EVIDENCE FOR SEASONAL VARIATION IN δ^{13} C and δ^{18} O profiles of *baculites* and implications for growth rate

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Abstract: The life histories of ammonites and the life strategies they employed are difficult to assess without robust modern analogues but placing constraints on ammonite growth rates provides a fundamental first step to understanding this abundant, but poorly understood, fossil group. Here we interpret periodic variations in carbon and oxygen stable isotope profiles from Campanian and Maastrichtian ammonites (*Baculites*) as seasonally driven and use these records to determine their rate of shell precipitation. Several of these samples are housed in museums and were originally prepared using sealants for display and preservation but testing of these sealants indicated no alteration of the isotopic values of treated carbonate. Diagenetic alteration, as determined by shell microstructure, affected the preservation in less well-preserved

AMMONITES are among the most common marine invertebrate fossils of the Mesozoic, but surprisingly little is known with certainty about their ecology. The variation in ammonite morphotypes has been reasonably interpreted to represent differences in lifestyle strategies, but there are few tools available to unequivocally test these hypotheses. Stable isotopic analysis of shell carbonate, particularly comparing different ammonites with cooccurring foraminifera or benthic molluscs, has proven successful in determining the placement of ammonites within the water column in some settings (e.g. Moriya et al. 2003; Sessa et al. 2015) though these results may not capture the true extent of water column habitat if ammonites adopted similar depth migration patterns as the modern Nautilus (Dunstan et al. 2011; Linzmeier et al. 2016, 2018). Previous isotopic work has examined ontogenetic trends in δ^{13} C and δ^{18} O from planispiral ammonites, with varying interpretations depending on the taxonomic group studied (Lukeneder et al. 2010; Lukeneder 2015; Moriya 2015; Stevens et al. 2015), while work on Baculites has been limited by small samples sizes specimens, and the δ^{13} C signal is more robust than δ^{18} O. The periodicity of isotopic profiles from *Baculites* shells presented here suggest that these organisms grew at rapid rates (*c*. 340 mm per year), which may imply an r-type life strategy in which the animals reach maturity quickly, spawn large quantities of progeny, and die at a young age. Because of the potential mobility of *Baculites*, reconstructing palaeoenvironmental conditions from these isotopic records is challenging and should be conducted cautiously. Unfortunately, well-preserved *Baculites* shells much longer than 350 mm are rarely recovered, which complicates the statistical treatment of potential periodicity in isotopic profiles.

Key words: *Baculites*, sclerochronology, ammonite, palaeo-ecology, stable isotopes, seasonal signals.

(Fatherree et al. 1998) or short sample lengths (Landman et al. 2018).

In addition to uncertainties in their preferred habitats, little is known about the lifespan and/or growth rate of ammonites, as the lifespans of modern relatives range from as short as a year (squid) to as long as 20 years (Nautilus; Immenhauser et al. 2016). While Nautilus is the only extant externally shelled cephalopod, there are a variety of differences noted between it and ammonoids that have been used to argue for non-analogous lifestyles between the two groups (Jacobs & Landman 1993). Other cephalopods, such as Spirula, have been proposed as more appropriate analogues (Warnke & Keupp 2005; Lukeneder et al. 2008). Without a clear modern analogue, life span is a challenging question to address in most fossil groups, including ammonites. While some molluscs, most notably bivalves, record annual banding in their shells, no study has yet related any seasonality to physically manifested growth banding in ammonite shells. Several methods have been employed to estimate lifespan in ammonites, which have been summarized well in the recent reviews

(Lukeneder 2015; Moriya 2015) but none provide unequivocal answers to ammonite growth rate or lifespan.

Here we present isotopic data that provide consistent estimates of growth rate in several species of *Baculites*. Our approach relies on examining periodicity in stable isotopic signals from fossil shell material and requires exceptional physical and geochemical preservation, which places limitations on the use of this technique. Our data support a growth rate of approximately 340 mm/a, which is rapid but not unreasonable when compared to some modern mollusc shell growth rates. However, this growth rate makes locating specimens long enough with multi-year isotopic records challenging, which complicates statistical interpretations. These constraints on growth rates further provide a means of estimating baculitid longevity and evaluating their probable life strategies, though it is unclear if these estimates translate to other genera of ammonoids.

Baculites

Baculites is notable among ammonite genera in that it has primarily orthoconic morphology, which provides some benefits to sequential sampling techniques employed here, but caution should be taken when extrapolating these results to other ammonite genera. Ammonites, like other molluscs, build accretional carbonate shells, but the mobility of ammonites makes interpreting growth records as environmental proxies more challenging when compared to obligately benthic organisms like bivalves (e.g. Immenhauser et al. 2016). Bivalves will inherently record changing environmental conditions (temperature, water chemistry, etc.) in their shells since they are largely unable to migrate geographically or in the water column (e.g. Buick & Ivany 2004; Schöne & Gillikin 2013; Immenhauser et al. 2016). Most bivalves have preferences for temperature (or other environmental variables) of shell construction that lead to seasonal cessations in growth with corresponding bands marking annual increments (Ivany 2012). Sequential stable isotopic sampling of bivalve shells generally supports the interpretation of these bands as seasonal markers and records variation in temperature and other water chemistry variables over the course of a growth season.

