

REGIONAL-SCALE MARINE FAUNAL CHANGE IN EASTERN AUSTRALIA DURING PERMIAN CLIMATE FLUCTUATIONS AND ITS RELATIONSHIP TO LOCAL COMMUNITY RESTRUCTURING

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ABSTRACT

Marine invertebrates are at risk of extinction if climate changes outpace their ability to adapt to thermal stress, and cold-adapted taxa may be especially vulnerable because of their specialized physiologies and because their high-latitude distributions permit only limited poleward migration. Here, we use a database of 1437 early and middle Permian eastern Australian fossil collections from the Paleobiology Database to test for latitudinal range shifts, extinctions, and faunal invasion among high-latitude marine invertebrates during climate changes in the late Paleozoic ice age. Latitudinal range shifts are not apparent, either because genera were unable to migrate or, more likely, because sampling noise or the scale of analyses prevent their recognition. Extinction rates were moderately elevated during the largest climate shifts, however, possibly suggesting that at least some taxa were unable to respond to the rate or magnitude of climate change. Although recognition of range shifts within Australia is difficult, warm-water brachiopods, bivalves, and ammonoids invaded the region during pronounced warming in the Artinskian, highlighting the importance of temperature on faunal distribution. That faunal invasion was coincident with substantial restructuring of local paleocommunities, but both likely resulted from the common cause of increasing temperature rather than having a causal relationship. Temperature warming would have stressed cold-adapted stenotherms, triggering changes in local dominance and allowing immigration of warm-water taxa. These local and regional shifts in dominance and distribution imply that physiological stresses from even gradual climate change can be sufficient to trigger biotic change.

INTRODUCTION

The ability of organisms to adapt to stresses due to climate change has major implications for predictions of extinction risk. Species can evolve or migrate when faced with changing environmental conditions (Davis and Shaw, 2001; Walther et al., 2002; Root et al., 2003; Perry et al., 2005; Parmesan, 2006); however, if they are unable to adapt they are vulnerable to extinction (e.g., Thomas et al., 2004; Maclean and Wilson, 2011) via habitat loss (Thomas et al., 2004), direct thermal effects on respiratory physiology (Pörtner, 2001), changing ocean chemistry including ocean acidification (Pörtner et al., 2004; Orr et al., 2005), and altered biotic interactions (Clarke, 1993; Harley et al., 2006). Although predictions of future extinction risk have large uncertainties (Thuiller et al., 2004; Botkin et al., 2007) and many organisms are adapting through range shifts (Walther et al., 2002; Perry et al., 2005; Parmesan, 2006), there is concern that ongoing climate warming may increase extinction in the 21st century (Thomas et al., 2004).

Although geographic range shifts can be an adaptive response favoring survival of a species, they can also have negative consequences for other species in the community as invasion reshuffles and creates new interspecific interactions, thus altering the competitive landscape

and potentially leading to extinctions and changes in species dominance (Clarke, 1993; Harley et al., 2006). Furthermore, the potential for invasion by exotic species can be enhanced by climate warming (Stachowicz et al., 2002; Rahel and Olden, 2008). These indirect effects from species invasion or temperature-mediated ecological interactions (e.g., Sanford, 1999) can exacerbate direct physiological stresses and contribute to extinction (Clarke, 1993). Warmer temperature stresses marine invertebrates through its effects on their respiratory physiology. As temperature increases, baseline oxygen demand increases but the rate of oxygen supply is limited by the organism's physiology, gradually reducing aerobic scope (excess energy available for growth, reproduction, or other activities, beyond baseline demands) until the thermal tolerance is reached (Pörtner, 2001). Despite apparently broad thermal tolerances, however, physiological stresses from direct thermal effects can be important to invertebrates that live close to their temperature threshold, as is the case for many shallow subtidal to intertidal species (Hughes et al., 2003; Harley et al., 2006). These physiological limitations are also particularly important for cold-adapted taxa, many of which have highly limited aerobic scopes (Peck et al., 2004; Pörtner et al., 2007).

The fossil record provides a long-term history of the interaction between climate change and the biosphere, documenting extinction and adaptation during episodes of climate warming in deep time. Adaptation via range expansion and contraction has been reconstructed in greatest detail for certain Pleistocene marine and terrestrial taxa (Kitamura et al., 2000; Hellberg et al., 2001; Roy et al., 2001; Harrison and Prentice, 2003) and, to a lesser extent, in tropical forest ecosystems during late Paleozoic Milankovitch glacial-interglacial cycles (Falcon-Lang, 2004; DiMichele et al., 2009). Dynamic climate fluctuations during the Permo-Carboniferous late Paleozoic ice age (LPIA) included a complete icehouse-greenhouse climate shift following the earliest Permian ice maximum, followed by three younger and more localized glacial episodes centered in eastern Australia (Fig. 1; Isbell et al., 2003; Fielding et al., 2008a, 2008b). Although Milankovitch-scale temporal resolution is not possible, as in Pleistocene marine communities (Kitamura et al., 2000), similar signals may be observable over longer timescales in the Permian. In the marine realm, there is evidence that the biogeographic boundary between tropical and cool-water faunas occurred at lower latitudes in the peak LPIA glacial episode than it does today (an interglacial interval) (Angiolini et al., 2007), but the details of how, or if, the geographic distributions of warm- and cool-adapted genera shifted in response to Permian climate fluctuations are not known. The taxonomic composition of high-latitude marine paleocommunities changed substantially (Clapham and James, 2008), but it is not clear whether that restructuring was synchronous with extinction or range shifts and invasion.

