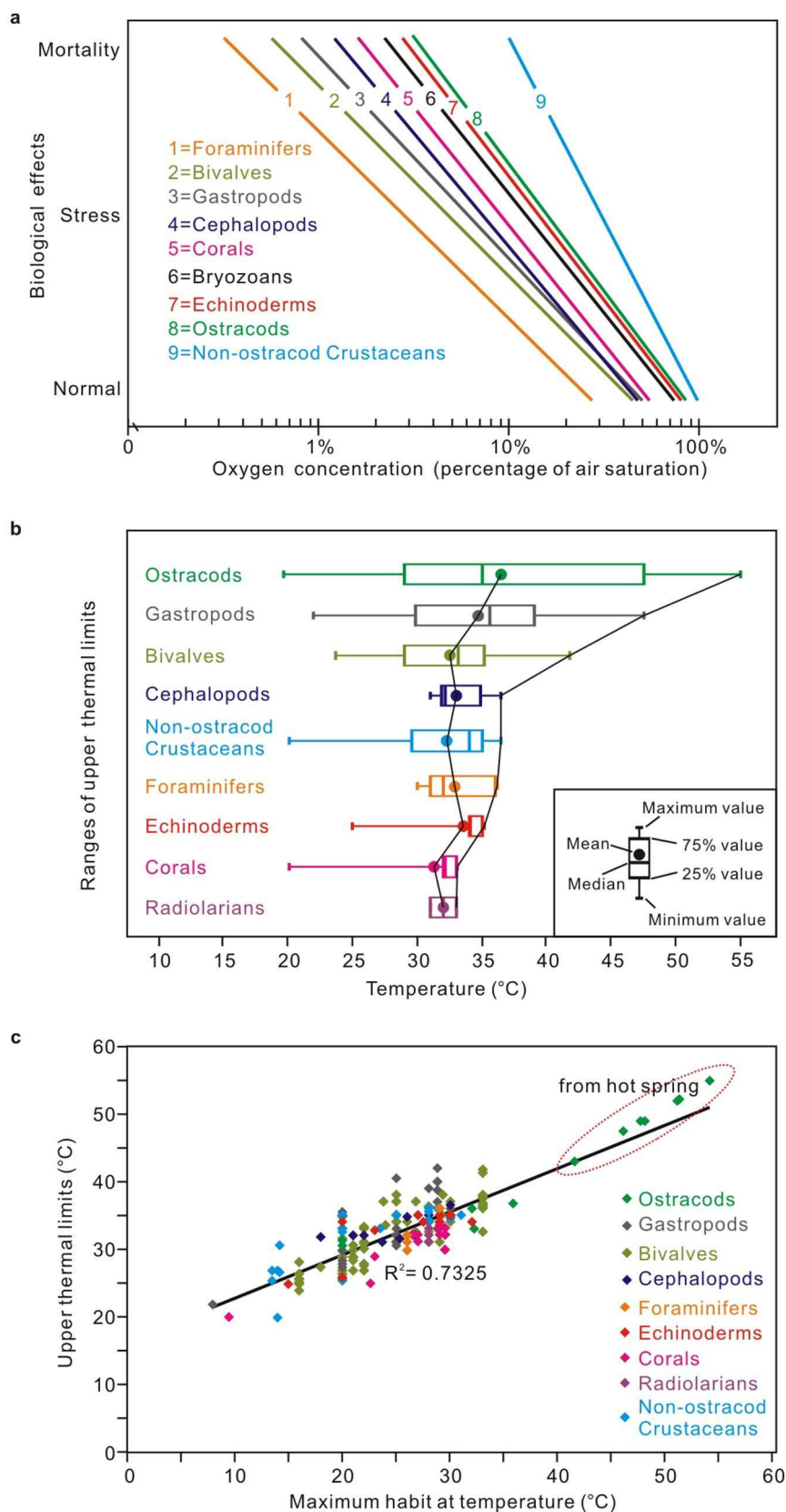
Figure 1 | Biological effects of decreased oxygen concentration and increased temperature. (a), Generally, crustaceans are more sensitive to reduced oxygen concentrations than bryozoans and echinoderms, followed by corals. Foraminifers and molluscs are the most tolerant. (b), Upper thermal limits are higher in ostracods and bivalves than in foraminifers, echinoderms, gastropods and non-ostracod crustacean, and are lowest in corals and radiolarians. (c), The relationship between the upper lethal thermal limits and the maximum habitat temperature of selected animals shows a