Using GIS to examine biogeographic and macroevolutionary patterns in late Paleozoic cephalopods from the North American Midcontinent Sea (#31237)

First revision

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Using GIS to examine biogeographic and macroevolutionary patterns in late Paleozoic cephalopods from the North American Midcontinent Sea

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Geographic range is an important macroevolutionary parameter frequently considered in paleontological studies as species' distributions and range sizes are determined by a variety of biotic and abiotic factors well known to affect the differential birth and death of species. Thus, considering how distributions and range sizes fluctuate over time can provide important insight into evolutionary dynamics. This study uses Geographic Information Systems (GIS) and analyses of evolutionary rates to examine how in the Cephalopoda, an important pelagic clade, geographic range size and rates of speciation and extinction changed throughout the Pennsylvanian and early Permian in the North American Midcontinent Sea. This period is particularly interesting for biogeographic and evolutionary studies because it is characterized by repetitive interglacial-glacial cycles, a global transition from an icehouse to a greenhouse climate during the Late Paleozoic Ice Age, and decelerated macroevolutionary dynamics, i.e. low speciation and extinction rates. The analyses presented herein indicate that cephalopod species diversity was not completely static and actually fluctuated throughout the Pennsylvanian and early Permian, matching findings from other studies. However, contrary to some other studies, the mean geographic ranges of cephalopod species did not change significantly through time, despite numerous climate oscillations; further, geographic range size did not correlate with rates of speciation and extinction. These results suggest that pelagic organisms may have responded differently to late Paleozoic climate changes than benthic organisms, although additional consideration of this issue is needed. Finally, these results indicate that, at least in the case of cephalopods, macroevolution during the late Paleozoic was more dynamic than previously characterized, and patterns may have varied across different clades during this interval.

Using GIS to Examine Biogeographic and Macroevolutionary patterns in Late Paleozoic Cephalopods from the North American Midcontinent Sea

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Abstract

Geographic range is an important macroevolutionary parameter frequently considered in paleontological studies as species' distributions and range sizes are determined by a variety of biotic and abiotic factors well known to affect the differential birth and death of species. Thus, considering how distributions and range sizes fluctuate over time can provide important insight into evolutionary dynamics. This study uses Geographic Information Systems (GIS) and analyses of evolutionary rates to examine how in the Cephalopoda, an important pelagic clade, geographic range size and rates of speciation and extinction changed throughout the Pennsylvanian and early Permian in the North American Midcontinent Sea. This period is particularly interesting for biogeographic and evolutionary studies because it is characterized by repetitive interglacial-glacial cycles, a global transition from an icehouse to a greenhouse climate during the Late Paleozoic Ice Age, and decelerated macroevolutionary dynamics, i.e. low speciation and extinction rates.

The analyses presented herein indicate that cephalopod species diversity was not completely static and actually fluctuated throughout the Pennsylvanian and early Permian, matching findings from other studies. However, contrary to some other studies, the mean geographic ranges of cephalopod species did not change significantly through time, despite numerous climate oscillations; further, geographic range size did not correlate with rates of speciation and extinction. These results suggest that pelagic organisms may have responded differently to late Paleozoic climate changes than benthic organisms, although additional consideration of this issue is needed. Finally, these results indicate that, at least in the case of cephalopods, macroevolution

during the late Paleozoic was more dynamic than previously characterized, and patterns may have varied across different clades during this interval.

Introduction

Much work has focused on the relationship between geographic range size and rates of speciation and extinction (e.g., Vrba, 1980; Jablonski, 1986; Eldredge, 1989; Stanley, 1990; Lieberman, 2000; Jablonski & Roy, 2003; Rode & Lieberman, 2004, 2005; Kiessling & Aberhan, 2007; Liow, 2007; Payne & Finnegan, 2007; Abe & Lieberman, 2009; Stigall, 2010; Myers & Saupe, 2013; Myers, MacKenzie, & Lieberman, 2013; Dunhill & Wills, 2015; Jablonski & Hunt, 2015; Orzechowski et al., 2015; Saupe et al., 2015; Castiglione et al., 2017; Pie & Meyer, 2017; Simões et al., 2016; Lam, Stigall, & Matzke, 2018; Schneider, 2018). Furthermore, the use of Geographic Information Systems (GIS) has greatly facilitated investigations into this macroevolutionary relationship (Stigall & Lieberman, 2006; Hendricks, Lieberman, & Stigall, 2008; Dunhill, 2012; Myers, MacKenzie, & Lieberman, 2013; Dunhill & Wills, 2015; Lieberman & Kimmig, 2018). Here, we focus on how geographic range size and rates of speciation and extinction changed throughout the Pennsylvanian and early Permian in the North American Midcontinent Sea in the Cephalopoda, an important clade of pelagic invertebrates (Landman, Tanabe, & Davis, 1996; Monnet, De Baets, & C. Klug, 2011; Korn et al., 2015), using GIS. This time interval is particularly interesting for biogeographic and evolutionary analysis because it is characterized by repetitive glacial-interglacial cycles, a global transition from an icehouse to greenhouse climate during the Late Paleozoic Ice Age (LPIA) (Montañez & Poulsen, 2013). Further, it is generally considered a time of sluggish macroevolutionary dynamics, i.e. low speciation and extinction rates and low degrees of faunal turnover, that have been demonstrated in studies of other marine invertebrate taxa (Sepkoski, 1998; Stanley & Powell, 2003; Bonelli & Patzkowsky, 2011). However, Balseiro (2016) did document the existence of some profound evolutionary turnover in bivalves and brachiopods over the course of this interval in regions closer to the ice sheets, such as present-day western Argentina. Furthermore, recently Segessenman & Kammer (2018) showed that advanced cladid crinoids do display elevated rates of evolution and turnover during this time interval (although three other subclasses of crinoids do show subdued evolutionary rates), and fusulinid foraminifera also fit the pattern shown in the advanced cladids (Groves & Lee, 2008; Groves & Yue, 2009; Segessenman & Kammer, 2018).