Although the tempo of climate change during the LPIA was almost certainly slower than the current rate of anthropogenic warming, the faunal response can nevertheless provide data on extinction and adaptation to natural rates of climate change. Investigation of biotic changes during longer-term LPIA climate warming and the consequent stresses on respiratory physiology complements studies of the more abrupt Guadalupian and end-Permian extinctions, which selected

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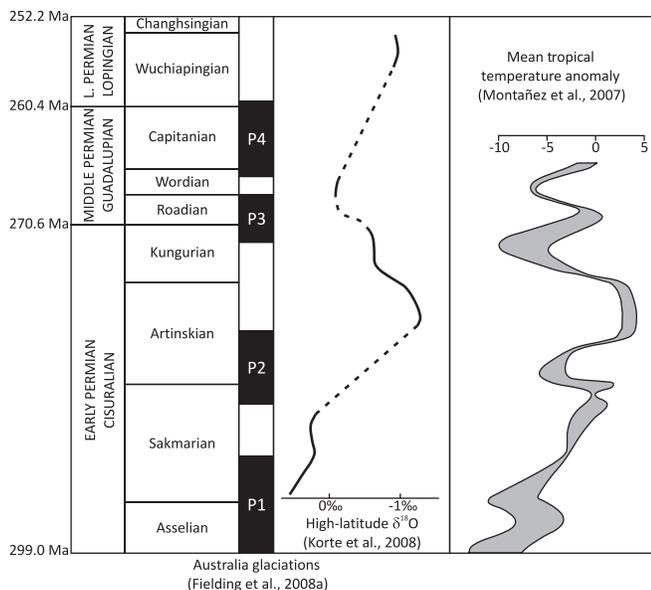


FIGURE 1—Permian timescale showing timing of glacial and nonglacial episodes in eastern Australia (based on the correlations of Fielding et al., 2008a), oxygen isotope paleotemperature trend based on eastern Australian brachiopods (from Korte et al., 2008), and reconstructed tropical paleotemperature changes based on North American brachiopods (from Montañez et al., 2007).

primarily for traits related to respiratory physiology (Clapham and Payne, 2011). As physiological adaptations among modern marine invertebrate groups will be critical for their success in ongoing climate warming, ocean acidification, and hypoxia, it is important to understand species- and community-level response during ancient crises, of varying magnitudes, that were also triggered by physiological stresses.

We focus on the Permian of eastern Australia (Fig. 2), encompassing the LPIA acme, deglaciation, and subsequent climate fluctuations in the early and middle Permian (P2–P4 glacials of Fielding et al., 2008a), the same time interval that Clapham and James (2008) used to document local paleocommunity change in that region. We compiled a database of 4301 marine invertebrate occurrences from 1437 fossil collections in the Permian of eastern Australia, available in the Paleobiology Database (www.paleodb.org), to (1) quantify extinction and adaptation via migration in marine invertebrate genera, (2) investigate the role of thermal limitation and physiological constraints on Permian marine invertebrates, and (3) test the relationship between local community change and range shifts and/or faunal invasion.

METHODS: QUANTIFYING REGIONAL FAUNAL CHANGE

We quantified migration and extinction with data from the Paleobiology Database (www.paleodb.org), comprising 4301 occurrences from 1437 collections in eastern Australia (Queensland, New South Wales, Victoria, and Tasmania), spanning the Asselian–Capitanian interval (Table 1 and Supplementary Data 1¹). A collection is a single taxonomic list from a discrete stratigraphic interval at a specific location; an occurrence is the record of a particular taxon in that collection. We only included collections that could be resolved to the stage level, which is often difficult in eastern Australia because conodonts and fusulinids are absent and ammonoids are mostly restricted to one interval (discussed in more detail below), and excluded questionably identified genera (those qualified with ? or “”; for download metadata, see Supplementary Data 2¹). We used the correlations of Fielding et al. (2008a), based on the brachiopod zonation of Briggs (1998), because most formations can be placed in the



FIGURE 2—Late early Permian (ca. 280 Ma) paleogeographic map showing location of eastern Australia study area, spanning the paleo-Antarctic circle.

zonation from data in Briggs (1998) and Fielding et al. (2008a). These intraregional correlations are not universally accepted, however, and alignment of this regional scheme with the global timescale is even more tenuous. An alternative set of zones and correlations has been proposed by Waterhouse (2008), using samples from measured sections and based on detailed revision of the brachiopod taxa. Because our analyses compare migration and extinction to glacial-nonglacial cycles also based on the eastern Australian record, the choice of correlation does not alter the conclusions.

We tested for migration by quantifying shifts in the maximum, mean, and minimum paleolatitude of each genus’s occurrences in eastern Australia. Many genera also ranged outside of eastern Australia, but we restricted our analysis to their eastern Australian record in order to investigate latitudinal range shifts along the high-latitude, north-south oriented continental margin. We assessed latitudinal range shifts both from occurrences binned by glacial-nonglacial intervals and at the stage level (e.g., Asselian to Sakmarian), excluding genera that did not have at least five occurrences in each of the two intervals being compared. We calculated three-timer extinction rates (Alroy, 2010) for each stage, after standardizing the data with the shareholder quorum subsampling method (quorum of 0.7, counting one-reference taxa and ignoring most common taxon and largest collection, and drawing fewer collections from large references) (Alroy, 2010).