Unlike bivalves, ammonites, whether they are demersal, pelagic or planktonic, possessed some ability to move or migrate and may therefore never record obvious annual banding because they did not have to remain in conditions that are suboptimal for growth. While no physical structures may be preserved, ammonites probably experienced some form of seasonal variation from seasonal migration, either vertically in the water column or geographically, or from varying environmental conditions in their habitat. *Baculites* in particular is thought to have adopted a demersal lifestyle (Sessa *et al.* 2015) which may

negate complications from vertical migration. However, modern demersal cephalopods (*Sepia*) are known to undertake significant lateral seasonal migrations (Wang *et al.* 2003). While migration makes interpretation of isotopic records as environmental conditions challenging, periodicity in isotopic signals can still be informative with respect to reconstructing growth rates as migration cycles probably occur annually. This study was prompted by an earlier study (Fatherree *et al.* 1998) that undertook stable isotope sampling of a single *Baculites* specimen and found data that were 'suggestive of seasonal variation.'

MATERIAL AND METHOD

Modern samples

Several of the *Baculites* fossils sampled in this study are housed in museum collections and have been prepared for display. In some cases, this preparation included coating the fossil in a sealant, and testing was required to ensure that this did not affect isotopic results. Several modern bivalves were used to test the effects of the museum preparation techniques on measured stable isotopic values in aragonite. These specimens of *Mercenaria* spp. were collected alive from estuarine conditions on St Catherine's Island, GA, USA in 1994. These organisms have clear growth lines, which allowed targeted isotopic sampling of isochronous growth intervals at various locations on the shell.

Fossil samples

Six different *Baculites* fossils (summarized in Table 1) were analysed using sclerochronological isotopic techniques, five of which were analysed by the authors and the sixth was previously published (Fatherree *et al.* 1998; AMNH 66330). All samples are late Campanian in age, except one specimen from the early Maastrichtian, and were collected from the Western Interior Seaway or Mississippi Embayment (Fig. 1). Each of these fossils are described below.

MPPM 2018.2.1. This specimen is a *B. undatus* body chamber collected from the Coon Creek Formation and is housed at the Pink Palace Museum, in Memphis TN (Fig. 2A). Samples (n = 71) were taken roughly every 5 mm along 393 mm of shell. The specimen had been coated with a sealant for display and preservation reasons. Tests to determine whether this sealant might affect isotopic measurements are described below (see Sealant Results, below).

MPPM 1977.22.3. This specimen is also a *B. undatus* body chamber collected from the Coon Creek Formation and is housed at the Pink Palace Museum (Fig. 2B). It

Specimen	Species	Locale	Formation	PI Score	δ ¹⁸ O Period ¹ (mm)	δ^{18} O Period Subsamples ² (mm)	δ ¹³ C Period ¹ (mm)	δ^{13} C Period Subsamples ² (mm)
MPPM 2018.2.1	B. undatus	Mississippi Embayment (TN)	Coon Creek	4.1 (?)	374* (428/331)	378, 372	330* (393/285)	333, 329
MPPM 1977.22.3	B. undatus	Mississippi Embayment (TN)	Coon Creek	4.1	629 (2153/232)	6245, 369	338* (421/282)	352, 352
AMNH 66330	B. compressus	WIS (SD)	Pierre Shale	4.5	367* (396/343)	363, 375	334* (422/276)	313, 369
USNM PAL 720528	B. scotti	WIS (SD)	Pierre Shale	3.9	676 (1646/157)	113, 329	315* (486/233)	336, 301
UWBM- 108201	B. compressus	WIS (MT)	Bearpaw Shale	3.3	39 (42/36)	160, 205	105 (130/88)	101, 60
USNM PAL 720527	B. compressus	WIS (SD)	Pierre Shale	3.9	1896 (3852/57)	668, 3162	129* (148/114)	129, 129

TABLE 1. Details of analysed Baculites specimens.

¹Best fit period length with the asymmetrical 95% confidence bounds in parentheses: (Upper Boundary/Lower Boundary).

²Period subsamples are the best fit period lengths to two subsamples of the original data set, each containing half the original data (see Data Analysis).

*Period lengths with an asterisk are considered to be good fits while periods without an asterisk did not pass validation tests and are considered to not have been appropriately fitted.

MT, Montana; SD, South Dakota; TN, Tennessee; WIS, Western Interior Seaway.

FIG. 1. Fossil specimen localities. The central shaded area represents approximate extent of the Western Interior Seaway in the Campanian (after Kauffman 1984; Lillegraven & Ostresh 1990; Slattery *et al.* 2015). Note that two samples come from the same location in the Mississippi Embayment. Colour online.



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was previously figured by Larson (2012, pl. 3, fig. 1a–b) who assigned it a late Campanian age. This sample was coated with a sealant for display and preservation purposes. Isotopic samples (n = 35) were collected from this specimen over a distance of 309 mm.

AMNH 66330. This sample of *Baculites compressus* was collected from the Pierre Shale (AMNH Location 3383) and analysed isotopically by Fatherree *et al.* (1998). Here we re-analyse the isotopic data generated in their study. The fossil was approximately 280 mm in length, but due to excellent preservation the authors were able to extend the effective length of the organism by sampling at different locations along the flank as *Baculites* shells have a curved aperture (Fig. 2C).

USNM PAL 720528. This specimen of *B. scotti* phragmocone is on loan from the USGS invertebrate palaeontology collections in Denver CO, USA. However, this collection is in the process of being transferred to the National Museum of Natural History palaeontology collections, and this specimen has been assigned a number to reflect its future repository. This specimen was collected from the Red Bird Silty Member of the Pierre Shale in South Dakota (USGS Location D1411). The overall fossil is 294 mm in length, but preserved shell material for sampling was only present over 218 mm, from which 38 samples were taken (Fig. 2D). This sample does not appear to have been prepared using any sealants.

UWBM-108201. This specimen of *B. compressus* phragmocone was collected from the Bearpaw Shale in central Montana on the shores of the Fort Peck Reservoir (UWBM Location B8808). Like most fossils from this location, it was preserved in an early diagenetic concretion. Samples (n = 20) were taken roughly every 10 mm along 184 mm (Fig. 2E). This sample was also treated with a sealant (polyvinyl butyral) to stabilize the fossil for transport which was examined for its isotopic effects below.

