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Influence of dissolved oxygen on secular patterns of marine microbial carbonate abundance during the past 490 Myr

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ABSTRACT

Shallow marine benthic microbial carbonate sediments declined episodically during the Phanerozoic. They were relatively abundant during the Cambrian/mid-Ordovician, late Devonian/Mississippian, mid-Permian/mid-late Triassic, and to a lesser degree in the late Jurassic/early Cretaceous. They were least abundant when invertebrate, especially reef, diversity was relatively high in the mid-Ordovician/late Devonian, early-mid Permian, late Triassic, mid-late Jurassic, and early Cretaceous to present-day. These intervals of microbial carbonate abundance and invertebrate diversity generally alternate transitionally with one-another; but 'lows' and periods of overlap also occur. 'Lows', when benthic microbial carbonate abundance and invertebrate diversity both declined, are apparent during the Pennsylvanian and early-mid Jurassic. Overlaps, when microbial carbonates and invertebrates were both relatively common, occur in the early Cambrian and late Jurassic. Overall, these patterns broadly support suggestions that microbial carbonate abundance declined as calcified invertebrates increased. To further explore these relationships, we compared microbial carbonate abundance and invertebrate diversity with estimates of changes in sea-surface temperature and marine dissolved oxygen for the past 490 Myr. This analysis suggests that invertebrate diversity varied directly with oxygen availability. Invertebrate diversity was low when dissolved oxygen was low in the early Ordovician, late Devonian, early Triassic, and early-mid Jurassic. It appears that, by reducing invertebrate diversity, low oxygen levels favored microbial carbonates. At the same time, low oxygen levels likely stimulated anaerobic metabolisms favoring carbonate precipitation. This study suggests that dissolved oxygen was a major control on secular patterns of marine microbial carbonate abundance during the Phanerozoic, together with marine temperature and carbonate saturation state.

1. Introduction

Benthic microbial carbonates form by the calcification of bacterial-algal mats and biofilms (Burne and Moore, 1987; Dupraz et al., 2009) and have been common components of marine limestones and dolostones since the Archean (Peters et al., 2017). Their development was significantly affected by changes in marine life and environments during the Phanerozoic (the past 541 Myr). Microbial carbonates remained abundant and widespread in shallow seas during the Cambrian but subsequently declined and have been relatively scarce for the past 100 Myr (Fischer, 1965; Garrett, 1970). This decline was not linear; peaks of microbial carbonate abundance (~500, ~370, ~250, and ~150 Ma; Kiessling, 2002) alternate with intervals of increased invertebrate diversity and successively decrease in magnitude (Riding, 2005). The Phanerozoic decline of microbial carbonates is thought to mainly reflect the combined effects of reduced seawater carbonate saturation and increased invertebrate competition (Fischer, 1965; Garrett, 1970; Webb, 1996; Riding, 2005; Riding and Liang, 2005a; Yao et al., 2016). Seawater carbonate saturation state is mainly governed by calcium and carbonate ion activity (Plummer and Sundquist, 1982), but the factors that drive long-term changes in invertebrate abundance and diversity are more debatable. To further elucidate long-term controls on microbial carbonates, and particularly their relationships with invertebrates, we compared estimates of sea-surface temperature (SST) and dissolved oxygen in tropical seawater, with microbial carbonate abundance and benthic invertebrate diversity (as a proxy for competition) from the late Cambrian (~490 Ma) to the present-day (see Methods, below). This approach was stimulated by research that has

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linked the transition from microbial carbonate to skeletal carbonates during the early–mid Ordovician to changes in temperature and oxygenation (Berry and Wilde, 1978; Webby, 2002; Servais et al., 2008, 2010, 2016; Trotter et al., 2008; Saltzman et al., 2011; Kah et al., 2016; Rasmussen et al., 2016; Young et al., 2016; Edwards et al., 2017; Lee and Riding, 2018). A strong reciprocal relationship between oxygen and life (Nursall, 1959; Berkner and Marshall, 1964; Cloud, 1968; Holland, 1994; Berner et al., 2007; Knoll, 2014) has profoundly influenced the diversity of both invertebrates (Childress and Seibel, 1998; Levin, 2003; Seibel, 2011; Verberk et al., 2011; Ferguson et al., 2013; Wood and Erwin, 2018) and vertebrates (Berner et al., 2007). The rise of eukaryotes, particularly invertebrates, has been attributed to marine oxygenation (Nursall, 1959; Sperling et al., 2013; Knoll, 2014; Reinhard et al., 2016). Oxygen levels are thought to have risen significantly in the Neoproterozoic, ~800 Ma (Och and Shields-Zhou, 2012; Lenton et al., 2014; Lyons et al., 2014), but then more slowly during the early Paleozoic (Dahl et al., 2010; Lenton et al., 2016). Elevated ('greenhouse effect') temperatures during the mid-late Cambrian (Fischer, 1984; McKenzie et al., 2014) resulted in low levels of dissolved oxygen in seawater, and marine oxygenation probably did not recover until the mid-Ordovician (Edwards et al., 2017; Lee and Riding, 2018). Oxygen levels at or above those of the Cenozoic probably did not occur until the Silurian (Royer et al., 2014, their Fig. 2b) or Devonian (Wallace et al., 2017), and remained subject to periods of significant reduction until the Early Cretaceous (Berner, 2009; Lu et al., 2018).