It is also necessary to assess the climatic affinity of the marine invertebrate genera to determine the temporal and spatial distribution of warm-water genera in the Permian of eastern Australia. This method was applied only to brachiopods and mollusks, because they have sufficiently large numbers of occurrences in Australia and globally for the analysis. We applied the method used by Clapham (2010) to quantify the preferred paleolatitude of genera, with a small modification to account for the underlying distribution of fossil occurrences. This method pools all global Permian occurrences of a genus (see Supplementary Data 3¹, also obtained from the Paleobiology Database with the same download procedures, other than the geographic restriction) to increase sample size (the median number of occurrences per genus after pooling is six) and reduce the influence of random noise in the data, and calculates the mean paleolatitude of its occurrences. The mean value (paleolatitude score) is indicative of the preferred temperature of the genus (its preferred temperature range, i.e., whether it is stenothermal or eurythermal, is not assessed by this method). Although relative differences in paleolatitude score are reliable, the absolute scores are biased toward lower latitudes because the distribution of all marine invertebrate occurrences is also biased toward low latitudes (Fig. 3) (Clapham, 2010). As an example, the raw mean paleolatitude score of the brachiopod genus *Megousia*, typically considered to be a cooler-water genus, is 24° because it is an uncommon constituent of the heavily sampled low-latitude faunas (Fig. 3). We corrected for this low-latitude bias for each genus by fitting a density function to the genus occurrence data and to the overall occurrence

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TABLE 1—Taxonomic coverage of the eastern Australia dataset analyzed here.

Taxonomic group	Number of occurrences
Brachiopoda	2903
Bivalvia	643
Bryozoa	362
Gastropoda	249
Crinoidea	63
Rostroconchia	25
Anthozoa	20
Conulariida	15
Cephalopoda	11
Trilobita	5
Hyalitha	3
Scaphopoda	1
Blastoidea	1

data (after converting paleolatitude to its absolute value, both density functions fitted 512 points with a smoothing bandwidth of 1.5 and were truncated poleward of 80 degrees paleolatitude because no fossil collections are found in those regions). We normalized the genus density function to the overall occurrence density function by dividing genus density values by overall density (Fig. 3), and calculated an adjusted paleolatitude score by converting the normalized genus density function into expected counts at each paleolatitude and calculating the mean paleolatitude of those values. The raw and adjusted paleolatitude scores are strongly correlated ($r = 0.966$) but 96.8% of genera have an adjusted paleolatitude score that shifted to higher latitudes relative to their raw score. The adjusted paleolatitude score for *Megousia* is 47° , a better representation of its cool-water affinity (although the large adjustment is not typical; the mean difference between adjusted and raw scores is 3.5°). We used adjusted paleolatitude scores for the analyses and considered genera with scores less than 40° to be warm-water taxa.

We compared faunal changes to previously published climate reconstructions for the early and middle Permian, which are based on proxies for both sea surface temperature (marine conditions) and ice volume (terrestrial or atmospheric conditions) (e.g., Montañez et al., 2007; Fielding et al., 2008a; Korte et al., 2008). As marine and atmospheric conditions are inexorably linked in the climate system, we do not differentiate between the two and instead use the term climate change for simplicity, to refer to temperature changes in the oceans and/or atmosphere.

RESULTS

Migration and Extinction in Eastern Australia

Seawater temperatures fluctuated with the waxing and waning of ice sheets during glacial and nonglacial intervals (*sensu* Fielding et al., 2008a) in the Permian of eastern Australia (Korte et al., 2008). If those temperature shifts were of sufficient magnitude, they should either have caused similar shifts in the latitudinal range of marine invertebrate genera (if the organisms were able to adapt and track their preferred temperature regime) or led to elevated extinction rates (among organisms unable to adapt). Shifts in the highest paleolatitude, mean, and lowest paleolatitude occurrence of genera (Fig. 4A) are highly variable after accounting for shifts in the overall distribution of fossil occurrences (Fig. 4B), despite restricting comparisons to genera with at least five occurrences in each interval. The mean paleolatitude of genera did not exhibit any consistent trends in response to climate change; most shifts were close to zero, indicating no preferential migration.

Shifts in the highest and lowest-paleolatitude occurrences also did not differ from zero in most cases. However, interpretation of the highest and lowest paleolatitudes is complicated by a number of factors. First, genera should be rare near the extremities of their range, rendering shifts in highest and lowest latitude of genera more volatile than shifts in their central tendency. Second, we corrected for sampling

