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Ammonoid extinction versus nautiloid survival: Is metabolism responsible?

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ABSTRACT

Understanding the mechanism of selective extinction is important in predicting the impact of anthropogenic environmental changes on current ecosystems. The selective extinction of externally shelled cephalopods at the Cretaceous-Paleogene (K-Pg) mass extinction event (ammonoids versus nautiloids) is often studied, but its mechanism is still debated. We investigate the differences in metabolic rate between these two groups to further explore the causes of selective extinction. We use a novel metabolic proxy—the fraction of metabolic carbon in the stable carbon isotope ratio of shell material (C_{meta})—to determine metabolic rate. Using this approach, we document significant differences in C_{meta} among modern cephalopod taxa (*Nautilus* spp., *Argonauta argo*, *Dosidicus gigas*, *Sepia officinalis*, and *Spirula spirula*). Our results are consistent with estimates based on oxygen consumption, suggesting that this proxy is a reliable indicator of metabolic rate. We then use this approach to determine the metabolic rates of ammonoids and nautiloids that lived at the end of the Cretaceous (Maastrichtian). Our results show that the nautiloid *Eutrephoceras*, which survived the K-Pg mass extinction event, possessed a lower metabolic rate than co-occurring ammonoids (*Baculites*, *Eubaculites*, *Discoscaphites*, and *Hoploscaphites*). We conclude that the lower metabolic rate in nautiloids was an advantage during a time of environmental deterioration (surface-water acidification and resulting decrease in plankton) following the Chicxulub asteroid impact.

INTRODUCTION

Understanding the relationship between environmental perturbations, physiological traits of organisms, and their evolutionary consequences is important because it allows us to predict the impact of anthropogenic climate change on current ecosystems. Mass extinction events can provide important insights, and a large number of studies have attempted to determine the biotic and/or abiotic factors, kill mechanisms, and selective nature of such events (e.g., Schulte et al., 2010). One of the "Big Five" mass extinction events that has attracted the attention of both the general public and researchers is the Cretaceous-Paleogene (K-Pg) mass extinction.

In the marine realm, ammonoids and nautiloids, both of which possessed an external shell, are iconic examples of selective extinction. Although ammonoids were more diverse and abundant than nautiloids during the Late Cretaceous, ammonoids became extinct at the K-Pg boundary (or shortly thereafter; see Landman et al., 2014), whereas nautiloids have survived to the present day. One possible explanation for this selective extinction is the difference in life cycles between the two groups. Ammonoids hatched at a smaller size (~1 mm) and probably spent some time in the plankton after hatching (Tajika et al., 2018), whereas nautiloids hatched at a larger size (~10 mm) and were nektobenthic after hatching (Gallagher, 1991). Therefore, ammonoids would have been more vulnerable to surface-water acidification following the Chicxulub asteroid impact, as proposed by Alegret et al. (2012) and Henehan et al. (2019).

Metabolic rate is another trait that can affect differential survival (Tajika et al., 2020). It dictates the energy requirements of an organism to sustain minimum activity and, thus, is linked to the energy allocation within an environment. Evidence for metabolic rate is not directly preserved in the fossil record, and a proxy must be used to reconstruct the metabolic rates of extinct organisms, especially those with no living descendants. Chung et al. (2021) proposed a new proxy to determine the metabolic rate in modern cephalopods using the stable carbon isotope composition of the shell. The principles of this method are: (1) the isotope ratio $^{13}C/^{12}C$ (expressed as $\delta^{13}C$) is a function of the isotope composition of carbon in the dissolved inorganic carbon (DIC) reservoir in which the shell formed as well as carbon incorporated via metabolism (McConnaughey et al., 1997), and (2) the fraction of metabolic carbon in the $\delta^{13}C$ of the shell is correlated with metabolism-related factors such as temperature and developmental stage.

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We apply this method to determine the metabolic rate in a variety of modern shell-bearing cephalopods and compare our results with published estimates of metabolic rate based on oxygen consumption in order to validate the approach. We then apply this method to Late Cretaceous shell-bearing cephalopods, namely ammonoids and nautiloids, to reveal their enigmatic ecology.