Our comparisons indicate that during the past 490 Myr, invertebrate diversity was highest when dissolved oxygen levels were relatively high, whereas microbial carbonates were most abundant when dissolved oxygen levels were low, so long as carbonate saturation state was high. It appears that microbial carbonate abundance declined as invertebrate diversity increased with dissolved oxygen. In addition to competition for space, it is likely that invertebrate skeleton formation also reduced the $CaCO_3$ available for microbial carbonates. Our comparisons further suggest that intervals of microbial and invertebrate carbonate abundance over the past 490 Mya have not simply alternated between one another. In addition to *transitions* between intervals of microbial carbonate and invertebrate abundance, there are examples of *overlap* and also extended 'lows'. 'Lows', when microbial carbonate abundance and invertebrate diversity were both reduced, 323–299 and 201–170 Ma, may at least in part be due to lower temperatures. Examples of *overlap*, when invertebrates and microbial carbonates were both relatively abundant, occur ~525–510 and 164–152 Ma.

These long-term patterns suggest that invertebrates interacted competitively with microbial carbonates at several levels, and also responded to different physicochemical influences. Whereas oxygen promoted marine invertebrate diversity, microbial carbonate abundance increased when oxygen was low. In addition to reducing invertebrate diversity, low oxygen could have favored microbial carbonate formation by promoting anaerobic metabolisms. A further effect involves increased temperature, which tends to both raise carbonate saturation and decrease the level of dissolved oxygen. Thus, elevated temperature (e.g., in the late Cambrian and during the Permian–Triassic transition) would be expected to have inherently favored microbial carbonate formation, in addition to reducing invertebrate diversity.

We therefore propose that Phanerozoic patterns of microbial carbonate abundance and invertebrate diversity largely reflect the interplay of physicochemical factors. Microbial carbonate formation has tended to increase with carbonate saturation state, whereas invertebrate diversity has increased with the level of dissolved oxygen level. These results help to clarify the factors underlying the distinctive fluctuating pattern of abundance of microbial and invertebrate shallow marine carbonate sediments since the Cambrian. By influencing invertebrate diversity, dissolved oxygen has significantly influenced the abundance of marine microbial carbonates throughout the Phanerozoic.

2. Methods

We examined relationships among dissolved oxygen, sea-surface temperature, invertebrate genus richness (as a rough proxy for abundance/competition) and microbial carbonate abundance, over the past 490 Myr.

2.1. Microbial carbonate abundance

Stromatolite decline, measured by reduction in number of form taxa during the Neoproterozoic (Awramik, 1971) and reduction in overall abundance since the early Ordovician (Cloud and Semikhatov, 1969), has been linked to increased eukaryote competition and reduced calcification (Fischer, 1965, pp. 1208–1209). In addition to stromatolites (Peters et al., 2017, their Fig. 2), calcified cyanobacteria (Riding, 1992; Arp et al., 2001), reefal microbial carbonates (Kiessling, 2002, their Fig. 16) and microbialites in general (Myshrall et al., 2014, their Fig. 6.2) together, all exhibit a markedly episodic non-linear pattern of decline over the past 500 Myr. Microbial carbonates are locally abundant in the Silurian (e.g., Soja and Riding, 1993; Sheehan and Harris, 2004; Peters et al., 2017, their Fig. 2) and early Devonian (e.g., Matysik et al., 2015), with a minor peak ~420–410 Ma (Kiessling, 2002, his Fig. 16). However, the main peaks of microbial carbonate (MC) abundance (Kiessling, 2002, his Fig. 16; see Riding, 2005, 2006) recognized here are MC1: Cambrian/mid-Ordovician (541–465 Ma), MC2: latest Devonian/Mississippian (372–323 Ma), MC3: mid-Permian to mid-late Triassic (265–227 Ma) and MC4: late Jurassic–early Cretaceous (164–133 Ma). These peaks, respectively 76, 49, 38, and 31 Myr in duration and 93, 58, and 63 Myr apart, steadily diminish in magnitude over time (Fig. 1A). These data are currently the best available. Their improvement by future compilation of Phanerozoic microbial carbonate occurrences will doubtless refine and inform the conclusions reached here.

2.2. Invertebrate diversity

We compared these microbial carbonate abundance data (Kiessling, 2002, his Fig. 16; Riding and Liang, 2005b, their Fig. 1) (Fig. 1A), with published assessments of marine invertebrate diversity data (Mayhew et al., 2012, 'shareholder quorum subsampling' (SQS) values from supplementary data; Zaffos et al., 2017, their Fig. 2a) (for details of shareholder quorum subsampling see Alroy, 2010), and also with a compilation of bryozoan, cnidarian and poriferan diversity data (from http://fossilworks.org/ accessed 8th May 2018; see Supplemental Data) to represent invertebrate reef-builders (Fig. 1C). Throughout our discussion we use the terms 'richness' and 'diversity' interchangeably. Based on these data compilations we recognize the following main intervals of elevated invertebrate (I), particularly reefal, genus diversity: I1: 465–372 Ma (mid-Ordovician/late Devonian), I2: 299–265 Ma (early/mid Permian), I3: 227–201 Ma (late Triassic), I4: 170–152 Ma (mid/late Jurassic), I5: 133–0 Ma (early Cretaceous/present day) (Fig. 1). As with the microbial carbonate abundance data, future compilations that refine these intervals will modify the conclusions reached here.

2.3. Temperature and oxygenation

We used sea-surface temperatures (Mayhew et al., 2012; Royer et al., 2004), marine dissolved oxygen values calculated from atmospheric oxygen estimates of Royer et al. (2014), and seawater carbonate saturation state values calculated by Riding and Liang (2005b, their Fig. 1) (Fig. 1B). Numerical geological ages used throughout are those of the International Chronostratigraphic Chart (Cohen et al., 2013).