latitudinal relationship, with warm-adapted forms the most tolerant. Relationships and ranges data are given in Tables S1–S3.
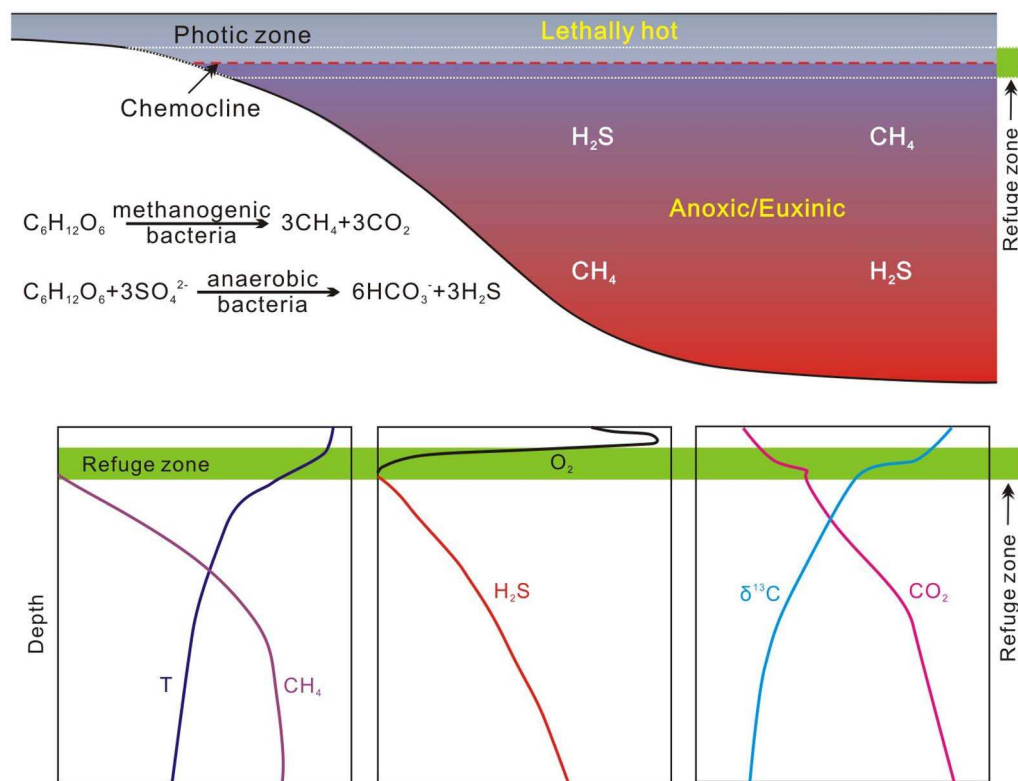
Figure 2 | PTB mass extinction dead water model showing the only refuge zone for the crisis lay in a narrow refuge zone of intermediate water depths. The chemocline separated anoxic and sulfidic deep waters from oxygenated surface waters and could move up and down during the Permian-Triassic interval[14], causing the refuge zone to shift vertically following the chemocline. Bulk parameters in the water column are based on modern Black Sea[15,16].