There have been a variety of hypotheses proposed for the postulated decelerated macroevolutionary dynamics of the LPIA. Some studies contend that this pattern is a result of environmental changes linked to glacial cycling while others point to tectonic activity (Stanley and Powell, 2003; Powell, 2005; Fielding, Frank, & Isbell, 2008; DiMichele et al., 2009; Falcon-Lang & DiMichele, 2010; Bonelli and Patzkowsky, 2011; Cecil, DiMichele, & Elrick, 2014; Segessenman & Kammer, 2018). To date, many of the studies focusing on the macroevolutionary dynamics of the LPIA have concentrated on benthic marine invertebrates (e.g., Stanley & Powell, 2003; Powell, 2007; Bonelli & Patzkowsky, 2011; Balseiro, 2016; Segessenman & Kammer, 2018) as they are highly diverse and very abundant. However, it is valuable to explicitly investigate evolutionary patterns in pelagic marine invertebrates as these are also diverse and abundant organisms in late Paleozoic marine ecosystems (Landman, Tanabe, & Davis,1996; Monnet, De Baets, & Klug, 2011; Korn et al., 2015). In particular, given the significant role that geographic factors play in speciation (Mayr, 1942; Eldredge & Gould, 1972;

Jablonski, 1986; Brooks & McLennan, 1991; Wiley & Lieberman, 2011; Jablonski & Hunt, 2015; Pie & Meyer, 2017), we might expect that pelagic organisms, because of their innately greater dispersal ability (at least as adults), might show different patterns relative to taxa that were benthic (Rojas et al., 2017; Yacobucci, 2017). This greater dispersal ability might allow pelagic organisms to more fully occupy potentially available habitats than benthic organisms, which could lead to larger geographic ranges and also less change in geographic ranges through time. It also could potentially influence patterns of speciation and extinction by dampening opportunities for geographic isolation and creating larger effective population sizes.

This study focuses on cephalopods from the Pennsylvanian-early Permian (Morrowan, Atokan, Desmoinesian, Missourian, Virgilian, and Wolfcampian) in the Midcontinent Sea of the United States as knowledge of the systematic affinities, geographic distribution and overall diversity of cephalopods during this interval is relatively well understood (Miller, Dunbar, & Condra,1933; Newell, 1936; Plummer & Scott, 1937; Miller & Youngquist, 1949; Nassichuk, 1975; Landman, Tanabe, & Davis, 1996; Kröger, 2005; Korn et al., 2015), the stratigraphy of the region is well constrained (Heckel, 2008, 2013), and there are extensive exposures of fossiliferous units in the region. Moreover, at this time the Midcontinent Sea was bordered by the Antler Orogeny to the north, the Ancestral Rocky Mountain Orogeny to the west/northwest and the Ouachita Mountain belt to the south/southeast (as well as various structural arches), such that it constituted a distinct biogeographic region for marine invertebrates (Wells et al., 2007; Nelson & Lucas, 2011; Joachimski & Lambert, 2015).

The Late Paleozoic Ice Age (LPIA) was the longest lived glacial period of the Phanerozoic and is relatively well understood due to numerous stratigraphic, sedimentologic, paleontologic, and isotopic studies (e.g., Mii, Grossman, & Yancey,1999; Isbell, 2003; Stanley & Powell, 2003; Raymond & Metz, 2004; Montañez, 2007; Powell, 2007; Tabor & Poulsen, 2007; Fielding, Frank, & Isbell, 2008; Heckel, 2008; DiMichele et al., 2009; Bonelli & Patzkowsky, 2011; Montañez & Poulsen, 2013; Balseiro, 2016; Roark et al., 2017; Segessenman & Kammer, 2018). Glacial cycling in the midcontinent region has received much study (e.g., Isbell, 2003; Heckel, 2008, 2013). Modern synthesis of the glacial history indicates that the Morrowan to early Desmoinesian represented a localized glacial period, the late Desmoinesian to early Virgilian represented a widespread interglacial period with minor glaciation, and the late Virgilian to early Wolfcampian represented the apex of widespread glaciation (Montañez & Poulsen, 2013). Modeling predicts that sea-level oscillations in the late Pennsylvanian were between 50-100 meters depending upon the number and volume of melting ice sheets, and that water temperatures are estimated to have been between 4-7°C cooler during glacial maxima than inter-glacial periods (Heckel, 1986; Isbell, 2003; Montañez, 2007; Tabor, 2007; Heckel, 2008; Cecil, DiMichele, & Elrick, 2014). The sea-level and temperature changes were likely to have had an important influence on species distribution and geographic range size during this time (Waterhouse & Shi, 2010). Though perhaps pelagic taxa would be less influenced by glacial sea-level cycles than benthic taxa, as these cycles are also known to cause variation in seafloor ventilation, with concomitant dysoxia/anoxia that is more severe for benthic taxa (A. Dunhill, pers. comm., 2018).