We calculated dissolved O_2 in tropical surface seawater for the past

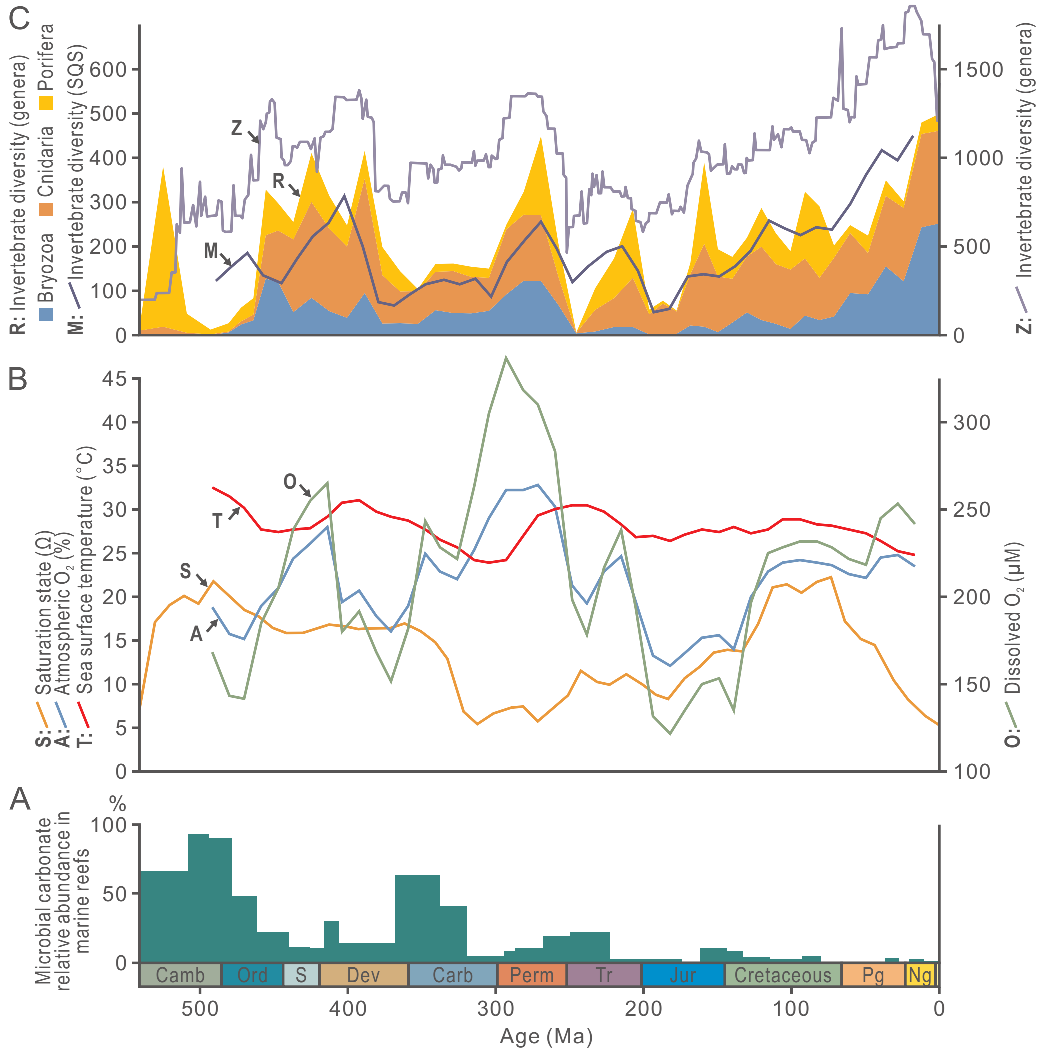

Fig. 1. (A) Microbial carbonate relative abundance in marine reefs, from Kiessling (2002, his Fig. 16), using Golonka and Kiessling's (2002, his Fig. 1, pp. 13–18) time intervals for supersequences (see Riding, 2005, his Fig. 1). Main peaks of abundance occur in the Cambrian–earliest Ordovician (541–465 Ma), latest Devonian–mid-Mississippian (372–323 Ma), mid-Permian to mid-late Triassic (265–227 Ma) and late Jurassic–early Cretaceous (164–133 Ma). These peaks, separated by intervals of lower abundance, steadily decline in magnitude throughout the Phanerozoic. Geological time-scale from Cohen et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
(B) Sea-surface temperature (Royer et al., 2004, their Fig. 4, their red curve, compiled by Mayhew et al., 2012, their supp. data), marine dissolved oxygen calculated from atmospheric oxygen estimates of Royer et al. (2014, their Fig. 2b), and seawater calcite saturation state calculated by Riding and Liang (2005b, their Fig. 1).
(C) Three estimates of Phanerozoic marine invertebrate genus richness. M: shareholder quorum subsampling (SQS) values from the supplementary data in Mayhew et al. (2012). Z: Range-through marine invertebrate generic richness calculated in million-year increments (Zaffos et al., 2017, their Fig. 2a); R: compilation of bryozoan, cnidarian and poriferan genus richness data to represent invertebrate reef-builders. This latter compilation includes all fossilized members of these phyla, mainly reef-building organisms. Porifera include archaeocyaths, hexactinellids, lithistids, sclerosponges, sphinctozoans and stromatoporoids. Cnidaria include rugose, tabulate, and scleractinian corals. Bryozoa include gymnolaemates and stenolaemates.