USNM PAL 720527. This specimen of *B. clinolobatus* phragmocone is also on loan from the USGS invertebrate palaeontology collections and will be transferred to the National Museum of Natural History. This specimen was collected from a lower Maastrichtian interval of the Pierre Shale in South Dakota (USGS Location D4986). It was sampled at a higher spatial resolution, with 104 samples over 116 mm (Fig. 2F). This sample does not appear to have been prepared using any sealants.

Modern bivalve specimen preparation

Two of the *Baculites* specimens (MPPM 2018.2.1 and MPPM 1977.22.3) studied here were on loan from the Pink Palace Museum, and their shells were coated with a sealant, specifically Future Floor Polish (now called Pledge[®] Floor Care Multi-Surface Finish). One specimen (UWBM-

FIG. 2. The five *Baculites* body fossils sampled in this study (A, B, D, E, F) and a sixth fossil designated as AMNH 66330 (Fatherree *et al.* (1998). A, MPPM 2018.2.1. B, MPPM 1977.22.3. C, AMNH 66330. D, USNM PAL 720528. E, UWBM-108201. F, USNM PAL 720527. Circles indicate specific locations of isotopic sampling. Samples A and E are preserved in surrounding rock matrix which has been digitally removed from the photograph. Scale bar represents 5 cm. Colour online. 108201) was coated with polyvinyl butyral, better known by the brand name Butvar[®], which is a more commonly used fossil shell consolidant. To test for any effects of these sealants on the oxygen and carbon isotope signals, a test using modern bivalve shells was conducted. Modern bivalve specimens were thoroughly washed to remove any surficial detritus from the shells. Once dry, the shells were partitioned into three sections with a marker so that each growth band had A, B and C sections (Fig. 3). Two coats of sealant were applied to the surface of the shells in the central 'B' sections with at least 24-hour periods of drying between coats and prior to any sampling.

Sampling methods

A handheld rotary tool paired with carbide dental drill bits were used to generate powder samples for isotopic analysis of *Baculites* and modern bivalves. The lowest drilling speeds able to produce sufficient powdered shell samples were used to mitigate the risk of thermal alteration of samples. Drill bits were cleaned with delicate task wipers and ethanol between drillings, and excess powder was removed from the workstation with compressed air to prevent cross-contamination. Using a microbalance, powder samples were then weighed (50–100 μ g) and placed into Exetainers[®] (Labco). Samples generated from modern bivalves were taken in suites of three corresponding samples. These suites consist of samples taken in each



FIG. 3. Example of one of four modern bivalves (ACE16) sampled to test for the effects of museum preparation sealants. Sections A and C were untreated, but section B was treated with a consolidant. Circles indicate sampling pits for isotopic analysis, where a single growth line was sampled across all three sections. Further sampling (not analysed in this case) can be seen towards the ventral margin. Scale bar represents 1 cm. Colour online.

of the sections (A, B and C) along the same growth band (Fig. 3). Samples procured from *Baculites* shells were taken in sequence of ontogenetic history parallel to the organism's growth axis (Fig. 2). Variable sampling resolutions were tested and range from 1 to 10 mm intervals.

SEM methods

Analysis of shell microstructure has proven to be one the most effective methods for assessing diagenesis in fossil carbonate material (Cochran et al. 2010; Lukeneder et al. 2010; Knoll et al. 2016) and has been used to ensure adequate ammonite shell preservation in similar studies (e.g. McArthur et al. 1994; Kruta et al. 2014; Landman et al. 2018). Small shell fragments (c. 1-3 mm diameter) were broken off from the specimens sampled (with the exception of MPPM 2018.2.1 as it was sampled in-house at the Pink Palace Museum) to assess their level of preservation by SEM analysis. Shell fragments were gold coated (15 nm thickness) prior to SEM analysis but were otherwise unmodified. Photomicrographs (Fig. 4) of the shell fragments' surfaces (2000×-2500× magnification) and cross-sections (12 000 \times -15 000 \times magnification) were produced with a JEOL JSM-7000F SEM at the Central Analytical Facility of The University of Alabama.

The fossil shells were then assigned preservation rankings on a scale of 1 (poor) to 5 (excellent) using the SEM based preservation index (PI) for nacre established by Cochran *et al.* (2010). In addition to the authors, three other people were consulted and the average of all five rankings was taken. The presence of the tabular microstructure of aragonite seen in the cross-section view was the primary feature noted while assessing preservation quality. The presence and severity of amorphous calcite replacement, tablet rounding, tablet welding, void space or other dissolution textures were considered when assigning preservation indices to shell fragments. Cochran *et al.* (2010) deemed the minimum acceptable PI value for isotopic sampling to be in the 3.5–4.0 range, which is largely supported by this work (see Seasonality, below).

Isotopic methods

Sample powders generated through drilling were weighed and placed into Exetainers[®] (see Sampling Methods, above) for analysis at the Alabama Stable Isotope Laboratory (ASIL) at The University of Alabama. Samples were analysed with Thermo GasBench II connected via continuous flow to a Delta V Plus isotope ratio mass spectrometer (IRMS). Exetainers[®] were flushed with helium gas to remove atmospheric gas and then acidified at 50°C with 103% phosphoric acid to liberate CO₂

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FIG. 4. SEM micrographs of all specimens sampled as part of this study, excluding MPPM 2018.2.1, which could not be sampled. Scale bars represent: 1 μ m (cross-section views); 10 μ m (surface views).

gas, which was introduced to the IRMS via the Gas-Bench II peripheral. Shell samples were interspersed with NBS-19 standards for sample correction and standardization. Standard weights were varied over the acceptable mass range (50–100 µg) to correct for linearity effects. Aragonite has slightly different acid fractionation values for δ^{18} O when compared with the calcite standard, and samples were corrected using published relationships for aragonite and calcite (Kim *et al.* 2007). At the reaction temperature and δ^{18} O range examined here, this process effectively adds 0.34_{00}° to all initial δ^{18} O values, which does not meaningfully affect interpretation of trends in these results.