orders and even between species of the same order but nonetheless there are clear differences in hypoxia tolerance amongst higher taxa allowing a ranked order of relative susceptibility to be determined (Fig. 1). In overall order of intolerance to hypoxia, generally crustaceans (including ostracods) are more sensitive than bryozoans, echinoderms and corals whilst molluscs (i.e. cephalopods, gastropods and bivalves) are more tolerant and foraminifers are the most resilient of all (Table S1 and Fig. 1a).

High temperature tolerance also varies greatly among different types of organisms. Specifically, the upper thermal limits of corals and radiolarians is especially low, about 33°C compared to that of echinoderms, foraminifers, cephalopods and non-ostracod crustaceans (35°C) whereas ostracods, gastropods and bivalves are the most thermally tolerant groups: some can even survive temperatures > 40°C (Fig. 1b). In addition, biota living at higher temperatures have higher upper thermal limits (Fig. 1c). This suggests that global warming will impact animals inhabiting all latitudes. Only if tropical forms have sufficient time and a migration route to higher latitudes will they be able to avoid the effect of higher temperatures whilst polar forms will be especially vulnerable to temperature increase because their preferred temperature zone will be lost.

Both anoxia and high temperature can significantly impact marine ecosystems and they often act in lethal synergy because oxygen requirements increase with temperature[13]. However, the effects of these two variables vary within marine ecosystems allowing the role of each to be evaluated. Generally, seawater temperature declines with increasing water depth and thus the most severe temperatures are experienced in the shallowest waters. In contrast, anoxia develops in the mid-water column or the deepest waters of restricted seas and is unlikely to have a direct or prolonged affect in surface water because of the rapid exchange of oxygen with the atmosphere. The double whammy of anoxia and lethal temperatures, proposed for the PTB mass extinction, therefore predict there will be a potential refuge zone at intermediate water depths (Fig. 2).

Discussion