490 Myr (latest Cambrian to present-day) (Fig. 1B), using modeled atmospheric oxygen estimates from Royer et al. (2014, their Fig. 2b) and sea surface temperature anomaly data from Royer et al. (2004, see their Fig. 4, red curve), compiled by Mayhew et al. (2012, 'temperature' column in their supp. dataset SD01x.xlsx). Dissolved oxygen in surface seawater depends on atmospheric oxygen composition together with water temperature, pressure, and salinity. We made the following assumptions: present-day tropical sea-surface temperate 25 °C, water depth of 0 m (i.e., surface of seawater at 1 atm), and salinity 35 parts per thousand. According to Henry's law, at constant temperature and pressure, the amount of O_2 gas that dissolves in water is directly proportional to the partial pressure of O_2 gas in equilibrium with water. In seawater, the presence of salt lowers the dissolved O_2. A table of solubility of oxygen in seawater at $\sim 35^0/_{00}$ salinity and 20% partial pressure of oxygen gas is given by the Engineering ToolBox (https://www.engineeringtoolbox.com/oxygen-solubility-water-d_841.html) (Table S1, Supplemental Data).

To obtain the Henry's law constants for surface seawater any given temperature we derived a polynomial function as follows. Using the tabulated dissolved oxygen data (Table S1, Supplemental Data), we first calculated discrete K_H values corresponding to the given temperatures (every 5 °C) at 20% partial pressure of O_2 (Table S2, Supplemental Data). We then obtained a polynomial function by fitting the K_H versus temperature curve (Fig. S1, Supplemental Data):

$$K_H = -0.0047T^3 + 0.68T^2 - 42.6T + 1741 \quad (1)$$

where T is temperature in °C.

We used the above polynomial function and calculated the predicted K_H at a given temperature using sea-surface temperature values from Royer et al. (2004), compiled by Mayhew et al. (2012) with a baseline temperature of 25 °C.

Next, we used Henry's law equation to calculate the dissolved oxygen in μM (Table S3, Supplemental Data):

$$C = K_H \times p_{O2} \quad (2)$$

where the partial pressure of oxygen, p_{O2} is from Royer et al. (2014, their Fig. 2b). The computed dissolved oxygen values are displayed in Fig. 1B.

3. Results

3.1. Invertebrate diversity and dissolved oxygen

Oxygen levels broadly track our measures of invertebrate diversity for the past 490 Myr (Fig. 1B). Our comparison of Mayhew et al.'s (2012) diversity data (using *raw* values of 'shareholder quorum subsampling', SQS) and dissolved oxygen shows positive correlation: $r = +0.384$, $p(\alpha) = 0.01 < 0.05$, $n = 44$ (Table S4, Supplemental Data). Invertebrate diversity is generally high when dissolved oxygen is high, although a conspicuous exception is when oxygen was high and diversity low ~300 Ma. This could reflect the effect on diversity of Ice Age conditions at that time, such as low temperature and low sea-level. In contrast, diversity was generally low when oxygen was low, e.g., ~475, 370, 250, 180 Ma, likely reflecting the effect of increased tendency to seasonal and/or localized hypoxia. Based on our calculated values, dissolved oxygen levels near or below 150 μmol per liter (μM) coincide with low invertebrate diversity in the Floian–Dapingian (479–468 Ma), early Famennian (369 Ma) and early Jurassic (193–171 Ma) (Fig. 1).

3.2. Invertebrate diversity and temperature

Using standardized subsampling techniques Mayhew et al. (2012, p. 15141, and their Fig. 1D), reported positive correlation between diversity (SQS) and temperature, $r = +0.289$. However, using Mayhew et al. (2012)'s *raw* SQS values we find diversity and temperature to be poorly correlated: $r = -0.10$, $p(\alpha) > 0.05$, $n = 44$ (Table S4, Supplementary Data). Our comparisons suggest that invertebrate diversity and sea-surface temperature can correspond (e.g., both relatively high ~400 and 190 Ma; both relatively low ~300 Ma), and also diverge (e.g., ~500, 260, 20 Ma) (Fig. 1).

3.3. Microbial carbonates and dissolved oxygen

Broadly, peaks of microbial carbonate abundance (e.g., ~500, 370, 237, 150 Ma) occur when dissolved oxygen values were at or below ~170 μM (Fig. 1). This appears to reflect the effect of reduced invertebrate diversity (and therefore competition), in response to low oxygen levels, on microbial carbonate formation.

3.4. Microbial carbonates, temperature and carbonate saturation state

Microbial carbonate abundance is generally positively correlated with sea-surface temperature, which tends to raise carbonate saturation state, and intervals of microbial carbonate abundance also broadly correspond with increased levels of calculated carbonate saturation state (Fig. 1). However, extended periods occur when microbial carbonates were not very abundant even though calculated carbonate saturation was relatively high; notably the mid-Ordovician to mid-Devonian and mid–late Cretaceous. These discrepancies likely reflect increased biocontrolled calcification during these intervals, which was not taken into consideration in the saturation state values calculated by Riding and Liang (2005a, their Fig. 5) (see Section 4.5).

3.5. Invertebrate diversity and microbial carbonates

Broadly, peaks of microbial carbonate abundance correspond with low invertebrate diversity, and peaks of invertebrate diversity ~465–372, 299–265, 133–0 Ma correspond with low microbial carbonate abundance (Fig. 1). Conversely, there are at least two intervals when invertebrate diversity and microbial carbonate abundance were both low: ~323–299, 201–170 Ma. These are times when microbial carbonate abundance appears to have been depressed by low carbonate saturation state (Riding and Liang, 2005a, 2005b) and when low temperatures (together with low dissolved oxygen levels, ~201–170 Ma) can be expected to have lowered invertebrate diversity. Overall, therefore, on the scales of these data, microbial carbonates were more abundant when invertebrate diversity was low, except when temperature and/or carbonate saturation state were also low.