Data analysis

While specific analysis of the isotopic profiles from each fossil are presented below, here we briefly discuss the analytical approaches to examining these profiles. If seasonal cycles in either δ^{13} C or δ^{18} O are present, they are likely to manifest as either roughly sinusoidal or abbreviated sinusoidal curves in which a portion of the sinusoid is omitted due to growth cessation. Here we employed the curve fitting toolbox in MATLAB to fit a sinusoidal curve to the data. It should be noted that this tool requires that y-values of the data in question to be normalized to an average of 0 for a sinusoidal curve fit, but the data and fitted curves were shifted back to original values after fitting in Figures 5-10 below. Prediction bounds at the 95% level are also calculated in this method and plotted as dashed lines. Amplitudes for the fitted curves are reported as peak-to-trough amplitude (double the mathematical amplitude) as this number is more relevant when considering the potential range of seasonal variation in the conditions that may have caused the fluctuating isotopic

FIG. 5. Isotopic profiles for δ^{18} O (top) and δ^{13} C (bottom) for sample MPPM 2018.2.1; growth direction from left to right. See Data Analysis for generation of best fit sine curve (dashed line) and 95% prediction bounds (dotted lines). Both δ^{13} C and δ^{18} O curves are considered to be appropriate fits. Instrumental precision was 0.1‰ for δ^{18} O and 0.05% for δ^{13} C. Colour online.

values. Error ranges for amplitude described in the text (see *Baculites* Results, below) are reported as 95% confidence bounds. Error ranges for the calculated periods are non-symmetrical and reported as 95% confidence bounds in Table 1 (and see Fig. 11).

There is no standard test for deciding whether a sinusoidal curve is the most appropriate fitting tool in comparison with another type of fit, such as a linear or exponential fit. We opted for a few simple tests to determine whether the fitted sine curve was appropriate. First, if the period of the fitted curve was much greater than the sampling length, the data are probably better represented by a linear fit and a sine curve would be inappropriate. This is true despite the fact that the r^2 value of the linear fit may be lower, which is simply the result of the greater number of coefficients allowing the curve to be over-fit to the data. Second, if the period of the fitted curve is on the order of the sampling interval, then the fit is probably finding sinuosity in the noise within the data and a sinusoidal fit should be rejected. If the curves passed the first two tests, we evaluated whether the sinusoidal fit was preserved when the data was subsampled by removing every other data point. Both of the two subsampled half data sets were fit with a new curve, and if the period of those curves was within the error bounds of the whole data set it was considered valid. Below (see Baculites Results, below) we present all of the sinusoidal curve fits generated and discuss whether these curves pass these simple tests.

Institutional abbreviations. AMNH, American Museum of Natural History, New York NY, USA; MPPM, Pink Palace Museum, Memphis TN, USA; USGS, United States Geological Survey, Denver CO, USA; UWBM, University of Washington Burke Museum of Natural History & Culture, Seattle WA, USA; USNM PAL, United States National Museum, Paleobiology Collections, Washington DC, USA.





FIG. 6. Isotopic profiles for δ^{18} O (top) and δ^{13} C (bottom) for sample MPPM 1977.22.3; growth direction from left to right. See Data Analysis for generation of best fit sine curve (dashed line) and 95% prediction bounds (dotted lines). The δ^{18} O fitted curve is not a good fit given that the reconstructed period is more than twice as long as the sampling interval; the δ^{13} C curve is considered to be a good fit. Instrumental precision was 0.1‰ for δ^{18} O and 0.05% for δ^{13} C. Colour online.

FIG. 7. Isotopic profiles for δ^{18} O (top) and δ^{13} C (bottom) for sample AMNH 66330; growth direction from left to right. Data are from Fatherree *et al.* (1998). See Data Analysis for generation of best fit sine curve (dashed line) and 95% prediction bounds (dotted lines). Curves for both δ^{18} O and δ^{13} C are considered to be appropriate fits. Instrumental precision was 0.1% for δ^{18} O and 0.05% for δ^{13} C. Colour online.

RESULTS

Sealant results

Carbon and oxygen isotope analysis of modern bivalve shells treated with polyvinyl butyral and Pledge[®] floor finish did not result in evidence for any contamination or alteration of δ^{13} C or δ^{18} O values. Because bivalve δ^{18} O and δ^{13} C vary along ontogenetic trajectories, we accounted for alteration at specific growth increments (Fig. 3) before assessing any potential isotopic effects of the treatment. The control value was calculated by taking the average of the δ^{13} C or δ^{18} O values for the two control sections (A and C), while the treatment section value was the δ^{13} C or δ^{18} O value for the B section. The difference between the control value and the treatment value was our measure of how much the isotopic value was altered. No consistent pattern or offset was observed between the control and sealant sections for either δ^{18} O or δ^{13} C. Statistical tests failed to reject the null hypothesis that the observed control–sealant differences were significantly distinguishable from 0. The shells treated with Pledge[®] floor finish (ACE5, ACE16P, JLC15, JLC17) had a mean control–sealant δ^{13} C difference of $-0.03 \pm 0.31\%_{00}$ (1 σ) and a mean δ^{18} O difference of $-0.10 \pm 0.41\%_{00}$ (1 σ). A one-sample *t*-test of the mean difference values (versus 0) resulted in a *p*-value of 0.70 for δ^{13} C and a *p*-value of 0.31 for δ^{18} O (Ellis & Tobin 2019). These *p*-values indicate that the control– sealant differences in both δ^{13} C and δ^{18} O are not meaningfully different to 0, which implies that Pledge[®] had no effect on either δ^{13} C or δ^{18} O values.