Materials and methods

Taxa considered, stratigraphic correlation, specimens examined, and georeferencing: 79 species belonging to 26 genera (13 nautiloids and 13 ammonoids) of cephalopods in the Pennsylvanian-Permian North American Midcontinent Sea were considered (Table S1). These represent the most abundant, well preserved, and taxonomically well understood species. Range reconstructions relied on the occurrence records of specimens derived from a comprehensive consideration of the entire taxonomic literature on the taxa studied. In particular, the following publications were utilized: Cox (1857), Swallow (1858), McChesney (1860), Meek & Worthen (1860, 1870), White & St. John (1867), White (1889), Hyatt (1891, 1893), Keyes (1894), Miller (1892), Smith (1896, 1903), Girty (1911, 1915), Mather (1915) Böse (1919, 1920), Miller (1930), Sayre (1930), Miller, Dunbar, & Condra (1933), Miller & Cline (1934), Miller & Owen (1934, 1937, 1939), Foerste (1936), Miller & Thomas (1936), Newell (1936), Plummer & Scott (1937), Elias (1938a, b), Miller & Moore (1938), Smith (1938), Miller & Furnish (1940a, b, 1957), Teichert (1940), Clifton (1942), Miller & Unklesbay (1942), Young (1942), Sturgeon (1946), Miller, Lane, & Unklesbay (1947), Miller & Downs (1948, 1950), Miller & Youngquist (1947, 1949), Miller, Youngquist, & Nielsen (1952), Kummel (1953, 1963), Ruzhentsev & Shimanskiy (1954), Unklesbay (1954), Arkell et al. (1957), Unklesbay & Palmer (1958), Hoare (1961), Furnish, Glenister, & Hansman (1962), McCaleb (1963), Gordon (1964), Miller & Breed (1964), Teichert et al. (1964), Furnish & Glennister (1971), Ruzhentsev & Bogoslovskaya (1971), Nassichuk (1975), Sturgeon et al. (1982), Hewitt et al. (1989), Boardman et al. (1994), Kues (1995), White & Skorina (1999), Kröger & Mapes (2005), Furnish et al. (2009), and Niko & Mapes (2009) as well as from examination of all specimens, including types, housed in: the Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas (KUMIP); the University of Iowa Paleontology Repository (UI); and the Yale University Peabody Museum of

Natural History (YPM). These institutions house the most complete repository of cephalopod diversity from this region and time as well as contain many of the type specimens of the species examined. Moreover, all specimens used in the analysis were personally examined and taxonomically-vetted via consideration of the literature, relevant type specimens, and other material, with species assignments and determinations made by the first author. Over 1,100 specimens were identified to species level in this study (Kolis, 2017). We chose to focus on the particular species considered, rather than downloading data from the Paleobiology Data Base (PBDB), as we wanted to be able to personally validate the taxonomic identity of specimens using collections data in conjunction with the literature in order to present more rigorously corroborated hypotheses about the geographic distributions of species. We consider this approach to be complementary to those approaches that utilize the PBDB in paleobiogeographic studies. On the one hand, our approach did limit the number of species we were able to consider. On the other hand, we believe it is quite important to evaluate hypotheses about systematic affinities of fossil specimens, the actual data of the fossil record themselves, in detail and thereby accurately define the taxonomic units considered. Given that species represent key macroevolutionary units in nature (Eldredge, 1989; Wiley & Lieberman, 2011; Hendricks et al., 2014), correctly characterizing them taxonomically, and thus validating the scope of their geographic distributions, is critical. Moreover, it has recently been shown by Marshall et al. (2018) that incorporating museum specimen data in the manner that our study has can greatly expand, enhance, and improve knowledge of geographic distributions of fossil species, relative to studies that only utilize data from the PBDB.

Specimens were assigned to the Virgilian, Missourian, Desmoinesian, Atokan, Morrowan, or Wolfcampian stages using the USGS National Geologic Map Database (U.S. Geological Survey, 2017), Sawin et al. (2006, 2008, 2009), Zeller (1968), Pope (2012), and Heckel (2013). The temporal boundaries of stages were derived from Davydov, Korn, & Schmitz (2012) (Table S2). All specimen localities were georeferenced during the course of the study. *GEOLocate* (Rios and Bart, 2018) and the *MaNIS Georeferencing Calculator* (Wieczorek, 2015) were used to obtain coordinates and uncertainty radii. All points were calculated in decimal degrees within the WGS84 model in the *GEOLocate* (Rios & Bart, 2018) world topo layer to ensure consistency and accuracy in determinations. Most uncertainty radii were less than 10 kms. Any specimens with questionable locality information were excluded from analyses, as were specimens with an uncertainty radius larger than the county they were contained within. This left 950 specimens (Table S1) to use in range reconstruction and statistical analysis of geographic range through geologic time. All statistical analyses were performed using Minitab® Statistical Software *Minitab v. 17* (Minitab, 2016) and *R-Studio Version 3.4.0* (2017).

Range reconstruction using GIS: Methods for range reconstruction follow Rode & Lieberman (2004, 2005), Stigall & Lieberman (2006), Hendricks, Lieberman, & Stigall (2008), Myers & Lieberman (2011), Myers, MacKenzie, and Lieberman (2013), and Dunhill & Wills (2015). In particular, after specimen occurrence data were georeferenced and assigned to temporal bins, *Excel* CSV files were compiled for the occurrence points for all specimens within species. CSV files were imported into *ArcGIS v. 10.3* (ESRI, 2014) and layers were created using geographic coordinate system 'WGS 1984' and projected coordinate system 'WGS 1984 World Mercator' (Fig. 1). These layers were input into *PaleoWeb* (The Rothwell Group LP, 2016) to rotate coordinates into continental configuration and geographic position of the midcontinent region during the Pennsylvanian-early Permian (Fig. 2). These paleo-coordinate layers were then re-projected into *ArcMap* (ESRI, 2014).

Geographic range values were calculated for each species (Table S3) using minimum bounding geometry. This method has been shown to provide the most accurate method for reconstructing changes in geographic range, especially for fossil taxa (Darroch & Saupe, 2018). Convex hulls or buffers were given to every specimen occurrence point in each species and these shapefiles were re-projected in ‘South America-Albers Equal Area Conic’. This model was used to accommodate the rotation of species occurrence coordinates into the southern hemisphere during the Late Paleozoic. Species with three or more occurrence points were given a convex hull that spanned the entire area between occurrences. In this way, multiple occurrence points were combined to recreate the geographic range of a single species. Species with only one occurrence point were given a 10km^2 buffer; species with just two occurrence points were given a 10km^2 wide buffer which was used, in conjunction with their distance, to derive an area value (following Rode & Lieberman [2004, 2005], Hendricks, Lieberman, & Stigall [2008], Myers & Lieberman [2011], and Myers, MacKenzie, and Lieberman [2013]).