3.6. Transitions, 'lows', overlaps

Our data support the observation that intervals of microbial and invertebrate carbonate abundance have broadly alternated with one another over long time scales during the Phanerozoic (Riding, 2005). In addition, our more precise delimitation of variations in invertebrate diversity also indicate three types of change between these intervals: transitions, 'lows', overlaps. Well-defined *transitions* occur between intervals of microbial carbonate and invertebrate abundance in the mid-Ordovician, late Devonian, late Permian, and mid-Triassic. An early Cretaceous transition is less well-defined due to the lower abundance of microbial carbonates at that time. Extended 'lows', when microbial carbonate abundance and invertebrate diversity were both reduced 323–299 and 201–170 Ma may, at least in part, be due to low temperatures. *Overlaps*, when invertebrates and microbial carbonates were both relatively abundant, occur ~525–510 and 164–152 Ma. Both of these examples involve sponges and microbial carbonates: mainly archaeocyaths in the Cambrian and mainly hexactinellids and lithistids in the late Jurassic. This may reflect the ability of sponges to tolerate conditions that also favored microbial carbonate formation (Lee and Riding, 2018). Further studies of microbial-invertebrate transitions are likely to reveal additional details and complexities.

3.7. Summary of intervals

Four intervals when microbial carbonate (MC) abundance was increased and invertebrate diversity was reduced occur during the Phanerozoic: MC1: Cambrian/mid-Ordovician (541–465 Ma), MC2: latest Devonian/Mississippian (372–323 Ma), MC3: mid-Permian/mid-late Triassic (265–227 Ma), and MC4: late Jurassic/early Cretaceous (164–133 Ma) (Fig. 1). These MC intervals alternate - often transitionally - with intervals of relatively high invertebrate (I), especially reef, genus diversity when microbial carbonates were less common (Fig. 2). The main intervals of increased invertebrate diversity are I1: mid-Ordovician/late Devonian (465–372 Ma), I2: early/mid Permian (299–265 Ma), I3: late Triassic (227–201 Ma), I4: mid/late Jurassic (170–152 Ma), I5: early Cretaceous/present day (133 − 0) Ma (Fig. 2). In addition to transitions, there are lows' between some of these intervals when microbial carbonates and invertebrates were both relatively reduced, e.g., during the Pennsylvanian (323–299 Ma) and early Jurassic (201–170 Ma). There are also at least two periods of *overlap* when invertebrates and microbial carbonates were both relatively abundant: early-mid Cambrian (~525–510 Ma), within MC1, when archaeocyaths were common, and late Jurassic (164–152 Ma), between I4 and MC4, also when sponges were common (Fig. 2).

4. Discussion

4.1. Invertebrate diversity and dissolved oxygen

Our comparisons suggest that marine invertebrate diversity has broadly tracked marine oxygenation since the Cambrian. Diversity was low when dissolved oxygen levels were low (and SST high), ~475, 370, 250, 180 Ma (Fig. 1). In addition, our comparison with Mayhew et al.'s (2012) *raw* shareholder quorum subsampling (SQS) data shows that diversity and oxygen are significantly correlated: $r = +0.384$ ($p(\alpha) < 0.05$, $n = 44$; see Section 3.1). Marine oxygenation has been linked to late Proterozoic and Cambrian animal evolution (see Introduction, above) and it has been proposed that 'oxygen was the chief limiting factor on the density of animal populations' in the Early Paleozoic (Fischer, 1965, p. 1211). However, whereas oxygen levels have been invoked to interpret terrestrial evolution (Berner, 2006), patterns of marine invertebrate diversity during the Phanerozoic as a whole have more often been linked to factors such as continental flooding, nutrient supply, temperature, tectonics, seafloor spreading rate, and global biogeography (e.g., Martin, 1996; Mayhew et al., 2008; Benton, 2009; Cárdenas and Harries, 2010; Hannisdal and Peters, 2011; Cermeño et al., 2017), as well as to 'intrinsic traits of animal taxa' (Stanley, 2007).

Despite relatively high present-day levels of atmospheric oxygen (Berner, 2009), zones of low oxygenation associated with upwelling