The smaller number of shells treated with polyvinyl butyral (ACE16B, JLC16) had a mean δ^{13} C difference of 0.28 ± 0.41‰ (1 σ) and a mean δ^{18} O difference of 0.28 ± 0.44‰ (1 σ). A one-sample *t*-test of the mean difference values (vs 0) resulted in a *p*-value of 0.27 for δ^{13} C and a *p*-value of 0.17 for δ^{18} O (Ellis & Tobin 2019). As

FIG. 8. Isotopic profiles for δ^{18} O (top) and δ^{13} C (bottom) for sample USNM PAL 720528; growth direction from left to right. See Data Analysis for generation of best fit sine curve (dashed line) and 95% prediction bounds (dotted lines). The δ^{18} O fitted curve is not a valid fit given that the reconstructed period is much longer than the sampling interval; the δ^{13} C curve is considered to be valid. Instrumental precision was 0.1‰ for δ^{18} O and 0.05% for δ^{13} C. Colour online.

FIG. 9. Isotopic profiles for δ^{18} O (top) and δ^{13} C (bottom) for sample UWBM-108201; growth direction from left to right. See Data Analysis for generation of best fit sine curve (dashed line) and 95% prediction bounds (dotted lines). Neither the δ^{13} C nor δ^{18} O profiles are reliable given the poor PI value assigned to the specimen and the poor quality of the fitted curves (see *Baculites* Results; Fig. 4). Instrumental precision was 0.1_{00}^{*} for δ^{18} O and 0.05% for δ^{13} C. Colour online.



above, this test suggests that Butvar[®] does not affect isotopic values of carbonate. Given that neither Butvar[®] nor Pledge[®] appear to alter isotopic values, the results and conclusions of this manuscript operate on the assumption that the isotopic values of the *Baculites* specimens are unmodified by the museum preparation methods involving Pledge[®] floor finish or polyvinyl butyral.

Baculites results

Here we report the diagenetic assessments and isotopic results for each of the six *Baculites* specimens discussed above in order of preservation quality (from best to worst). The implications of these results are subsequently discussed in the following section.

AMNH 66330. We did not have physical access to this specimen and did not acquire our own SEM micrographs of the microstructure of the fossil. Fortunately, Fatherree *et al.* (1998, fig. 3) provided a cross-sectional view of the nacreous tablets that can be used to place the specimen within the preservation index system. We assessed this image to determine a PI value, ranked here at 4.5, or very well-preserved. Additionally, there is no correlation ($r^2 = 0.04$) between δ^{13} C and δ^{18} O, which is consistent with a well-preserved shell.

Potential periodicity in both the δ^{13} C and δ^{18} O was qualitatively recognized by the original authors, and here we quantify their observation by fitting a sine curve to both isotopic profiles (see Data Analysis, above). We found sinusoidal curves with similar periods in both δ^{18} O (367 mm) and δ^{13} C (334 mm; Fig. 7). Both fitted curves were considered to be valid, as the reconstructed periods were not close to the sampling interval or significantly longer than the sampling length. Additionally, curves fitted to the subsampled data were consistent with the full data set for both δ^{13} C (334 mm; subsampled data: 313 and 369 mm) and δ^{18} O (367 mm; subsampled data: 363 and 375 mm). Additionally, the correspondence between the periods in the two isotopic systems lends support to the interpretation of them as seasonally



FIG. 10. Isotopic profiles for δ^{18} O (top) and δ^{13} C (bottom) for sample USNM PAL 720527; growth direction from left to right. See Data Analysis for generation of best fit sine curve (dashed line) and 95% prediction bounds (dotted lines). The δ^{18} O isotopic profile was poorly constrained, and interpretation of the δ^{13} C profile is complicated (see *Baculites* Results). Instrumental precision was 0.1‰ for δ^{18} O and 0.05% for δ^{13} C. Colour online.

4.6

4.6

FIG. 11. Reconstructed period lengths and associated uncertainties at 95% confidence level for $\delta^{18}O$ (top) and $\delta^{13}C$ (bottom) are plotted against a measure of diagenesis (preservation index). Better preserved samples show consistent period lengths near 340 mm. Samples below 3.5 are assumed to be altered based on Cochran *et al.* (2010) as indicated by darker grey box. Lighter grey and gradient reflect area of potential alteration based on our data. Oxygen isotopic values may be more prone to resetting. Samples with similar PI values are slightly staggred to separate data points. Dashed lines represent 340 mm period length. Colour online.

derived. The peak-to-trough amplitude of the fitted sine curve is 0.83 \pm 0.34% for $\delta^{13}C$ and 1.67 \pm 0.16% for $\delta^{18}O$.

MPPM 2018.2.1. We had limited sampling access to this specimen and no fragments were available for SEM analysis. However, samples from the Coon Creek Formation have been known to be well-preserved geochemically, including preservation of the organic material within the shell (Weiner *et al.* 1976). Additionally, specimen MPPM 1977.22.3 (discussed below) from the same site was assessed using SEM techniques and recorded a PI value of 4.1. No correlation was observed in the isotopic cross plot ($r^2 = 0.01$; Fig. 12). While the evidence is circumstantial, this context implies that the sample is likely to be reasonably well preserved, and we assume that it has a PI similar to that of MPPM 1977.22.3. Sine curves fitted to the

sequential isotopic sampling of MPPM 2018.2.1 reveal periodicity in both δ^{13} C (330 mm; subsampled data: 333 and 329 mm) and δ^{18} O (374 mm; subsampled data: 378 and 372 mm) of similar magnitude to that of AMNH 66330 (Fig. 5). These fitted curves also pass the validation tests described in Data Analysis, above.