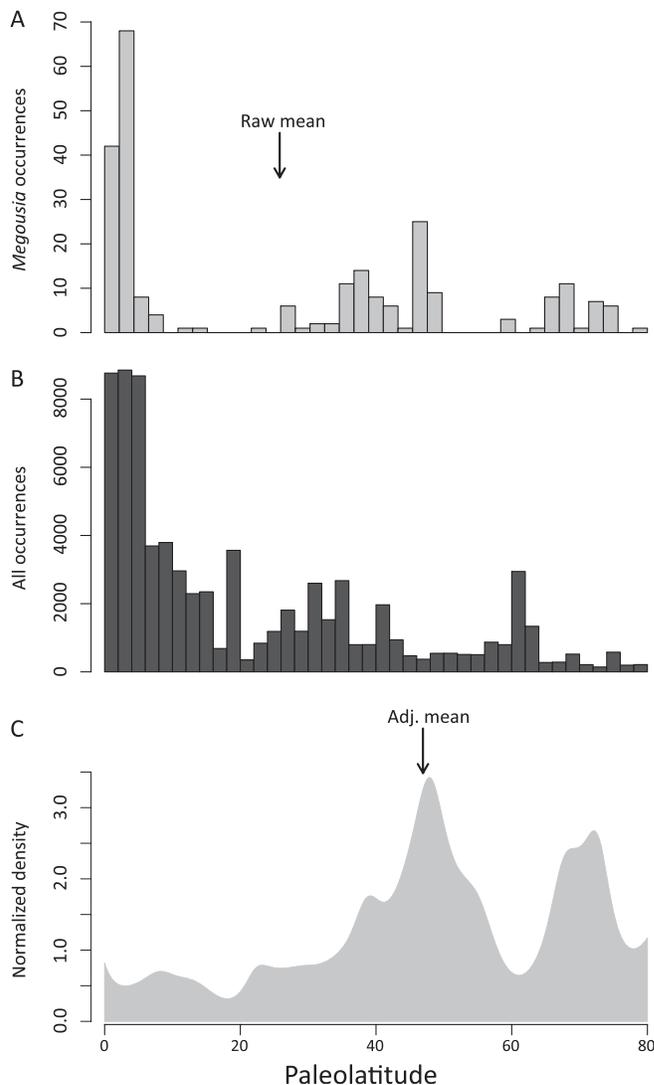


FIGURE 3—Example outlining the procedure for normalizing genus occurrences by the underlying global distribution of occurrences. A) Histogram showing paleolatitude distribution of Permian occurrences of the brachiopod genus *Megousia* from the Paleobiology Database. B) Histogram showing the paleolatitude distribution of Permian occurrences of all marine invertebrate genera, also from the Paleobiology Database. C) Normalized density function for the occurrences of *Megousia*, generated by normalizing the genus density function (based on histogram in A) by the overall density function (based on histogram in B). See text for more details on the density functions and normalization.

effects by adjusting for the shift in the mean position of collections; however, in some intervals the highest or lowest paleolatitude shifted more or less than the mean position. For example, the P3 glacial to nonglacial transition was characterized by a large equatorward shift in the mean position of collections but an even greater equatorward shift in the highest-latitude collection (Fig. 4B). Finally, shifts in highest and lowest paleolatitude tended to be in opposite directions, indicating that range expansion or contraction, rather than range shifts, was the primary signal. Times of range expansion (poleward shift in highest paleolatitude, equatorward shift in lowest paleolatitude) coincided with increases in the number of occurrences (Fig. 4C), whereas range contraction occurred when the number of occurrences decreased from one interval to the next. These factors imply that shifts in the highest or lowest paleolatitude of occurrences are more likely to reflect sampling artifacts than true biological responses.

Although the onset and termination of glacial episodes did not coincide precisely with stage boundaries, we also binned data at the

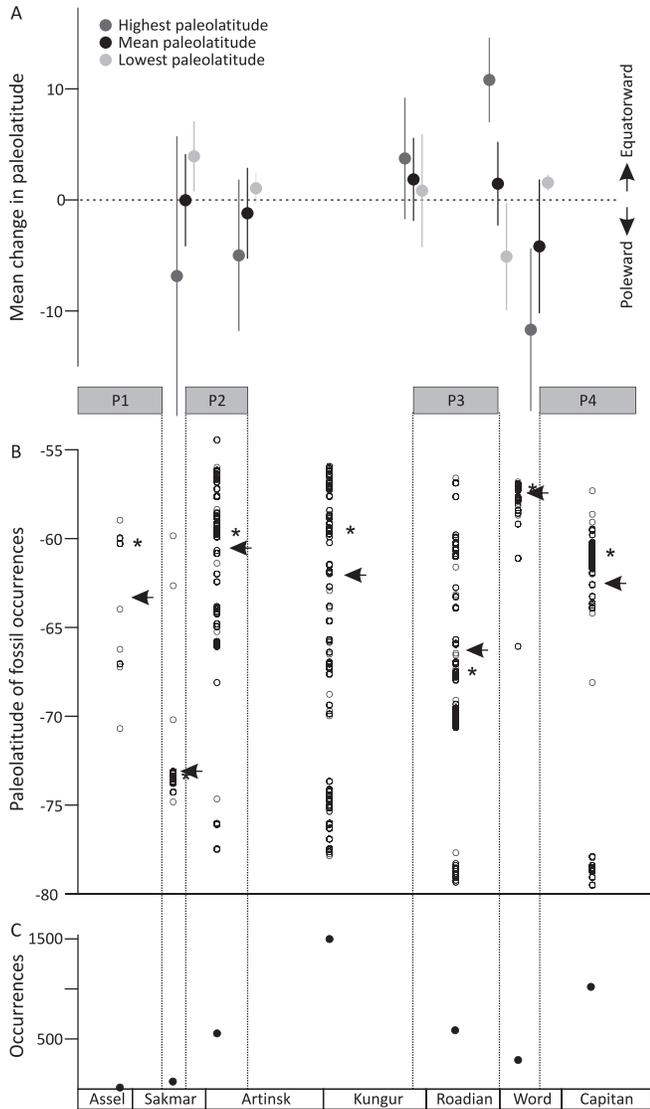


FIGURE 4—Glacial-nonglacial changes in the paleolatitudinal distribution of eastern Australian invertebrate taxa. A) Mean shift in the highest-latitude, mean, and lowest-latitude recorded paleolatitude of genera. Genera with fewer than five occurrences in each stage were excluded. Paleolatitudinal shifts were adjusted for the distribution of samples by subtracting the shift in the mean position of all fossil occurrences. Error bars are one standard deviation. B) Paleolatitudinal distribution of all marine invertebrate occurrences in eastern Australia. Arrows mark the mean occurrence, and stars the median. C) Total number of occurrences in each glacial and nonglacial interval.

stage level to compare evidence for migration to evidence for extinction (Fig. 5). Like analyses of glacial-nonglacial changes, there were no consistent shifts in highest, mean, or lowest paleolatitude across stage boundaries (Fig. 5A). There is some support, however, for faunal turnover and extinction during times of more pronounced warming and cooling in the Permian. Extinction rates were higher across the Sakmarian/Artinskian boundary, close in time to warming after the P2 glacial episode (Fielding et al., 2008a; Korte et al., 2008), and across the Kungurian/Roadian boundary, coincident with cooling at the onset of the P3 glaciation (Fielding et al., 2008a; Korte et al., 2008), than in the Artinskian/Kungurian or Roadian/Wordian (Fig. 5B). Extinction between the Wordian and Capitanian was inflated by the loss of the marine record in Tasmania and the Sydney Basin. The short duration of the time series (only four data points, excluding the Wordian/Capitanian because of the bias from record truncation) makes it