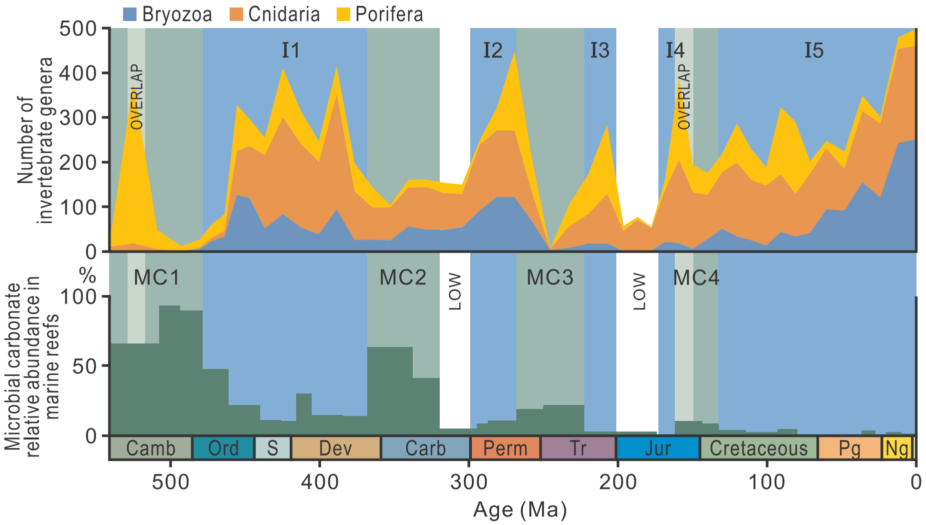

Fig. 2. Phanerozoic Intervals characterized by microbial and invertebrate skeletal carbonate. Geological time-scale from Cohen et al. (2013). There are four intervals of increased microbial carbonate abundance: MC1: 541–465, MC2: 372–323, MC3: 265–227, and MC4: 164–133 Ma. These alternate with intervals of relatively high invertebrate, especially reef, diversity when microbial carbonates were less common: I1: 465–372, I2: 299–265, I3: 227–201, I4: 170–152, I5: 133–0 Ma. 'Lows', when microbial carbonates and invertebrates were both relatively reduced, occur 323–299 and 201–170 Ma. Two intervals of overlap, when invertebrates and microbial carbonates were both relatively abundant, occur within MC1, ~525–510 Ma, and between I4 and MC4, 164–152 Ma.

and stratification are locally and seasonally common in restricted seas, especially where there is nutrient influx, and develop seasonally as oxygen-minimum zones (OMZs) in the open ocean (Stramma et al., 2008; Levin, 2018). Some organisms, such as many sponges, tolerate low oxygen. Present-day hexactinellids, for example, tolerate hypoxia (< 1.4 mL/L) (Chu and Tunnicliffe, 2015) and can survive anoxia (oxygen concentrations < 0.2 mL/L) (Tunnicliffe, 1981). However, many invertebrates are stressed by these conditions (Levin et al., 2009; Rabalais et al., 2010; Stramma et al., 2010), and even water conventionally regarded as only marginally hypoxic (2 mg O_2/L) may be lethal or sublethal for many species (Vaquer-Sunyer and Duarte, 2008). In present-day reefs, the coral *Acropora yongei* can be significantly harmed by low oxygen (2–4 mg/L) (Haas et al., 2014), and coral species richness is reduced below 2 mg/L (Altieri et al., 2017, their Fig. 2). In addition to absolute levels of oxygen, short-term variability in oxygen concentration can also be severely limiting (Matabos et al., 2012). Several mass extinction events have been specifically linked to low dissolved oxygen, e.g., Frasnian–Famennian, Permian–Triassic, and end-Triassic (Meyer and Kump, 2008; van de van de Schootbrugge and Wignall, 2015; Jost et al., 2017; Levin, 2018, their supp. Fig. 3). Over time, it is likely that variations in dissolved oxygen have strongly influenced marine sessile invertebrate reef-builders, and intervals of anoxia broadly correspond with increased abundance of microbial reefs (Knoll and Fischer, 2011, their Fig. 4.1). Under the low atmospheric values calculated for some past intervals, particularly when overall temperatures were increased, similar low-oxygen conditions and their effects, are likely to have been expanded in time and space, e.g., late Cambrian–early Ordovician, late Devonian, Early Triassic, and Jurassic–Early Cretaceous (Fig. 1).

Exceptionally preserved biotas (Allison and Briggs, 1993) and oceanic anoxic events (OAEs) (Jenkyns, 2010) also tend to occur within extended intervals with low levels of dissolved O_2. Well-known examples include mid–late Cambrian and early Ordovician Burgess Shale type faunas (Butterfield, 1995; Van Roy et al., 2010; Lerosey-Aubril et al., 2017), Late Devonian Kellwasser events (Bond et al., 2004), Mississippian Shrimp Beds (Aldridge et al., 1993), the late Permian mass extinction (Brennecka et al., 2011; Lau et al., 2016), and the early Toarcian event (Posidonienschiefer, T-OAE, ~183 Ma) (Jenkyns, 2010).

We propose that oxygenation exerted a significant influence on marine invertebrates; specifically, that low levels of dissolved oxygen limited diversity. This is consistent with recognition that present-day low oxygen (hypoxia) can reduce marine invertebrate diversity (e.g., Vaquer-Sunyer and Duarte, 2008; Levin et al., 2009; Rabalais et al., 2010; Stramma et al., 2010). In addition to its direct effect, oxygenation can increase availability of key nutrients such as phosphorus (Laakso and Schrag, 2017). The Cambrian-Ordovician transition from microbial to invertebrate carbonates (Adachi et al., 2009) exemplifies these inferred effects. In the late Cambrian and early Ordovician, microbial carbonates were abundant whereas invertebrate diversity appears to have been limited by low levels of dissolved oxygen that reflect the combined effects of elevated marine temperatures (Trotter et al., 2008) and relatively low atmospheric oxygen levels (Webby, 2002; Edwards et al., 2017, their Fig. 2). During the early–mid Ordovician, microbial carbonate abundance declined and invertebrates diversified, as temperature declined and dissolved O_2 is estimated to have increased from 100 to 150 µM (Lee and Riding, 2018). These changes were the prelude to a protracted phase that lasted until the beginning of the late Devonian, during which – very broadly – invertebrate diversity tended to be high and microbial carbonate abundance low. Subsequent episodes of increased microbial carbonate abundance (~372–323, 265–227, 164–133 Ma) coincided with low levels of dissolved oxygen and low invertebrate diversity (Fig. 1). We therefore suggest that the distinctive oscillating pattern of microbial carbonate abundance and invertebrate diversity that characterizes much of the Phanerozoic was underpinned by changes in marine oxygenation that significantly affected invertebrates and, thereby, microbial carbonates. Provided carbonate saturation was elevated, microbial carbonate abundance increased when low dissolved oxygen levels limited invertebrate diversity.