Assessing fossil record bias: A common concern when studying the fossil record is that there might be biases that could lead to inaccurate or artifactual findings. This concern can be manifold, but the two most pertinent issues here involve incomplete sampling and/or issues of stratigraphic bias. While it is important to be aware of the fact that the fossil record is incomplete, it is worth recognizing that there is a large body of research that demonstrates many of the biogeographic patterns preserved in the fossil record, particularly in marine settings, represent real biological phenomena, rather than taphonomic artifacts (Myers & Lieberman, 2011; Rook, Heim, & Marcot, 2013; Dunhill & Wills, 2015). Further, it is also prudent to realize that sampling bias is a common issue in studies of extant biodiversity and species distribution, and much work needs to be done in this area to alleviate the biases of the extant biota (Lieberman, 2002; Carrasco, 2003).

The possibility that biases in the fossil record might lead to artifactual results was assessed in a few different ways. First, the relationship between outcrop availability and the geographic range of Pennsylvanian and Permian cephalopods was determined (see Myers & Lieberman, 2011). A percent coverage table of the range size of species overlaid against temporal outcrop availability was created using *ArcGIS v. 10.3* (ESRI, 2014). A low percentage of overlap between range size and outcrop area would suggest species distributions are more likely to reflect 'real' biogeographic patterns while a high percentage of overlap would suggest the presence or absence of outcrop was significantly influencing results (Myers & Lieberman, 2011; Myers, MacKenzie, & Lieberman, 2013; however, see also Dunhill, 2012 for an alternative viewpoint). The second test used was an "n-1" jackknifing analysis. This procedure sub-sampled species range size within each temporal bin to test the resilience of data to outliers. Mean range size estimations were generated for each temporal bin; these were input into a one-way ANOVA to compare jackknife estimates with the initial geographic range size estimates (Myers & Lieberman, 2011; Myers, MacKenzie, & Lieberman, 2013). Finally, a Pearson rank correlation test was performed to test the association of occurrence points and geographic range size; a close correlation would indicate that reconstructed ranges were very much dependent on sampling and suggest that reconstructed biogeographic patterns might be an artifact of a biased fossil record (Myers, MacKenzie, & Lieberman, 2013).

Speciation and extinction rate calculations: Speciation and extinction rates were calculated in order to consider macroevolutionary dynamics in cephalopods from the Late Paleozoic Midcontinent Sea. Macroevolutionary rates were calculated using the following equation, presented in Foote (2000) and Rode & Lieberman (2005):

$$N_f=N_0e^{rt}$$

where N_0 is the species richness at the beginning of a temporal bin, N_f is the species richness at the end of a temporal bin, t is the duration of a temporal bin, and r is the total rate of diversity change. The temporal bins used were North American stages (Table S2). Species richness values (N_f) were determined for each temporal bin and were parsed into 'carry-over' (N_0) and 'new' species richness values to ensure the accuracy of speciation and extinction rate calculation. In this way, it was possible to calculate the rate of diversity change between bins. For example, $r_{Atokan}= (\ln N_{0\text{-}Desmoinesian} - \ln N_{0\text{-}Atokan})/ t_{Atokan}$. Speciation rate within each temporal bin was calculated using the equation $S_{Atokan}= (\ln N_{f\text{-}Atokan} - \ln N_{0\text{-}Atokan})/ t_{Atokan}$, and extinction rate within each temporal bin was calculated using the equation $E_{Atokan}= S_{Atokan} - r_{Atokan}$ for each temporal stage (Foote, 2000; Rode & Lieberman, 2005).

Results

Paleobiogeographic patterns: Geographic range data were analyzed separately across all cephalopods and individually for both nautiloids and ammonoids. Species geographic range size data were tested for normality within each temporal stage using the Anderson-Darling normality test. Range size data within each temporal stage were not normally distributed for any data combination ($P < 0.005$). Instead, distributions were left skewed across all temporal stages for every data grouping. Data were subsequently log-transformed to normalize data, and statistical analyses were performed on both original and transformed data.

In general, geographic range size (either mean of transformed data or median of original) of ammonoids and nautiloids increases during the Missourian and Virgilian stages (Fig. 3), which was a time of sea-level rise due to warming during an interglacial (Isbell, 2003; Montañez & Poulsen, 2013), such that there may be an association between the sea-level rise and the increase in geographic range. Another possibility is that there was some change in taphonomic conditions that occurred during the Virgilian that made it easier to discern the actual biogeographic distributions of species at this time, relative to other time intervals (G. Pineiro, pers. comm., 2018). However, none of the changes in geographic range were statistically significant, so it is not possible to infer strong correlation between the sea-level rise, or possible taphonomic factors, and the range expansion. For instance, Mann-Whitney U tests found no statistically significant changes (at $P \leq 0.05$) in median geographic range size for any temporal stages separately across all cephalopods, as well as individually for nautiloids and ammonoids, even prior to correction for multiple comparisons. This is because with the Mann-Whitney U test median range values are considered, and for all cephalopods the median range values are constant through time ($79 km^2$).

The same was true for two-sample t-tests performed on log-transformed data which again found no statistically significant changes (at $P \leq 0.05$) in mean geographic range size though time, even prior to correction for multiple comparisons. Again, recall that *mean* range size data are shown in Figure 3, and the differences among log-transformed data through time are far less substantial (and ultimately not significant). Furthermore, a one-way ANOVA, either with or without the assumption of equal variance, failed to find any significant differences (at $P \leq 0.05$) between stages for log-transformed mean geographic range size across all cephalopods as well as individually for nautiloids and ammonoids.