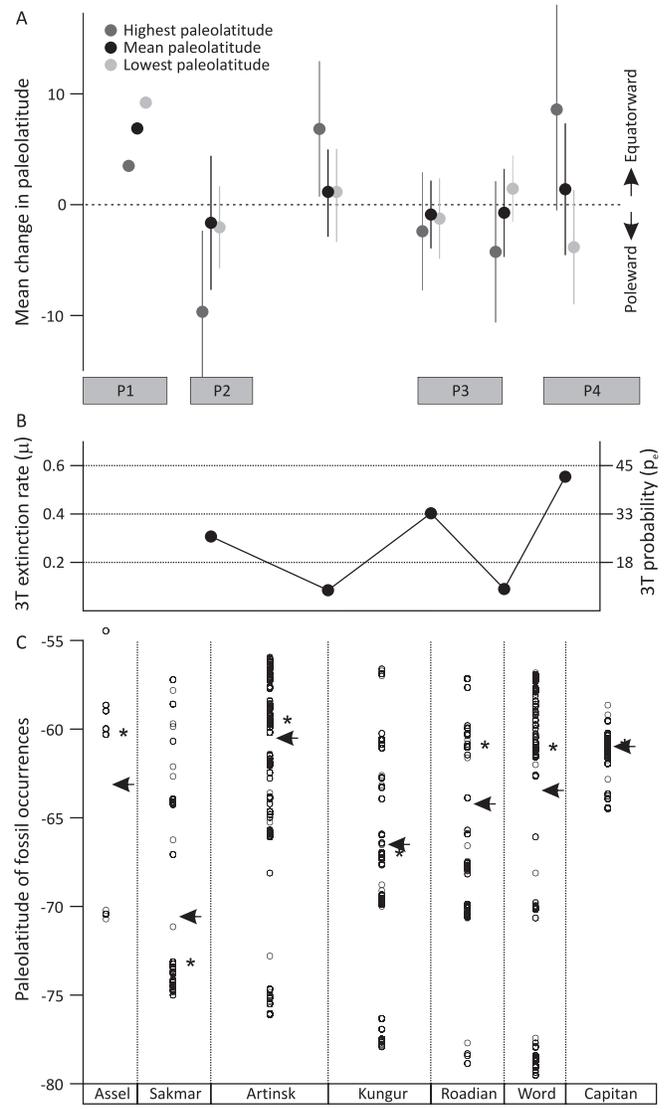


FIGURE 5—Stage-to-stage changes in the paleolatitudinal distribution of eastern Australian invertebrate taxa. A) Mean shift in the highest-latitude, mean, and lowest-latitude recorded paleolatitude of genera. Genera with fewer than five occurrences in each stage were excluded. Paleolatitudinal shifts were adjusted for the distribution of samples by subtracting the shift in the mean position of all fossil occurrences. Error bars are one standard deviation. B) Three-timer extinction rate calculated from SQS standardized diversity data (Alroy, 2010). Three-timer extinction probabilities were calculated from equations in Alroy (2010). C) Paleolatitudinal distribution of all marine invertebrate occurrences in eastern Australia. Arrows mark the mean occurrence, and stars the median.

difficult to determine whether elevated Sakmarian and Kungurian extinctions were random fluctuations or real signals.

Faunal Invasion in Eastern Australia

Evidence for migration of genera within eastern Australia is equivocal, but it is possible that changing climate allowed warm-water taxa to migrate into eastern Australian communities. Although resident cold-water genera, such as the brachiopods *Trigonotreta*, *Echinalosia* and relatives, and *Terrakea* and relatives, or the bivalve *Eurydesma*, were the dominant taxa (albeit at different times) throughout the succession (Waterhouse, 1987; Clapham and James, 2008), warmer-water brachiopods such as *Martinia* and *Spiriferellina* were present locally (e.g., Waterhouse, 1987) and ammonoids occurred but were extremely rare