4.2. Invertebrate diversity and temperature

Links between invertebrate diversity and temperature (Fischer, 1960) continue to be debated (Currie, 1991; Clarke and Gaston, 2006; Mittelbach et al., 2007; Kiessling, 2009; Gillman and Wright, 2014). Using standardized subsampling techniques, Mayhew et al. (2012, p. 15141, and their Fig. 1D), found positive correlation between invertebrate diversity (SQS) and seawater temperature, $r = +0.289$, for the Phanerozoic as a whole. However, the same diversity and temperature data show times of both broadly positive correlation (e.g., ~400, 300, 190 Ma) and negative correlation (e.g., 500, 260, 20 Ma), and using Mayhew et al. (2012) *raw* SQS values, we calculate overall slightly negative correlation, $r = -0.10$ ($p(\alpha) > 0.05$, $n = 44$; see Section 3.2), between diversity and temperature. Two conspicuous divergences that occur between diversity and temperature, ~500 and 260 Ma, may respectively reflect diversity decline as elevated temperatures depressed dissolved oxygen levels. Conversely, increased diversity during the great Ordovician biodiversification event (GOBE) can be linked to a combination of temperature decline and increased oxygenation (Webby, 2002; Trotter et al., 2008; Edwards et al., 2017, their Fig. 3; Lee and Riding, 2018, their Fig. 7).

4.3. Microbial carbonates and dissolved oxygen

These links between dissolved oxygen and invertebrate diversity affected microbial carbonate abundance (Fig. 1). Our comparisons suggest that microbial carbonate abundance increased when invertebrate competition was reduced by low dissolved O_2 levels. In addition, many microbes not only tolerate but are well-adapted to low O_2. Thus, correspondence between microbial carbonate abundance and low levels of dissolved oxygen could reflect increase in anaerobic bacterial metabolisms that can promote carbonate precipitation (Grotzinger and Knoll, 1995; Higgins et al., 2009; Schrag et al., 2013; Sun and Turchyn, 2014), such as sulfate reduction. Overall, Phanerozoic microbial carbonates appear to have responded positively to a combination of low dissolved O_2, elevated temperature, and increased carbonate saturation state, and to absence of invertebrates, just as they seem to have done in the Precambrian. As the Phanerozoic progressed, these conditions became scarcer. Present-day normal marine carbonates are overwhelmingly dominated by the skeletal remains of algae and invertebrates (Leeder, 1982; Schneider et al., 2000), whereas benthic microbial carbonates are much more restricted. Microbial crusts in Quaternary reefs exemplify an anaerobic marine heavily calcified stromatolite ‘refuge’, now declining as natural acidification lowers carbonate saturation state (Riding et al., 2014).

4.4. Invertebrate diversity and microbial carbonate abundance

The inverse relationship between microbial carbonate abundance and invertebrates based on Sepkoski Jr.'s (1997) data (Riding, 2005, his Fig. 2; Riding and Liang, 2005a; Riding, 2006), is supported here by comparisons with recent compilations of invertebrate diversity (Mayhew et al., 2012, SQS from their supplementary data; Zaffos et al., 2017), as well our compilation of reef invertebrate diversity data (Fig. 1). Overall, intervals characterized by increased microbial carbonate abundance correspond with lower invertebrate diversity: Cambrian–earliest Ordovician (541–480 Ma), latest Devonian–Mississippian (372–323 Ma), mid-Permian–late Triassic (265–227 Ma), and late Jurassic–earliest Cretaceous (164–133 Ma). Despite lack of clear correlation between all mass extinctions and increased microbial carbonate abundance (Riding, 2005), this pattern is consistent with the long-held view that invertebrate competition has significantly limited microbial carbonate abundance (Fischer, 1965; Garrett, 1970; Awramik, 1971). Fischer (1965) suggested that, in addition to competition, stromatolite may have declined since the Ordovician because they ‘became less mineralized’. Microbial carbonate abundance broadly correlates positively with calculated seawater carbonate saturation state (Riding and Liang, 2005a).

The likelihood that microbial carbonate abundance reflects a response to both competition and carbonate saturation state raises the question of the relative importance of these influences (Riding, 2005). Microbial carbonates were not always abundant when invertebrate diversity was low (e.g., ~300 and 200 Ma), and this can tentatively be attributed to low carbonate saturation state and/or low temperatures. Conversely, microbial carbonates were not always abundant when carbonate saturation state was high, for example the Silurian to late Devonian. Since this was an interval of generally increased invertebrate diversity, it seems reasonable to conclude that increased benthic invertebrate competition limited microbial carbonates by competing for both space and calcium carbonate, similar to the effect on seawater carbonate saturation of the Mesozoic-Cenozoic rise of calcified plankton (Sandberg, 1975; Wilkinson and Walker, 1989; Riding, 1993; Webb, 1996; Riding and Liang, 2005a).