MPPM 1977.22.3. SEM photomicrographs for this specimen reveal well-preserved nacreous microstructure (Fig. 4) that was assigned a PI value of 4.1. This observation is supported by a lack of correlation in the isotopic cross plot ($r^2 = 0.0$; Fig. 12). A sine curve passing our validation tests was fitted to the δ^{13} C isotope profile, resulting in a period similar to those observed above (338 mm; subsampled data: 352 and 352 mm). The peak-to-trough amplitude was 1.22 $\pm 0.45\%$ (Fig. 6). Attempts to fit a sine curve to



FIG. 12. Cross plots of δ^{13} C– δ^{18} O for all specimens analysed here. Strong correlations may be indicative of diagenesis, though only one sample shows a moderate negative correlation. Sample UWBM-108201 shows no correlation between δ^{13} C and δ^{18} O, but SEM analysis indicates substantial alteration, emphasizing that cross plots are not sufficient for assessing diagenesis. Instrumental precision was 0.1_{∞}^{6} for δ^{18} O and 0.05% for δ^{13} C.

the δ^{18} O data for this specimen do not pass the validation tests, as the period of the fitted curve (629 mm; subsampled data: 2153 and 232 mm) is more than twice as long as the sampling interval, and there is no agreement between subsampled periods. Consequently, these δ^{18} O data would be more appropriately fit with a linear trend.

USNM PAL 720528. This specimen was fairly well-preserved, as indicated by a PI value of 3.9 (Fig. 4) and effectively no correlation between $\delta^{13}C$ and $\delta^{18}O$ values $(r^2 = 0.08;$ Fig. 12), though the PI score indicates a greater degree of alteration than those described above. The sine curve fitted to the δ^{18} O data did not pass our validation tests, with the reconstructed period more than double the sampling interval and no correspondence with subsampled data (676 mm; subsampled data: 1646 and 157 mm; Fig. 8). A sinusoidal curve for the δ^{13} C profile had a period of 315 mm (subsampled data: 336 and 301 mm), greater than, but not double, the 218 mm sampling interval. Much of the shape of this curve is determined by the last third of the sampling interval and, given the shorter sampling length, this curve should be cautiously interpreted, though the subsampled data sets do produce similar fitted curves. The peak-to-trough amplitude of this δ^{13} C fit was 0.81 \pm 0.30%.

USNM PAL 720527. This specimen showed similar preservation to the USNM sample above, with a PI value of 3.9 (Fig. 4) and a moderate negative correlation between δ^{13} C and δ^{18} O values ($r^2 = 0.31$; Fig. 12). This fossil was sampled at a much higher spatial resolution (c. 1 sample/mm) to identify variations that might have been overlooked in the lower resolution sampling of other specimens (c. 1 sample/cm). No high resolution variation was observed in δ^{18} O (Fig. 10); instead a fairly consistent unidirectional trend was observed. When a sinusoidal curve is fit to the $\delta^{18}O$ data, the period of the curve is >1500 mm for a 116 mm sampling interval (Fig. 10), which implies that a sine curve is poorly defined and is inappropriate here. The δ^{13} C profile of this sample was more ambiguous; there are suggestions of higher resolution variation on the order of 5-10 cm in some parts of the profile, but the fluctuations are not consistent. A sinusoidal curve with a period of 129 mm (subsampled 129 and 129 mm) was fit to the δ^{13} C data, with an amplitude of 0.50 \pm 0.09%. This δ^{13} C curve passes our validation tests.

UWBM-108201. This is the least well-preserved specimen analysed, with a PI value of 3.3 (Fig. 4). It should be noted that no correlation was observed between δ^{13} C and δ^{18} O ($r^2 = 0.01$; Fig. 12), which emphasizes the point that

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isotopic analysis alone is insufficient to reveal diagenesis. Both the δ^{13} C and δ^{18} O profiles are effectively flat (Fig. 9). In the case of δ^{18} O, the reconstructed period (39 mm) approaches twice the sampling interval, while the subsampled fitted curve periods are very different (160 and 205 mm) suggesting that the variation is probably noise. For δ^{13} C, the shape and period (105 mm) of the fitted sinusoid are strongly controlled by a few higher variance data points near the middle of the sampled interval, and the periods of subsampled curves are similarly variable (101 and 60 mm).

DISCUSSION

Periodicity

There are some notable patterns and consistent features of many of the isotopic profiles, but their interpretation is somewhat equivocal and should be approached with caution. All but one of the curves that were reasonably fit to the data and passed the validation tests had similar period lengths. Specifically, the most common periodicity observed was around 343 ± 45 (95%) mm (reflected in the δ^{18} O profiles of AMNH 66330 and MPPM 2018.2.1 and in the δ^{13} C profiles of AMNH 66330, MPPM 2018.2.1, MPPM 1977.22.3 and USNM PAL 720528). Most of the other isotopic profiles did not show a reliable sinusoidal fit (i.e. did not pass our validation tests) though there was one exception (see below). The fossil samples we examined exhibit some variation in their diagenetic quality, as measured by preservation index (PI = 3.3-4.5), that may explain the lack of periodicity observed in the isotopic profiles of the less well-preserved samples.