Extinction selectivity provides a powerful test for the underlying causes of extinction events[17] and, armed with our model (Fig. 2), we evaluate the fates of the marine biota during the PTB crisis in South China, which provides by far the best knowledge of the fortunes of the marine biota during this crisis. Recent study of numerous sections in South China has revealed a two-pulse crisis, 200 kyr apart, straddling the PTB that shows distinctive selectivity[18]. The first pulse, the long-recognised latest Permian extinction (LPE) coincides with a rapid temperature increase seen in the South China record[5] and a brief pulse of anoxia in deeper water sites of Tethys (whilst more prolonged dysoxia begins at this time in more northerly, Boreal latitudes)[19,20]. The second pulse, an earliest Triassic extinction (ETE), coincides with a continued warming trend and the global spread of oxygen-poor waters[3,21,22].

The LPE is characterised by high extinction rates of corals, calcareous algae, fusulinids, sponges, radiolarians and echinoderms whilst molluscs, conodonts, ostracods and small foraminifers and most fish show much lower extinction magnitudes[18,23,24]. This crisis was clearly devastating for inhabitants of shallow-water and planktonic (radiolarian) communities. Ostracods and foraminifers were diverse and widespread across a spectrum of water depths prior to the LPE and their relative fortunes at this time are especially informative. Deep-water ostracods were eliminated in the crisis whilst their shallow-water relatives fared much better[18]. In contrast, both shallow-water and deep-water foraminifers were wiped out in the LPE whilst examples from mid-water depths continued to thrive[18]. Ostracods are the most high temperature-tolerant of all modern marine invertebrates (Fig. 1b). We suggest that this tolerance was also present in the latest Permian and it allowed them to thrive in hot, shallow-waters that were lethal to the temperature-sensitive groups like radiolarians, calcareous algae and corals. However, ostracods are especially intolerant of hypoxia, which explains their disappearance from deeper water locations during the LPE. In contrast, foraminifers
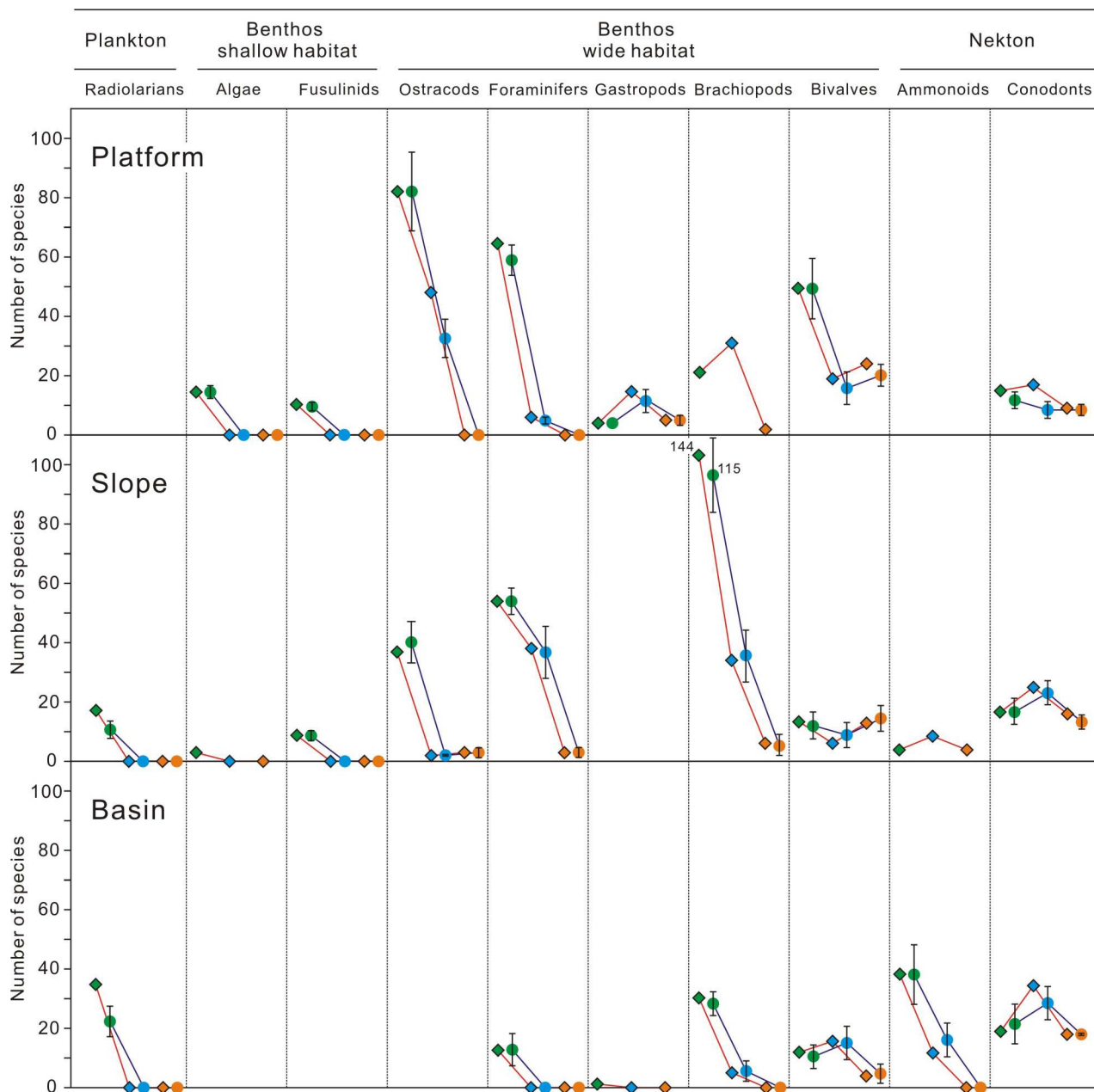
Figure 3 | Biodiversity curves in the platform, slope, and basin habitats near the PTB in South China. Diamonds show raw data whereas circles show subsampling data corrected for variation in sampling intensity by using UW method[25]. Plankton and benthos only found in shallow-water habitats completely disappeared during the latest Permian extinction, whereas nekton and eurytopic benthos underwent two pulses of extinction. Water-depth data and biotic data see Table S4. Diamond = raw species richness data and circle with bar = subsampling data with 95% confidence intervals. Green colour = data from pre-latest Permian extinction, blue colour = data from middle interval, and orange colour = data from post-earliest Triassic extinction.