4.5. The nature of competition

We used measures of diversity through time to represent invertebrate abundance and thereby competition with microbial carbonates. Competition for space and resources is often intense among benthic, especially reef, communities (McCook et al., 2001; Taylor and Wilson, 2003; Chadwick and Morrow, 2011; Svensson and Marshall, 2015). Organisms exhibit overgrowth, grazing and predation (Taylor and Wilson, 2003) and compete for limiting resources such as food, space and oxygen (Ferguson et al., 2013). Invertebrate competition with microbial carbonates has been suggested to include grazing and burrowing (Garrett, 1970), boring (Myshrall et al., 2014), substrate competition (Webb, 2005), and the effects of bioclastic and pelleted sediment production (Pratt, 1982). In addition, there could be competition not only for space but also for $CaCO_3$ supply. Carbonate saturation state values calculated by Riding and Liang (2005a) do not take account of biocontrolled $CaCO_3$ removal. Consequently, elevated saturation state levels calculated for the Ordovician to Devonian do not preclude the likelihood that increase in invertebrate biocalcification during that extended interval would have lowered seawater carbonate saturation sufficiently to limit microbial calcification. Riding (2005, p. 33) observed that ‘metazoan interference in microbial carbonate formation could include competition for the $CaCO_3$ required for microbial calcification’.

In addition, microbes can compete with metazoans (Webb, 2005). At the present-day, for example, cyanobacterial mats can inhibit coral recruitment and promote reef degradation (Ford et al., 2018). During the Cambrian, ability to exploit low-oxygen conditions may have enabled microbial carbonates to outcompete metazoan reef builders such as sponges and corals, whereas progressive Ordovician marine oxygenation subsequently promoted diversification of skeletal metazoans that could outcompete microbial carbonates for seafloor space (Lee and Riding, 2018). Reef competition is complex due to the variety of substrates and seafloor morphology, such as oxygen-poor crypts, sediment-filled crevices, current-swept surfaces and exposed hardgrounds. Consequently, even during protracted intervals when microbial carbonates appear to have been relatively scarce, such as much of the Devonian (~410–372 Ma), reefal microbial carbonates were locally abundant and thrived as cryptic crusts in reefs (Pratt, 1982, 1995; Soja and Riding, 1993; Soja, 1994; de Freitas and Mayr, 1995; Webb, 1996; de Freitas and Nowlan, 1998; Sheehan and Harris, 2004; Matysik et al., 2015; Peters et al., 2017, their Fig. 2).

If microbial carbonates decline as competition increases (Garrett, 1970; Awramik, 1971), then they could increase when invertebrates decline. Thus, Schubert and Bottjer (1992, 1995) suggested that Early Triassic stromatolites represent a temporary resurgence in the aftermath of the end-Permian mass extinction. However, microbial carbonates only appear to increase after some (e.g., Late Devonian, Permian–Triassic) rather than all (e.g., end-Ordovician, end-Triassic (but see Ibarra et al., 2016), end-Cretaceous) mass extinction events, indicating that factors in addition to competition influence microbial carbonate development. This implicates carbonate saturation state as the key control since, in mass extinction aftermaths, microbial carbonate abundance increased at times when saturation state was high (e.g., Late Devonian and end-Permian), but not when it was low (e.g., Late Cretaceous) (Riding, 2005, 2006). Based on comparison of metazoan diversity data (Sepkoski Jr., 1997) and calculated seawater carbonate saturation state (Riding and Liang, 2005a), Riding and Liang (2005b) suggested that a combination of changes in carbonate saturation state and metazoan competition could account for Phanerozoic episodes of microbial carbonate (Kiessling, 2002, his Fig. 16) and calcified cyanobacteria (Arp et al., 2001) abundance, which ‘broadly coincide with intervals when carbonate saturation state was elevated and metazoan diversity reduced.’ This supports Fischer's (1965) earlier inference. Thus, on the scales shown by these data, microbial carbonates were more abundant when invertebrate diversity was low, so long as carbonate saturation state was elevated.

5. Conclusions

Intervals of microbial carbonate abundance and reduced invertebrate diversity correspond with increased carbonate saturation state, elevated temperature, and low levels of dissolved oxygen (Fig. 1). Conversely, increased invertebrate diversity and lower microbial carbonate abundance occurred during intervals with lower temperatures and higher levels of dissolved oxygen. These secular patterns support previous inferences that, after the Cambrian, microbial carbonate abundance was limited by invertebrate competition and low seawater carbonate saturation state. In addition these patterns suggest a positive long-term link between invertebrate diversity and marine oxygenation. Low invertebrate diversity and increased microbial carbonate abundance correspond with low levels of dissolved oxygen, and invertebrate diversity increased and microbial carbonate abundance declined when dissolved oxygen levels increased. Significant influence of dissolved oxygen on invertebrate diversity, if confirmed, provides a valuable new insight into the development of Phanerozoic marine biotas.

Phanerozoic environmental factors that favored microbial carbonate formation are reminiscent of conditions inferred for much of the Archean and early-mid Proterozoic: elevated seawater saturation state, low O_2 and elevated temperature, as well as absence of invertebrate competition. During the past ~500 Myr, decline in microbial carbonate abundance appears to have reflected global long-term reduction in carbonate seawater saturation state and temperature, as atmospheric CO_2 declined, together with increase in marine oxygenation that favored invertebrate diversification and competition. During the past ~100 Myr, oxygen and invertebrate diversity increased, temperatures declined, and marine microbial carbonates became relatively scarce. These patterns underscore the importance of seawater saturation state and invertebrate competition, which previous research has recognized as significant influences on microbial carbonate abundance. Additionally, they identify dissolved oxygen as a key factor influencing invertebrate diversification. This contributes to fundamental understanding of the physicochemical factors underlying the alternating pattern of microbial and invertebrate carbonate intervals during the Phanerozoic.

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Appendix A. Supplementary data

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