With respect to δ^{18} O profiles, the two best preserved samples (PI = 4.5, 4.1; the second inferred from coeval sample) both show acceptable sinusoidal curve fits, while the four less well-preserved samples (PI = 4.1, 3.9, 3.9, 3.3) did not show good fits, which is also revealed by the increasing uncertainty in the period length calculations of these samples (Fig. 11). Since the best preserved samples show a well fit sinusoidal curve, it is likely that preservation of this variation represents the unaltered condition. Cochran *et al.* (2010) suggested that the cutoff point for well-preserved samples is between preservation index values of 3.5 and 4.0, while our evidence suggests that the loss of isotopic preservation in δ^{18} O occurs around a PI value of 4.1, at or above the top of the range indicated by Cochran *et al.* (2010).

The pattern in δ^{13} C is similar to that in δ^{18} O, except the transition from preserved periodicity to uninterpretable patterns occurs at slightly lower PI values (*c*. 3.9). The four best preserved samples (PI = 4.5, 4.1, 4.1, 3.9) showed similar length periods that were reasonably well constrained (Fig. 11) while the worst preserved sample (UWBM-

108201) did not show well constrained periodicity. Only one sample (USNM PAL 720527, PI = 3.9) does not fit this pattern well; a much shorter (134 mm), but reasonably constrained period was fit to this δ^{13} C profile. The sampling for this fossil was different from the others in two ways: it was sampled at a higher frequency and over a shorter total length; it is possible that one or both of these factors contributed to the different isotopic pattern observed. The differences could also be the result of undetected differential alteration of various sections of the fossil, or it could be a real primary isotopic signal that does not fit the overall pattern. Unfortunately, we cannot differentiate these possibilities at this time.

Given the higher threshold for preservation of δ^{18} O periodicity, our data imply that the δ^{18} O signal may be more prone to alteration than the δ^{13} C signal, which is preserved at somewhat lower PI values. This pattern is consistent with an understanding of diagenesis as a fluid mediated process, in which the much greater abundance of oxygen in water makes isotopic exchange between the fluid and shell material much more common than with carbon (Banner & Hanson 1990).

Seasonality

Ultimately, our hypothesis is that the observed periodicity in many of the isotopic profiles is real, based primarily on the observation that periodicity is revealed in well-preserved samples but not apparent in more altered specimens. Previous isotopic analysis of planispiral ammonites has also inferred seasonal variation from periodicity in isotopic profiles (Zakharov et al. 2005, 2011). The similarity of the period lengths recorded by all of the well preserved (PI > 3.8) specimens except one (USNM PAL 720527) provides additional, but circumstantial, support to this hypothesis. This similarity suggests a common cause to the periodicity, which is probably driven by annual variation as there are unlikely to be higher or lower frequency environmental or internal changes that would be recorded at a similar interval. Most importantly, two fossils (Figs 5, 7) preserve both δ^{13} C and δ^{18} O periodicity of similar lengths. If the isotopic profiles showed different periodicity within the same specimen, the seasonal signal hypothesis would be rejected.

Given their likely demersal position at 100–200 m water depth (Tsujita & Westermann 1998; Sessa *et al.* 2015) many environmental factors could plausibly fluctuate annually to drive isotopic variation, including but not limited to temperature (δ^{18} O), primary productivity (δ^{13} C) and relative terrestrial water flux (δ^{13} C, δ^{18} O). Alternatively (or in addition), *Baculites* themselves may have had internal seasonal variation due to metabolic changes that could affect the δ^{13} C of their extra-pallial fluid (McConnaughey & Gillikin 2008; Tobin & Ward 2015) or seasonal migrations that moved them between different water masses on an annual basis could affect the δ^{13} C and δ^{18} O. Given the recognition of periodicity in the isotopic profiles of *Baculites* shells of different ontogenetic positions, it is unlikely that the observed isotopic changes reflect a one-time life event like reaching sexual maturity, as has been observed in modern *Spirula* (Lukeneder *et al.* 2008; Price *et al.* 2009; Warnke *et al.* 2010). If migration is the driver of the observed isotopic periodicity, it is more likely to be the result of annual migrations, analogous to modern *Sepia* (Wang *et al.* 2003) which can record a migration history in their cuttlebones (Rexfort & Mutterlose 2006).

The magnitude of temperature variation inferred from the δ^{18} O amplitude (assuming a constant δ^{18} O_w) is less than or equal to 5°C, much lower than would be expected from simple seasonal fluctuation of surface water temperature in any of these locations. However, both a demersal lifestyle (Sessa et al. 2015) and the mobility of organisms in pursuing optimal growing conditions would substantially mute the overall seasonal signal expected. The recorded amplitude of the δ^{18} O signal probably reflects an inseparable combination of water depth, where deeper life position results in lower amplitude temperature swings, and geographical location, where higher latitudes would preserve greater seasonal temperature variability. Unfortunately, with only two samples showing δ^{18} O periodicity, addressing these potential factors is not possible. While there are more samples that show $\delta^{13}C$ periodicity, there are also more environmental variables that can influence δ^{13} C values, so interpretation is again challenging. Given the variety of possible inputs to the system, it is impossible for us to definitively point to one explanation for the seasonal variation observed in the isotopic profiles of baculites.

There are two samples that preserve periodicity in both δ^{13} C and δ^{18} O, but in one sample the two curves are in phase (MPPM 2018.2.1) and in the other they are more or less out of phase (Fatherree *et al.* 1998). This discrepancy suggests that the controls on at least one isotopic system are environmental and geographically variable. All of these samples were deposited in a relatively shallow epeiric seaway or a very long continental shelf (Fig. 1) for which there are no good modern analogues, which further complicates any useful environmental interpretation. Circulation and terrestrial water flux to the Western Interior Seaway is thought to be fairly complex (Petersen *et al.* 2016) and without further constraints, speculation on the meaning of the isotopic fluctuations would be largely unsupported.