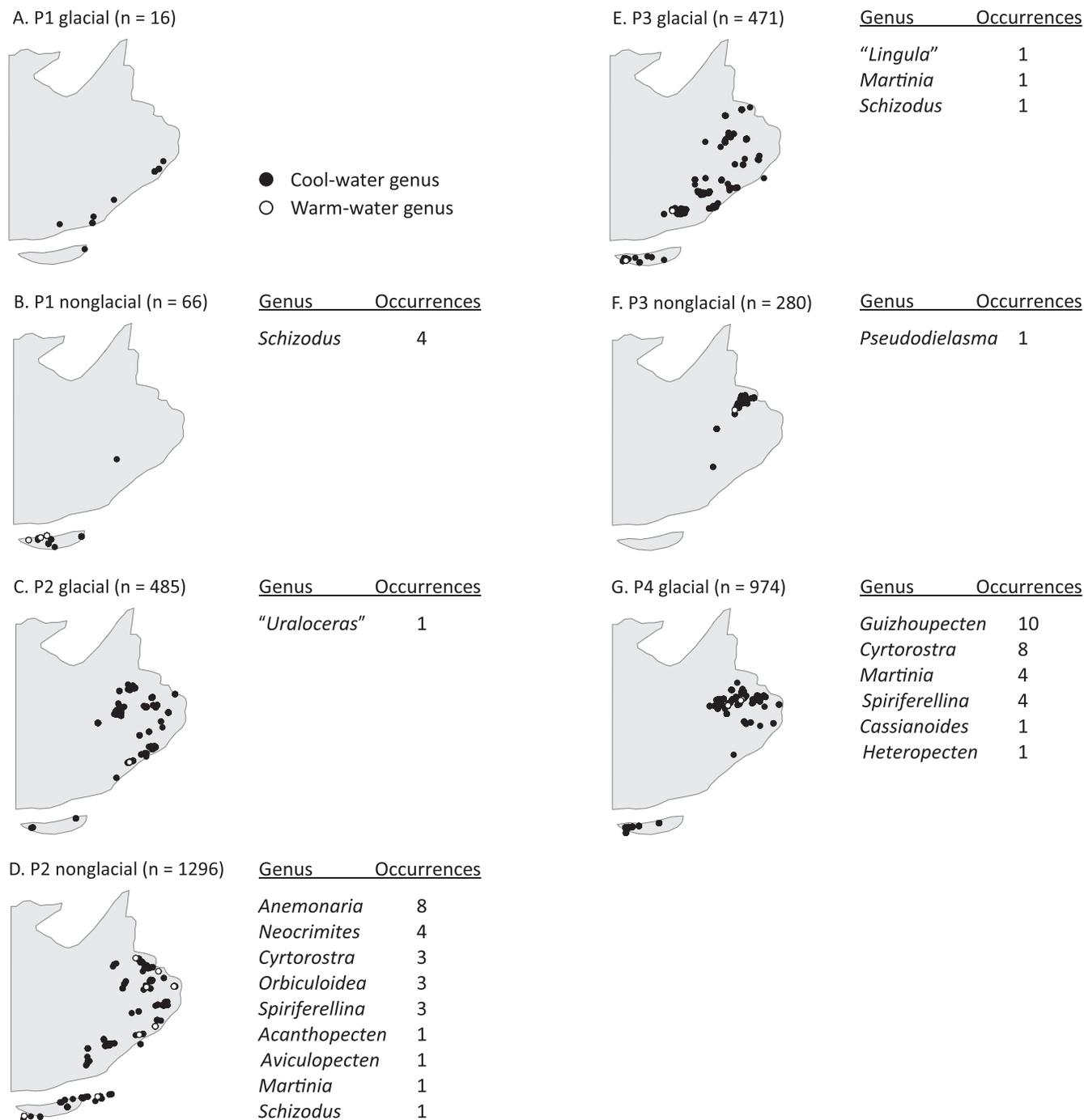


FIGURE 6—Paleogeographic maps showing occurrences of cool-water brachiopods and mollusks (black circles) and warm-water brachiopods and mollusks (white circles, defined as those with an adjusted preferred latitude less than 40°) during glacial-nonglacial intervals in the Permian of eastern Australia. The total number of occurrences in each interval is listed and the adjacent table lists the genus name and number of occurrences for warm-water genera during each time.

(Armstrong et al., 1967). Bivalves exhibited a similar pattern; warmer-water genera such as *Guizhoupecten*, *Cyrtorostra*, and *Cassianoides* were restricted to certain intervals, whereas cold-water resident genera (e.g., *Etheripecten*, *Vacuella*, *Myonia*) occurred throughout the succession.

Brachiopods and mollusks with a warm-water affinity (not strictly tropical taxa but defined here as those with a paleolatitude score less than 40 degrees) were absent or sparse in eastern Australia in the earliest Permian glacials (P1 and P2) and the post-P1 non-glacial (Figs. 6A–B). Although they remained scarce, warmer-water genera became significantly more common (Fisher's exact test comparing counts in P2 glacial and nonglacial; $p = 0.004$) during climate warming following the P2 glacial (Fig. 6D).

Warm-water genera were less common in the P3 glacial and nonglacial (although the stage-to-stage changes are not statistically significant) and then became significantly more common again in the P4 glacial in Queensland (Fisher's exact test comparing P3 nonglacial and P4 glacial counts; $p = 0.01$).

Ammonoids, although not a strictly tropical group, were intolerant of cold waters and thus were extremely rare in eastern Australia during the Permian, represented by only six species from fewer than 10 collections (Armstrong et al., 1967). Most recorded occurrences are in Queensland, the lowest-latitude region of eastern Australia; only three specimens have been described from New South Wales (Teichert and Fletcher, 1943; Teichert, 1954) and none from Tasmania, located near

the paleo-Antarctic circle in the Permian. These rare ammonoid occurrences are clustered temporally as well as spatially. With the exception of “*Uraloceras*” *pokolbinense* (Teichert, 1954) from the Farley Formation, a unit deposited during the P2 glacial episode (Fielding et al., 2008a), all other ammonoid records come from Artinskian or Kungurian formations correlated to the post-P2 nonglacial. These include occurrences of *Neocrimites meridionalis* from the Elderslie Formation of the Sydney Basin (Teichert and Fletcher, 1943); *Archboldiceras lobulatum*, *Archboldiceras whitehousei*, and *Neocrimites* cf. *fredericki* from the upper part of the Homevale Formation in Queensland (Armstrong et al., 1967), and “*Uraloceras*” *cancellatum* from the Yarrol Formation in Queensland (Dear, 1966). The peak abundance of ammonoids during the post-P2 nonglacial coincides with the widespread invasion of warmer-water brachiopod and bivalve taxa, suggesting that these cold-intolerant groups were able to colonize eastern Australia only during the warmest intervals of the Permian.

DISCUSSION

Evidence for Climate-Driven Migration

Eastern Australian marine invertebrate genera did not exhibit consistent latitudinal shifts in response to Permian climate fluctuations, a result that seems inconsistent with evidence for climate-driven range shifts by Pleistocene and recent organisms (e.g., Kitamura et al., 2000; Walther et al., 2002). If true, the absence of migration may suggest that high-latitude Permian invertebrates were unable to cope with the rate of climate changes, an interpretation potentially supported by moderately elevated extinction rates during the two largest climate shifts. However, there are reasons to doubt the face-value interpretation of range-shift data, particularly as the temporal distribution of warm-water genera, common only in warmer time intervals, provides evidence that at least some taxa migrated as climate changed. Sampling limitations or effects of scale are likely important in masking range shift trends within eastern Australia, but the absence of consistent range shifts among most taxa could also indicate underlying biological or environmental differences between brachiopod-dominated communities in the Permian of eastern Australia and molluscan communities in the recent past.