Analysis of macroevolutionary rates: Speciation rate (S) and extinction rate (E) were calculated for the Atokan, Desmoinesian, Missourian, and Virgilian stages across all cephalopods and within nautiloids and ammonoids, respectively. The S and E presented across all cephalopods are comprised of two calculations; one calculation included taxa that only occurred in a single temporal stage (Table 1; Fig. 4), while the other calculation excluded taxa that occurred in a single temporal stage (Table S4). S and E was also calculated for ammonoids and for nautiloids including (Tables S5, S6) and excluding taxa that occurred in a single stage (Tables S7, S8). Note, due to the dependence of calculations on diversity metrics from both adjacent stages, it is not possible to accurately calculate the rate of biodiversity change (R), or S and E for the first stage considered, the Morrowan, nor R or E for the last stage considered, the Wolfcampian (these are thus left blank in Table 1 and Tables S4-S8). While it might have been possible to infer S and E using other methods, to do so would exaggerate the significance of edge effects and thus be problematic (Foote, 2000).

Across all cephalopods, S was high in the Atokan and Desmoinesian, fell in the Missourian, and reached very low levels in the Virgilian and Wolfcampian (Fig. 4). By contrast, E was low in the Atokan and Desmoinesian, began to rise in the Missourian, and reached even higher levels in the

Virgilian (Fig. 4). Essentially, across all cephalopods examined, when S is high, E is low, and when S is low, E is high. This is potentially contrary to the pattern expected with an ecological opportunity model of speciation (Simões et al., 2016), although the specific processes driving the diversification could not be determined at this time. However, it is possible that when S was high there may have been many short-lived species that could not be sampled that were actually going extinct, and this phenomenon would artificially depress E.

As expected, S and E are lower when singletons are excluded (see Tables 1, S4). (See Segesseman & Kammer [2018] for a recent discussion of how singletons can affect manifest patterns in these types of studies.) Notably though, S and E patterns diverge somewhat between ammonoids and nautiloids when considered individually. For instance, in nautiloids S is high in the Atokan and Desmoinesian, then declines to moderate in the Missourian, and is at its lowest in the Missourian and Wolfcampian (Table S6), whereas in ammonoids S is only high in the Atokan, declines to moderate in the Desmoinesian, declines somewhat more in the Missourian and then remains essentially constant through the Wolfcampian (Table S5). In addition, E is low in ammonoids during the Desmoinesian and Missourian but high in the Atokan and Wolfcampian (Table S5), whereas in nautiloids there are no observed extinctions during the Atokan; values remain quite low for nautiloids in the Desmoinesian, rise somewhat in the Missourian, and then rise again in the Virgilian (Table S6).

An important caveat regarding the calculation of S is that many of the species analyzed belong to genera that were widely distributed beyond the Midcontinent Sea during the Late Paleozoic. Thus, although none of the species considered in these analyses occurred outside of the

Midcontinent Sea, their close relatives did. It is conceivable that while speciation events and rates by necessity are treated as occurring *in situ* herein, this might not always have been the case. Instead, some speciation events could have occurred outside of the Midcontinent Sea with subsequent invasion events into that region. These invasions would appear as *in situ* speciation events in this analysis, although they actually were not. In the absence of phylogenetic hypotheses for the genera considered it is not currently possible to consider how much of the pattern pertaining to speciation rate shown in Fig. 4 is due to invasion instead of speciation. Further, a related phenomenon could affect the calculation of E: at times what were treated as extinction events might have simply been local extinctions in the Midcontinent Sea which could have included emigration to other regions. As mentioned previously, it does not appear that any of the species considered occur outside of the Midcontinent Sea, but a phylogenetic hypothesis for these groups would be valuable for considering this issue in greater detail.

Relationship between biogeography and macroevolutionary rates: Mean geographic range size increased during the Missourian and Virgilian and declined in the Wolfcampian (Fig. 3); speciation rates were high in the Atokan and Desmoinesian and fell in the Virgilian (Fig. 4); extinction rates were low in the Atokan and Desmoinesian and rose in the Virgilian (Fig. 4). The Pearson correlation test in *Minitab 17* (Minitab, 2016) was used to examine the association between geographic range and either speciation rate extinction rate in greater detail. No significant (at $P \leq 0.05$) correlation between speciation or extinction rate and range size was found across all cephalopods or within ammonoids or nautiloids individually (Table 2). However, in cases the values approach $P = 0.05$: for instance, the association between decreasing geographic range size and increasing extinction for all cephalopods and for ammonoids alone. Notably, an association between decreasing geographic range size and increasing extinction has been documented by numerous studies (e.g. Vrba, 1980; Jablonski, 1986; Eldredge, 1989; Stanley, 1990; Jablonski & Roy, 2003; Rode & Lieberman, 2004, 2005; Kiessling & Aberhan, 2007; Payne & Finnegan, 2007; Stigall, 2010; Dunhill & Wills, 2015; Jablonski & Hunt, 2015; Orzechowski et al., 2015; Saupe et al., 2015; Castiglione et al., 2017; Pie & Meyer, 2017; Lam, Stigall, & Matzke, 2018; Schneider, 2018) and thus is a very robust phenomenon in general and likely to be operating to some extent herein. However, over this time interval and for this particular group of species the association is not statistically significant (Table 2), probably because sample sizes are not large, and further this is likely because many taxa were culled by the late Mississippian extinction (M. Powell, pers. comm., 2018).