Growth rate

While the mobility of *Baculites* precludes use of the δ^{13} C and δ^{18} O profiles as direct environmental proxies, the

consistency of the periodicity within the isotopic profiles can still provide useful information regarding the growth rate of these organisms, even if the precise driver of the variation is unknown. Specifically, the average period of the well supported δ^{18} O and δ^{13} C profiles (see above) is $343 \pm 45 (95\%)$ mm, which implies that *Baculites* precipitated shell material at approximately 343 mm/year. Improved statistical evaluation of these trends would be accomplished with longer (>700 mm) isotopic profiles from well-preserved material, but we are currently unaware of any specimens that would meet the criteria for this type of sampling. At present, sampling multiple specimens is the only way to further test this hypothesis.

While the uncoiled morphology of *Baculites* facilitates the sampling process, their generally incomplete preservation makes acquisition of longer isotopic records impossible. Ontogenetic isotopic profiles from some planispiral ammonites have been completed with many interpretations drawn about ontogenetic habitat changes (Lécuyer & Bucher 2006; Lukeneder et al. 2010; Zakharov et al. 2011; Lukeneder 2015; Stevens et al. 2015). In some cases, a single whorl was sampled and changes in life habitat were drawn from isotopic variation of δ^{13} C and/or δ^{18} O (Lukeneder *et al.* 2010; Stevens et al. 2015). While in other cases, longer records were completed (Lécuyer & Bucher 2006; Lukeneder et al. 2010) with some authors inferring a seasonal variation (Stahl & Jordan 1969; Lécuyer & Bucher 2006). It is unclear whether Baculites occupied similar habitats or shared migratory behaviours with planispiral ammonites, and therefore it may be inappropriate to assign them similar growth rates based on our data. However, if the growth rates estimated from these Baculites specimens do apply to planispiral ammonites, previously inferred habitat changes may simply be seasonal variations captured in the shell, and the ammonite lifestyle/migration types defined by Moriya (2015) may warrant further consideration.

Despite a paucity of individual complete specimens, there are methods to estimate Baculites growth patterns. Tsujino et al. (2003) used large numbers of specimens to develop a formula to estimate total length from whorl height. This formula is species specific, but since we lack the sample size to create similar allometric growth charts for each species here, we employed the relationship between length (L) and whorl height (H) developed by Tsujino et al. (2003) ($L = 3.03 \times H^{1.50}$) to generate rough estimates for the total length of the largest (whorl height) Baculites specimen we examined. Sample MPPM 1977.22.3 is the largest sample in which the aperture is preserved and measurable, with an H of 53 mm and an estimated L of 1159 mm. If the growth rate estimates are correct, it would have reached this size in 3–4 years (3.4 \pm 0.5), assuming a constant growth rate. The longest composite baculitid specimen we know of (B. grandis) is 1550 mm (Westermann 2013), which would have reached maturity at 4-5 years with the estimated

growth rate. These estimates are similar to those derived from other approaches (Bucher *et al.* 1996) which place ammonite lifespan near five years (see Lukeneder 2015 for a review of other age estimate approaches).

As proposed by Fatherree et al. (1998), this rapid growth rate may be part of an ecological strategy for Baculites, which may have employed an r-selection growth strategy; but this assumes senescence shortly after the termination of shell growth. In this interpretation, large baculitid accumulations may result from spawning and subsequent mass death as observed in some modern cephalopods. However, the imbrication of Baculites shells that is commonly observed in these accumulations may indicate post-mortem transport of the animals. This creates greater uncertainty about the size of spawning events since shells could be transported from various locations before being deposited with other individuals. It is important to note that a three to five year period to a terminal growth point does not necessarily imply the end of life, but stable isotopic approaches cannot reveal any further age information without continued accretional growth. Even if Baculites continued to live at a mature growth size, the speed with which they reached physical maturity supplements the existing evidence demonstrating that the modern Nautilus is a poor analogue for ammonites (Jacobs & Landman 1993).

Landman et al. (2018) recently published ontogenetic stable carbon and oxygen isotopes in B. compressus specimens to address baculitid lifestyle and preferred habitat, primarily by comparing δ^{13} C values from *Baculites* fossils found at methane seep sites and at non-seep locations. While those ontogenetic data were useful in addressing questions regarding seep habitats, their analysed specimens were too short (<13 cm) to supplement our data. It is not known whether the samples analysed here were collected from methane seep sites or not, but specimens MPPM 2018.2.1, MPPM 1977.22.3 and AMNH 66330 show δ^{13} C values that suggest non-seep habitats, while δ^{13} C values for USNM PAL 720528, USNM PAL 720527, and UWBM-108201 lie within the proposed range for methane seep sites (Landman et al. 2018), though these interpretations should be made cautiously, especially in specimens shown to have undergone significant diagenesis. Alternatively, these isotopic variations could be the result of species specific vital effects (Dance et al. 2014).

CONCLUSIONS

We present here a case for growth rate reconstructions from ammonite isotopic profiles, though we recognize that interpretation of isotopic data from extinct taxonomic groups will always be challenging. Our interpretation hinges on two premises: (1) that the recognition of sinuosity in isotopic data is geochemically original; and (2) that this sinuosity is driven by seasonal variation. While it does not appear that the δ^{18} O of *Baculites* shells may be used as a viable seawater temperature proxy for seasonality in the Cretaceous, isotopic data from shell carbonate does offer valuable insight into their palaeoecology. Likely seasonal trends in carbonate isotope data are shown to be identifiable in ontogenetically sampled *Baculites* specimens that are well preserved (PI ≥ 4.1), with the δ^{18} O signal being more prone to alteration than δ^{13} C. The periodicity of positively identified seasonal signals in the individuals sampled are in close agreement with one another and suggest very rapid growth rates (>300 mm per year). Comparison with records of planispiral ammonites suggests that longer sampling records may be necessary to separate developmental habitat changes from seasonal variations.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.27tn2gs

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