are the most hypoxia-tolerant group and so were able to thrive at intermediate water depths at this time (but not in the truly anoxic conditions of deeper waters). The relative success of most fish groups could be attributable to their upper water column life site above the anoxic deeper waters.

The interval between the two extinction pulses was characterised by unusual marine communities that lacked shallow-water specialists and diverse radiolarians in low latitudes (Fig. 3), although this planktonic group remained diverse and abundant in higher latitude, cooler southern oceans[26]. Nonetheless benthic communities diversified at this time in South China, notably amongst groups tolerant of high temperatures (ostracods, gastropods and bivalves). The second pulse of extinction – the ETE – brought this radiation to an end. The

wide spread of anoxic facies at this time was enough to cause the demise of the high-temperature (but not hypoxia) tolerant ostracods. Only species tolerant of both high temperature and hypoxia, namely bivalves and gastropods (Fig. 1), were able to thrive in large numbers (but not high diversity) in the aftermath of this second extinction event (Fig. 3).

The refuge zone concept has great utility in explaining trends in the South China data. Unfortunately no other regions are known in such detail but comparisons can still be attempted. The high southern latitude peri-Gondwana region (South Tibet, Pakistan and Kashmir) provide highly fossiliferous, shallow-water PTB sections[27] but the paucity of deep-water sections makes it difficult to evaluate preferential survival relative to depth preference. Nonetheless there is
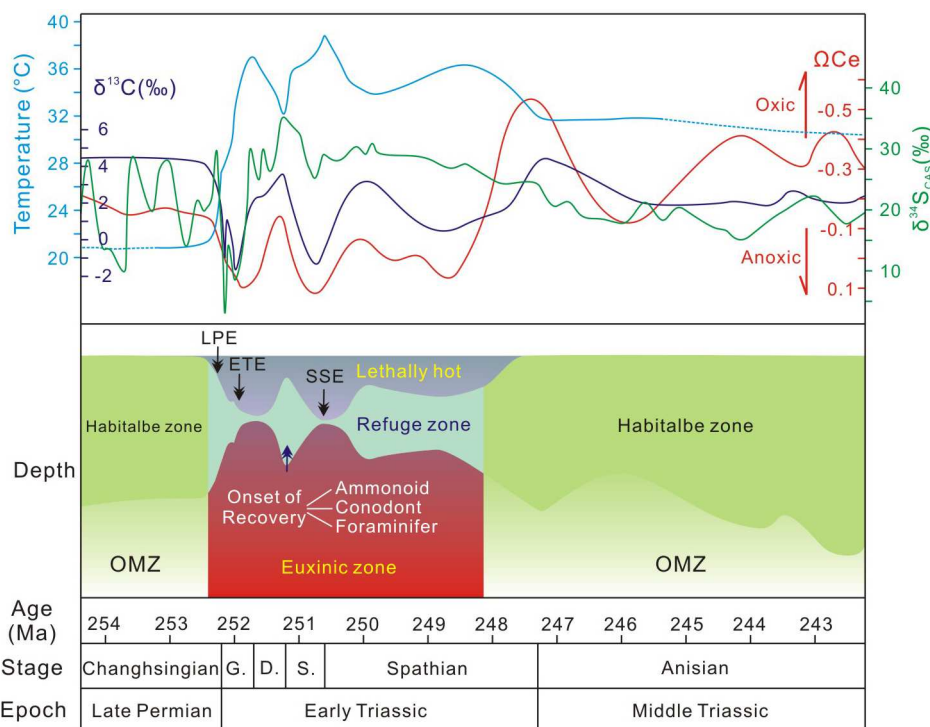
Figure 4 | The evolution of the mid-water refuge zone during the Early Triassic. Carbon isotope data[3,7,29], sulfur isotope data[30,31], temperature data[3,5], and conodont ΩCe data showing redox conditions[22] are all from South China. Environmental data in the Changhsingian and PTB strata are from Meishan section whereas those in the Lower and Middle Triassic are from Nanpanjiang Basin. Age data are from Figure S1. Abbreviation: G. = Griesbachian, D. = Dienerian, S. = Smithian, OMZ = oxygen minimum zone, LPE = latest Permian extinction, ETE = earliest Triassic extinction, and SSE = Smithian-Spathian extinction.

compelling evidence that the refuge zone concept is applicable. Immediately prior to the LPE the diverse benthic faunas of peri-Gondwana consist of brachiopods, bryozoans, corals and echinoderms (especially crinoids) whilst in the immediate aftermath the fauna is dominated by bivalves, ammonoids, ostracods, foraminifers, and a modest diversity of brachiopod survivors[28]. With the exception of the molluscs, all these taxa disappear in the earliest Triassic, contemporaneous with the ETE of South China. The eradication of corals and bryozoans (but not ostracods) during the LPE suggests a role for high temperatures in the shallow-waters of peri-Gondwana. This notion is supported by the observation that numerous warm-water taxa including brachiopods and calcareous sponges, foraminifers and brachiopods migrate into the region at this time[28]. The succeeding ETE occurred during a phase of rapid transgression and the loss of all but the mollusc groups suggests a role for deeper-water anoxia in the second kill phase.

The refuge zone concept can also be used to evaluate the subsequent Early Triassic radiation and recovery. The evolution of this zone is based on seawater temperature, redox proxy data, carbon and sulphur isotope data (Fig. 4), which reveals that, as well as the two phases of shrinkage on either side of the PTB there was also a contraction around the Smithian-Spathian boundary during a peak of warmth (Fig. 4). As with the earlier phases, the Smithian-Spathian refuge zone contraction also coincides with an extinction event[32]. The refuge zone expanded during the Dienerian-Smithian boundary during a cooling trend (Fig. 4) that coincided with evidence for recovery in several groups, e.g. conodonts[33], ammonoids[33,34] and foraminifers[35]. This is interpreted here to reflect radiation into expanding habitats. That the radiation is best seen in deeper waters[35] further suggests the recovery was driven more by the retreat of anoxic waters into deeper depths rather than the opening up of shallow waters by cooling.