The coarser stage-level resolution of our analyses may obscure migration trends, such as those observed over much shorter timescales in the Pleistocene and recent, because stage-level ranges are likely already a time-averaged signal incorporating range shifts that occurred over Milankovitch timescales. Time averaging of shifting ranges will not necessarily bias the mean recorded paleolatitude of a genus, assuming that Milankovitch-scale range shifts were symmetrical around the longer-term mean, but only if the geographic and temporal scope of sampling is sufficiently dense. Regardless of its effects on the mean recorded paleolatitude, time averaging of ranges will increase the variance of occurrences recorded in a stage. The details of Milankovitch-scale range shifts, assuming they existed among Permian high-latitude marine invertebrates, are unknown, but the geographic distribution of Permian fossil localities is far from uniform and most genera are recorded from only a few occurrences per stage. As a result of the increased variance and shifting ranges, the very sparse sampling is much less likely to recover the true mean paleolatitude in each stage and will therefore obscure actual stage-to-stage shifts unless they are very large.

Taxonomic scale may also influence recognition of range shifts. Although species can migrate in response to climate change, the latitudinal distribution of a genus may not change or may change idiosyncratically due to shifts in the temperature preferences of its constituent species. Many of the common brachiopod genera contained species with short-lived durations (Waterhouse and Shi, 2010) relative to the timescale of glacial-nonglacial climate fluctuations (Fielding et al., 2008a), suggesting that adaptation via speciation could overprint the signal from migration.

It is likely that sampling noise and issues of scale can explain the lack of climate-driven range shifts within eastern Australia. There may, however, be biological or environmental reasons that favored stable paleolatitudinal distributions. Because thermal effects on metabolic oxygen demand are the primary physiological stress during climate warming (Pörtner, 2001), brachiopods may be less susceptible than bivalves because of their low metabolic rates and low oxygen demand, or perhaps more susceptible because of their low aerobic scope (i.e., an inability to supply oxygen when higher metabolic rates are required by activity, or by warmer temperatures) (Peck, 1996). If true, migration trends observed among more metabolically demanding mollusks (Kitamura et al., 2000; Hellberg et al., 2001) may not apply to the more metabolically austere brachiopods. Although brachiopods have extremely low oxygen demands, low metabolic rates are not necessarily beneficial when temperatures increase, however, because they are often accompanied by limited aerobic scope, particularly in cold-adapted stenothermal taxa (Pörtner et al., 2007). Living brachiopods have particularly limited aerobic scopes (e.g., Peck, 2008), implying that Permian genera may have been even more sensitive to warming than bivalves, even if the brachiopods were relatively eurythermal. Increased temperature sensitivity of high-latitude brachiopods would also be consistent with tentative evidence for elevated local extinction in eastern Australia during early Permian climate transitions.

Even if early Permian brachiopods were physiologically sensitive to warming, faunal migration may have been minimal if the climate in eastern Australia was isolated from global climate changes and remained cold. Regional temperature may have been decoupled from overall global warming in the early–middle Permian (e.g., Reid et al., 2007; Clapham, 2010) and the presence of glacially influenced sediments and the cool-water carbonate polymorph glendonite in lower–middle Permian sediments in eastern Australia implies persistent cold conditions, even after deglaciation elsewhere (Jones et al., 2006). The sedimentological evidence is consistent with continued cold temperatures, but only intermittently as part of glacial/nonglacial cycles in eastern Australia (Fielding et al., 2008a). The oxygen isotopic compositions of brachiopod shells also indicate fluctuating seawater temperatures, in particular a major warming trend from the Sakmarian to Artinskian, that broadly parallel the low-latitude record (Korte et al., 2008), rather than consistently cold temperatures.

Regional Climate Change in Eastern Australia

The climatic signature of eastern Australian marine faunas corroborates previously published interpretations for that region based on sedimentological and isotopic proxies, particularly related to the onset of climate warming, the timing of peak warmth, and seawater temperatures during less severe middle Permian (P3 and P4) glaciations. The colonization of eastern Australian basins by warmer-water genera during deglaciation after the P2 glacial (Fig. 6) suggests that this glacial-nonglacial transition was the time of greatest warming in eastern Australia, consistent with the oxygen isotope record (Korte et al., 2008). If P2 deglaciation occurred in the mid-Artinskian (Fielding et al., 2008a), major climate warming in eastern Australia appears to have postdated the mid-Sakmarian deglaciation recorded elsewhere in Gondwana. It is possible that substantial warming also occurred during the Sakmarian, but is not reflected in the distribution of tropical genera, if the temperature warmed but remained below a threshold required by the warm-water genera.

Warm-water brachiopods, bivalves, and ammonoids largely disappeared from eastern Australia with the return of cold conditions, likely linked to upwelling (Jones et al., 2006), in the middle Permian. As a result, the marine faunas of eastern Australia were isolated and decoupled from the overall global warming trend during the Permian, similar to the decoupled regional cooling in the middle and late Permian of northern and northwest Pangea (Reid et al., 2007; Clapham, 2010).