Analysis of fossil record bias: The low percentage of overlap between cephalopod species geographic ranges and available outcrop, less than 1% in 29 out of 30 species (Table S9; the one species with a larger percentage value, *Orthoceras kansasense*, occurs throughout the Midcontinent Sea), suggests the results are not simply an artifact of an incomplete fossil record, at least pertaining to outcrop availability. The "n-1" jackknifing analysis also supports the robustness of the reconstructed ranges, as no statistically significant differences were found between the mean of the reconstructed and subsampled range values for any time interval (all P-values > 0.9), suggesting that one or a few occurrence records are not having a major influence on biogeographic patterns. Similar results were found in other taxa and time periods by Hunt, Roy, & Jablonski (2005), Myers & Lieberman (2011), and Myers, MacKenzie, & Lieberman (2013), although Dunhill, Hannisdal, & Benton (2014) did find some association between outcrop area and diversity in the case of the marine fossil record of Great Britain. Finally, the Pearson correlation test shows no correlation (-0.055, P-Value = 0.789) between the number of occurrence points and geographic range size; this provides further evidence that the biogeographic signatures of Late Paleozoic cephalopods are unlikely to be simply an artifact of the fossil record.

Diversity patterns: Across all cephalopods, species richness increased from the Morrowan to the Atokan, peaked in the Desmoinesian, and decreased through the Wolfcampian (Fig. S1). A similar pattern is seen in the nautiloids (Fig. S2). However, the ammonoids (Fig. S3) demonstrate an earlier peak in the Atokan, followed by a Desmoinesian to Virgilian plateau, with a decrease in the Wolfcampian. Notably, previous studies of Late Paleozoic brachiopod communities in Bolivia showed a consistent trend between diversity and glacial cycling with increased diversity during glacial periods and decreased diversity during inter-glacial periods (Badyrka, Clapham, & Lopez, 2013). However, there seems to be less consistency between species richness trends and glacial cycling in the Midcontinent Sea. For instance, there is an increase in cephalopod species richness throughout the Morrowan to Desmoinesian associated with localized glaciation, and an interglacial period with generally minor glaciation is associated with a decrease in cephalopod species richness from the Desmoinesian to Virgilian, yet by contrast widespread glaciation is associated with a decrease in species richness from the Virgilian to the Wolfcampian. An important point, however, is that these are just raw diversity patterns and sample standardized diversity patterns show a different result (M. Powell, pers. comm., 2018).

Discussion

Geographic range shifts through time are one of the pervasive phenomena in the history of life; these are manifest both within species and higher-level clades, occur at a number of different time scales, and are frequently linked to climatic change (Wiley & Lieberman, 2011). Specific examples do come from the Late Paleozoic, a time of extensive climate change including profound glaciation along with numerous glacial and interglacial cycles (Montañez and Poulsen, 2013). Those changes impacted patterns of geographic range in both terrestrial plant (e.g., DiMichele et al., 2009; Falcon-Lang & DiMichele, 2010) and marine invertebrate ecosystems (e.g., Leighton, 2005; Powell, 2007; Waterhouse & Shi, 2010). When it comes to marine invertebrates from this time interval, most of the focus has been on the highly diverse benthic faunas (e.g., Stanely & Powell, 2003; Powell, 2007; Bonelli & Patzkowsky, 2011; Balseiro, 2016; Segessenman & Kammer, 2018); however, taxa that have a pelagic life style (as adults) are also worth examining. Herein, 79 pelagic species of cephalopods were examined for patterns of range size change using GIS and although in general these species exhibit some evidence for changes in geographic range size (Fig. 3), those changes were not statistically significant nor can they be directly tied to climate change. In a similar vein, many paleontological studies have demonstrated that species with larger geographic ranges tend to have lower extinction rates than species with narrower geographic range sizes (e.g., Vrba, 1980; Jablonski, 1986; Eldredge, 1989; Stanley, 1990; Rode & Lieberman, 2004; Stigall & Lieberman, 2006; Payne & Finnegan, 2007; Stigall, 2010; Hopkins, 2011; Dunhill & Wills, 2015). Again, this phenomenon was not found to be statistically significant in the case of the Late Paleozoic cephalopod species considered herein (Table 2).

There may be a few different explanations for these findings. First, it may be that cephalopod species were not significantly affected by the glacial-interglacial climatic cycles transpiring within the Late Paleozoic Midcontinent Sea. A second possible explanation, perhaps coupled to the first, is that since cephalopods are highly mobile relative to benthic marine invertebrates such as gastropods, bivalves, brachiopods, etc., they can more easily occupy a greater portion of their potential range relative to taxa that are benthic (at least as adults). Further, perhaps the available potential range of cephalopod species does not change much in glacial relative to interglacial regimes. This may seem unlikely given the vast fluctuations in sea level occurring at the time, but pelagic marine organisms, because of their ease of dispersal, may more easily maintain consistent geographic ranges relative to benthic counterparts. Another possible explanation for the pattern retrieved is that, given the limits of stratigraphic correlation, sample size, and the completeness of the fossil record, it was necessary for the analyses of species distribution conducted herein to focus on the time scale of geological stages, whereas in actuality there were climatic changes occurring within stages (Heckel, 2008, 2013); these probably did cause fluctuations in species' geographic ranges within stages, but simply could not be observed in the present study. A final set of explanations are related to the issue of sampling. For instance, it was more difficult for the analyses presented herein to detect a relationship between geographic range size and macroevolutionary rate because speciation and extinction rates could only be calculated for four stages. Further, a common concern when studying the fossil record is that there might be biases that can lead to inaccurate findings. This concern can be manifold, and although it is not entirely obviated by the results presented regarding the apparent quality of the fossil record suggested by the various tests presented, it does become harder to invoke as a specific, primary reason for results retrieved.