Physiological selectivity of marine extinctions is one of the most powerful tools available to assess causes of mass extinctions and this

approach has also been used to argue for hypercapnia (CO_2 poisoning) and acidification kill mechanisms for the PTB mass extinction[17,23]. Both these factors could act synergistically with hypoxia and temperature stresses because all are driven by elevated atmospheric CO_2 levels[13]. Regarding acidification, the preferential loss of heavily calcified and therefore supposedly poorly buffered taxa (e.g. corals, sponges, brachiopods, bryozoans and crinoids) is held as evidence for this extinction mechanism[17,23]. However, this analysis fails to account for other losses. These were extremely heavy amongst the cephalopod ammonoids[33]; a supposedly well-buffered group and silicified taxa should be relatively unaffected by acidification compared with heavily calcified forms. Indeed, Clapham and Payne state that "taxa with siliceous skeletons were significantly more likely to survive the end-Permian extinction" if it was caused by acidification[17]. This is a curious statement because Late Permian siliceous taxa (radiolarians, sponges) suffered severe losses at this time, the most severe crisis in their history, and it lead to the well-known "chert gap" of the Early Triassic[36]. Probably the most compelling evidence for acidification comes from the losses of corals, calcareous algae and echinoderms – all groups that are susceptible to lowered pH – but their losses can also be attributed to elevated temperatures and they are just a few of many groups to suffer severe extinction.

Hypercapnia-resistance should be best seen amongst infaunal taxa, because such conditions are regularly encountered in taxa that burrow within the sediment[13]. Thus Knoll and colleagues have argued that burrowers such as polychaetes worms and holothurians show 0% extinction during the PTB crisis[23]. However, we contend that the fossil record of both these groups during this crisis is too poorly known to draw such conclusions. The bivalves have both infaunal and epifaunal representatives and Clapham and Payne's study finds that infaunal forms were especially vulnerable to extinction[17] – the opposite pattern to that predicted for hypercapnic extinction. The loss of all large burrow types during the mass extinction[37] further argues against a role for hypercapnia in the crisis.

In summary, we consider that the concept of a refuge zone, sandwiched between lethally hot surface waters and poisonously anoxic deep waters, best explains the course of the PTB mass extinction and the style of (partial) recovery in the ensuing Early Triassic as seen in the well-known record of South China. A detailed analysis of other regions is yet to be undertaken but it appears extinctions in the southern hemisphere also accord with this extinction style. However, we note that the onset of prolonged, intense anoxia in latest Permian Boreal latitudes[19,20,38] may have made the "first strike" proportionally more devastating than seen in equatorial Tethys.

Methods

We searched the literature for reports of hypoxia and high temperature on Google Scholar and Web of Science using the keywords "hypoxia", "temperature", "marine", "tolerance" and the names of biotic groups that occurred in the Permian-Triassic oceans such as bivalves, gastropods, foraminifers, etc. to guide the search. This search got more than 10,000 published papers of responses of marine organisms to hypoxia and temperature, which were then examined further for the availability of experimental assessments. In total 141 papers reported the oxygen and upper temperature thresholds for marine invertebrates (Tables S1–S3).

The outcome of oxygen thresholds (Fig. 1a) was summarized using comparative experiments among biotic groups and indicators such as survival, growth, feeding, metabolism, and migration observed in the experiments and oceanographic survey (Table S1). The outcome of temperature threshold analyses (Fig. 1b, c) was summarized using the following indicators of upper thermal limits, e.g. ULT_{100} and ULT_{50}, representing the statistically-derived temperature at which 100% or 50% of organisms in a given population die, respectively, and Max HT, representing the maximum habitat temperature of selected organisms. The ranges of upper thermal limits for aquatic organisms were presented in maximum, minimum, mean, median, 75% and 25% values.

Two subsampling methods, i.e. lists unweighted (UW)[25] and lists occurrences weighted (OW)[39,40], were employed for the fossil data near the PTB. The UW method obtains its quota based on the number of combined fossil collections whereas the OW method derives its quota on the number of species occurrences. Standardization methods interpolate biodiversity levels by repeatedly subsampling sets of combined fossil collections or separated taxonomic occurrences. Thus, subsampling biodiversity curves are defined by choosing a fixed sampling quota and then counting the number of species in each temporal interval at this sampling level. Most of fossil groups had rather low species richness in the post-ETE interval, and some groups also had low species richness in the middle interval between LPE and ETE. So, the OW method was not suitable for these temporal intervals. Here, the UW method was applied for most fossil data and OW method was used for some fossil groups that have a relatively high diversity in each temporal interval (Figs. S2–S4).

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Author contributions

Ha.S. and P.B.W. conceived the study. J.T., Y.S., Hu.S. and W.H. participated in data preparation. D.C. and L.T. analyzed and interpreted the data. All the authors discussed the results and contributed to the manuscript.

Additional information