	Tasmania	Hastings Block	Gympie Block	New England Fold Belt	Denison Trough	Bowen Basin
P4	Capitanian					
	Wordian					
P3	Roadian		Curra/ Gigoomgam Limestone			
	Kungurian					
P2	Artinskian	Berriedale Lst	Mt Pleasant Lst Yessabah Lst	Leura Lst Carmila Beds	Dilly Beds	Elvinia Dresden
	Sakmarian	Darlington Lst				
	Asselian					

FIGURE 7—Temporal distribution of carbonate-dominated stratigraphic units in the Permian of eastern Australia (modified from James et al., 2009). With the exception of the Darlington Limestone and part of the Curra/Gigoomgam Limestones, carbonate-rich units are restricted to the Artinskian post-P2 nonglacial. Carbonate units interpreted as the Wordian Oxtrack Formation in James et al. (2009) are most likely the Dresden Limestone, based on the presence of *Eurydesma* bivalves.

Implications for Carbonate Sedimentation in Eastern Australia

Although the Permian succession in eastern Australia is dominated by siliciclastic deposits typical of high-latitude settings, cool-water carbonate units, dominated by brachiopod and bryozoan grains and lacking warm-water allochems like ooids or algae, are common in the upper Artinskian part of the section along the entire continental margin from Tasmania to Queensland (James et al., 2009). With the exception of Sakmarian limestones formed by the prolific accumulation of *Eurydesma* bivalves, carbonates are virtually absent from the rest of the eastern Australian Permian (James et al., 2009). The prevalence of carbonate facies in the late Artinskian and their near absence during other intervals (Fig. 7) mimics the spatial and temporal distribution of ammonoids and warmer-water brachiopod and bivalve genera, suggesting that warmer temperatures in the Artinskian promoted carbonate deposition, even though the carbonates were still cool-water facies. The fact that carbonate deposition was enhanced when temperatures were warmer is not surprising given the temperature dependence of carbonate saturation, but the paucity of limestones in the rest of the succession suggests that there may be a minimum temperature threshold below which carbonate accumulation rates are too low to outpace siliciclastic input (although potentially complicated by climate-driven changes in erosion and/or runoff), except in unusual circumstances such as the *Eurydesma* beds.

Relationship to Local Community Change

Marine communities in eastern Australia underwent substantial compositional change during Permian warming, shifting from dominance by spiriferid brachiopods and the cold-water bivalve *Eurydesma* to dominance by productid brachiopods such as *Echinalosia*, *Terrakea*, and related genera (Clapham and James, 2008). This shift from glacial to post-glacial faunas primarily occurred during the Artinskian post-P2 nonglacial interval, coincident with the invasion of warmer-water genera, and was accompanied by the development of unusual community types dominated by otherwise rare taxa (Clapham and James, 2008). Other examples of paleocommunity change also coincided with species invasions (e.g., Holland and Patzkowsky, 2007), although the role of species invaders in driving ecological change during climate warming is controversial even in modern ecosystems. Some workers argue that altered ecological interactions are more important than temperature changes in driving shifts in dominance (Clarke, 1993; Thomas et al., 2004), whereas others suggest that community change and species invasion could instead both be responding to environmental forcings (Didham et al., 2005; MacDougall and Turkington, 2005; Sax et al., 2007).

Increased seawater temperatures are a plausible common cause for both local dominance shifts and regional faunal invasion. First, warmer conditions would have stressed stenothermal, cold-adapted taxa and favored those with greater aerobic scope (Pörtner et al., 2007), likely leading to changes in local relative abundance. Second, active taxa with higher metabolic rates, such as ammonoids, would only have been successful in eastern Australia when temperatures were warm enough to support their metabolic demands. Cascading ecological effects from the introduction of invasive species may also have contributed to the paleocommunity disruption, beyond the effects of increased temperature, but it is difficult to assess causality.

CONCLUSIONS

Despite limits to the spatial and taxonomic resolution of analyses, the distribution of marine invertebrate groups in eastern Australia provides constraints on Permian climate change and insights into the regional-scale faunal response to post-glacial warming. Latitudinal range shifts cannot be detected in marine invertebrate genera along the eastern Australian margin, possibly because of the low-metabolism and limited-scope aerobic physiology of the dominant brachiopods, but more likely because the broader taxonomic and temporal scale of analyses obscure potentially subtle species-level shifts. Warm-water brachiopod, bivalve, and ammonoid genera entered the region during warmer intervals, however, providing evidence for climate-linked migration in at least some taxa and implying that thermal limits constrained the poleward extent of some Permian taxa. Extinction rates were moderately elevated during Sakmarian-Artinskian (cool to warm) and Kungurian-Roadian (warm to cool), the two largest climate shifts, which could indicate that the rate or magnitude of climate change outpaced the biotic response, possibly providing an alternative explanation for the absence of range shifts. Ammonoids, which likely had greater metabolic oxygen requirements and thus reduced cold-water tolerance because of their active life habits, were almost entirely restricted to the post-P2 nonglacial episode, suggesting that it was the warmest interval of the early or middle Permian in eastern Australia. That conclusion agrees with previously published oxygen isotope proxies (Korte et al., 2008) and with the distribution of carbonate lithofacies in eastern Australia (James et al., 2009).

The appearance of warm-water brachiopod, bivalve, and ammonoid genera was coincident with an episode of substantial paleocommunity restructuring and instability in the region (Clapham and James, 2008). The addition of invasive taxa may have contributed to paleocommunity restructuring via altered ecological interactions, but local and regional changes can both be explained by a common cause from increasing temperature and the resulting physiological stress from increased metabolic oxygen demand. That stress could both drive community restructuring, by promoting shifts in dominance from stenotherms adapted to persistently cold polar waters to more eurythermic groups tolerant of a warming climate, and enable invasion of higher-latitude regions by groups such as ammonoids with more active lifestyles. Similar, although more severe, stresses to respiratory physiology are implicated in the Guadalupian and end-Permian extinctions, but the eastern Australian record indicates that even gradual climate change can induce sufficient physiological stress to trigger substantial biotic changes, particularly among more vulnerable groups such as those living in high-latitude regions.

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