Another finding perhaps contrary to what might typically be expected for the Late Paleozoic is that there was at least some evolutionary diversification and turnover within cephalopods, such that species diversity did fluctuate throughout the Pennsylvanian and early Permian. Pennsylvanian rates of macrevolution are typically classified as 'sluggish' or 'stolid' across all marine animals, and Sepkoski (1998) formalized the notion that there was a marked decline in evolutionary rates of Carboniferous and Permian marine faunas. Stanley & Powell (2003) reiterated this result and identified low mean macroevolutionary rates for marine invertebrate taxa. Bonelli & Patzkowsky (2011) also documented a pattern of low turnover in the face of major episodes of sea-level rise and fall due to climatic change. The results from the analyses presented herein could indicate that macroevolutionary rate, at least in the case of Late Paleozoic cephalopods, was more dynamic than often thought. One possible reason for this result is that cephalopods are a fairly evolutionarily volatile group (Lieberman & Melott, 2013) relative to many other marine invertebrate groups and have relatively high rates of diversification (Stanley, 1979; Jacobs et al., 1994; Landman, Tanabe, & Davis,1996; Monnet, De Baets, & Klug, 2011; Korn, Klug, & Walton, 2015; Korn et al., 2015); thus, they would generally be expected to have higher rates of speciation and extinction than typical. However, this may not be the entire explanation, as other groups also seem to show elevated rates of speciation and extinction during this time interval. For instance, Balseiro (2016) did document evolutionary turnover at high latitudes, and elevated evolutionary rates have also been found in fusulinid foraminifera (Groves & Lee, 2008; Groves & Yue, 2009) and advanced cladid crinoids (Segessenman & Kammer, 2018). Ultimately, we support the contention raised by Segessenman & Kammer (2018) that patterns from a few individual groups do not refute the general pattern of sluggish macroevolution postulated for this time period in the history of life. The results may lend credence to the notion that macroevolutionary patterns across all marine animals are rarely unitary for any one time period in the history of life, and instead often tend to be variegated.

Conclusions

Patterns of range size change in late Paleozoic cephalopods from the North American Midcontinent Sea were investigated using GIS. These species do exhibit some evidence for changes in geographic range size through time, but the changes were not statistically significant nor could they be directly tied to climate change. Further, in contradistinction to what is usually found in the fossil record, cephalopod species with larger geographic ranges were not found to have lower extinction rates than species with narrower geographic ranges. These distinctive patterns may perhaps be related to the fact that cephalopods are pelagic and highly mobile, at least relative to many benthic marine invertebrates. Finally, the group shows more evolutionary diversification and turnover during the Pennsylvanian and early Permian than is typical of other marine invertebrate groups and this could be related to the fact that cephalopods are an evolutionarily volatile group.

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Figure Captions

Figure 1: Distribution of Pennsylvanian and early Permian cephalopods.

A) Distribution of Pennsylvanian nautiloid and ammonoid data points (red) and B) early Permian nautiloid and ammonoid data points (blue) across the midcontinent region of North America. Plotted using *ArcGIS v. 10.3* (ESRI, 2014) software at 1: 20,000,000.

Figure 2: Occurrence points of *Metacoceras* sp. and *Mooreoceras* sp.

For the Virgilian, shown on possible paleogeography of that stage, at 1:1,000,000,000 scale; plotted using *PaleoWeb* (The Rothwell Group LP, 2016).

Figure 3: **Mean geographic range size in km^2 of cephalopods through time.**

Nautiloid species (A) and ammonoid species (B) range changes occur but are not statistically significant when analyzed using non-parametric tests (note, median range size data not graphed but for all cephalopods they are 79km^2 for all time intervals, for ammonoids they are 78.5km^2 for the Desmoinesian and Wolfcampian and 79km^2 for all other time intervals, and for nautiloids they are 79km^2 for all time intervals) or when log transformed data are analyzed using parametric tests (note log transformed data not graphed but mean transformed values for all cephalopods are 5.51 [standard error 0.75] for the Morrowan, 4.05 [standard error 1.02] for the Atokan, 4.36 [standard error 0.49] for the Desmoinesian, 5.65 [standard error 0.49] for the Missourian, 5.96 [standard error 0.79] for the Virgilian, and 4.31 [standard error 0.52] for the Wolfcampian).

Figure 4: **Speciation and extinction rates through time.**

Values given in per Myr and derived from Table 1.

Table 1(on next page)

Speciation rates (S) per millions of years (Myr), extinction rates (E) per Myr, and rate of turnover (R) per Myr, for each stage across all cephalopods.

Species richness values, species carryover from the previous stage, new species originating in the stage, N_o, N_f, and duration (in Myr) also given.

Table 1:

Speciation rates (S) per millions of years (Myr), extinction rates (E) per Myr, and rate of turnover (R) per Myr, for each stage across all cephalopods, with species richness values, species carryover from the previous stage, new species originating in the stage, N_o, N_f, and duration (in Myr) also given.

Stage	Species Richness	Species Carryover	New Species	N_o	N_f	Duration	R	S	E
Wolfcampian	13	7	6	7	13	14		0.0442	
Virgilian	38	32	6	32	38	5	-0.3040	0.0343	0.3383
Missourian	55	33	22	33	55	3	-0.0103	0.1703	0.1805
Desmoinesian	41	12	29	12	41	3	0.3372	0.4096	0.0724
Atokan	15	7	8	7	15	2	0.2694	0.3811	0.1116
Morrowan	8	0	8	0	8	6			

Table 2(on next page)

Pearson correlation test for association between S and geographic range and E and geographic range across all cephalopods and for ammonoids and nautiloids individually.

Pearson’s r and P-values given.

Table 2:

Pearson correlation test for association between S and geographic range and E and geographic range across all cephalopods and for ammonoids and nautiloids individually, with Pearson's r and P-values given.

Taxon – Speciation	**Pearson's r**	**P-value**	**Taxon – Extinction**	**Pearson's r**	**P-value**
All Cephalopods – S	-0.541	0.347	All Cephalopods – E	0.925	0.075
Nautiloids– S	-0.463	0.432	Nautiloids – E	0.913	0.087
Ammonoids – S	-0.519	0.370	Ammonoids – E	0.803	0.197

Figure 1

Distribution of Pennsylvanian and early Permian cephalopods.

A) Distribution of Pennsylvanian nautiloid and ammonoid data points (red) and B) early Permian nautiloid and ammonoid data points (blue) across the midcontinent region of North America. Plotted using ArcGIS v. 10.3 (ESRI, 2014) software at 1: 20,000,000.

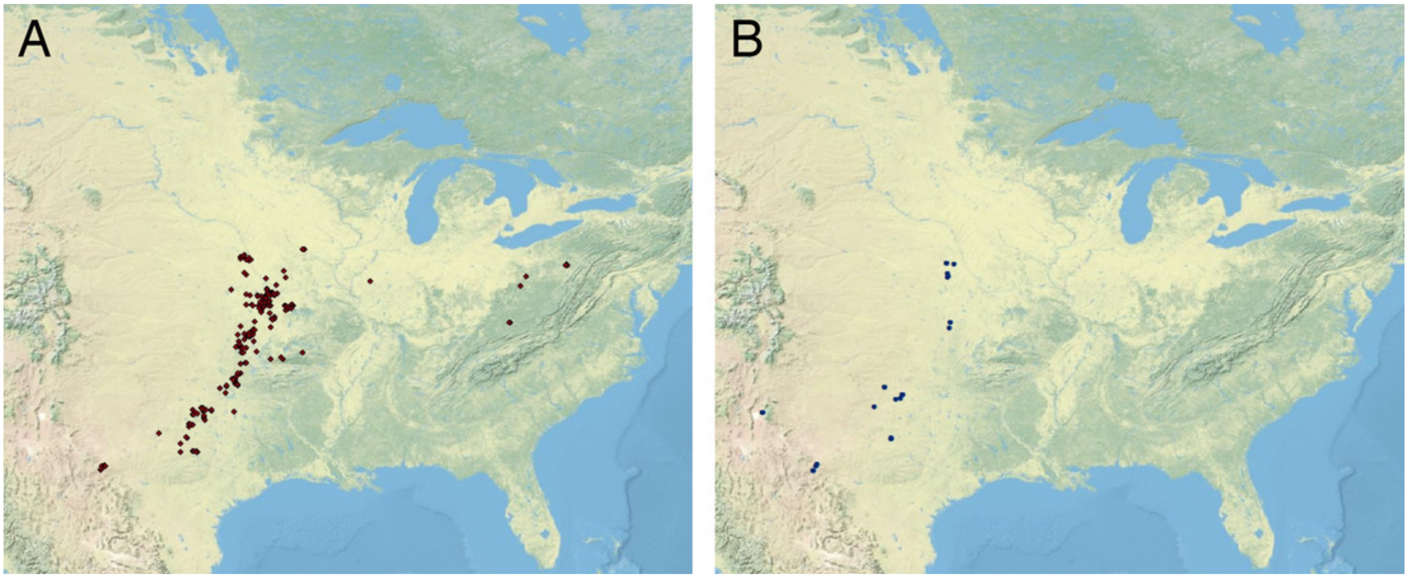

Figure 2

Occurrence points of Metacoceras sp. and Mooreoceras sp.

For the Virgilian, shown on possible paleogeography of that stage, at 1:1,000,000,000 scale; plotted using PaleoWeb (The Rothwell Group LP, 2016).

Figure 3

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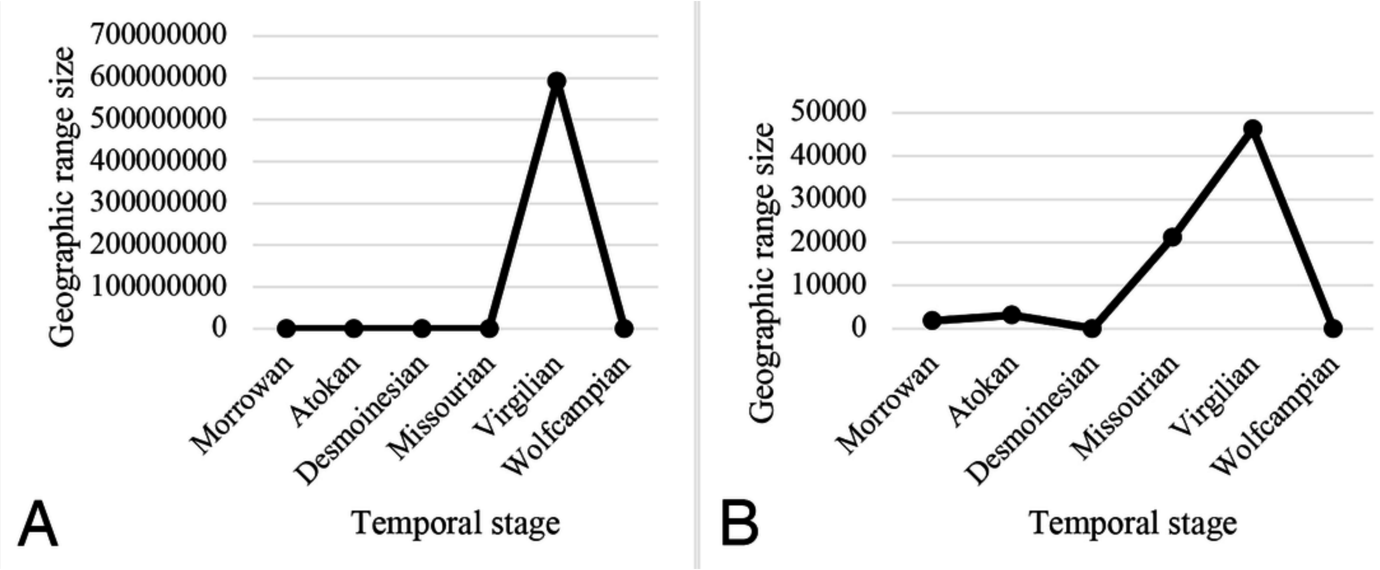

Figure 4

Speciation and extinction rates through time.

Values given in per Myr and derived from Table 1.