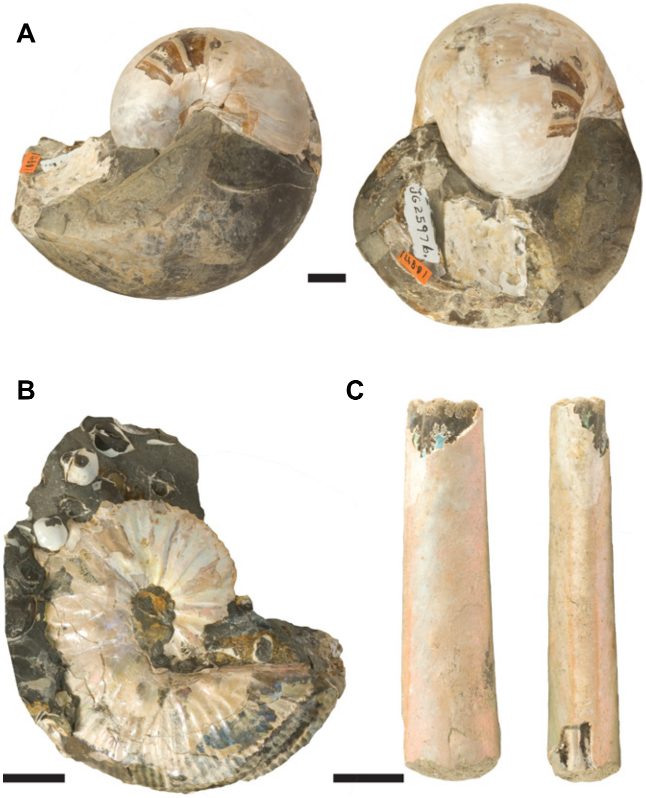

Figure 1. Fossil cephalopods used in this study. (A) *Eutrephoceras dekayi*, lower Maastrichtian Pierre Shale, Montana, USA (American Museum of Natural History [AMNH] specimen catalog 108471). (B) *Hoploscaphites criptonodosus*, upper Maastrichtian Owl Creek Formation, Mississippi, USA (AMNH 138977). (C) *Eubaculites latecarinatus*, upper Maastrichtian Owl Creek Formation, Mississippi, USA (AMNH 77515). Scale bars = 10 mm.

METHODS AND MATERIAL

For modern shell-bearing cephalopods, we selected 10 species (*Nautilus macromphalus*, *Nautilus pompilius*, *Argonauta argo*, *Illex illecebrosus*, *Dosidicus gigas*, *Architeuthis dux*, *Sepia elegans*, *Sepia orbignyana*, *Sepia officinalis*, and *Spirula spirula*), drawing on data from Chung et al. (2021). The sources of these specimens are listed in the Supplemental Material[1].

For fossil shell-bearing cephalopods, we chose three time-rock intervals: the upper Maastrichtian *Discoscaphites iris* Zone of the Owl Creek Formation in Mississippi, USA; the lower Maastrichtian *Baculites baculus–Baculites grandis* Zones of the Pierre Shale in Montana, USA; and the lower Albian *Douvilleiceras mammillatum* Zone of the Ambarimaniga Formation in Madagascar. For the upper Maastrichtian and lower Albian localities, we compiled data for $\delta^{13}C_{shell}$ for ammonoids, nautiloids, and bivalves based on previously published papers (Hoffmann et al., 2019; Sessa et al., 2015). For the lower Maastrichtian locality, in addition to the data published by Landman et al. (2018), we collected shell samples and analyzed them for $\delta^{13}C$ (Fig. 1; see the Supplemental Material for more details). All samples were composed of aragonite and were examined under scanning electron microscope (SEM) to determine the degree of alteration. We employed the preservation index (PI) of Cochran et al. (2010) and selected only samples with PI ≥ 3 (Supplemental Material).

The Maastrichtian study sites represent relatively shallow water. The upper Maastrichtian Owl Creek Formation in Mississippi was deposited in a nearshore environment between 70 and 150 m deep (Sessa et al., 2015). The lower Maastrichtian Pierre Shale in Montana was deposited in the Western Interior Seaway at a depth of <70 m (Landman et al., 2018). This locality was probably also influenced by freshwater influx associated with the progradation of the Sheridan Delta into the area during the late Campanian and early Maastrichtian (Landman et al., 2020). The fossils from the lower Albian Ambarimaniga Formation occur in a condensed section reflecting multiple transgressive systems tracts (Zakharov et al., 2016). The exact depth of deposition is unclear, but Hoffmann et al. (2019) suggested a depth of ~525 m, much deeper than the two Maastrichtian localities.

Calculation of the Fraction of Metabolic Carbon

We used the fraction of metabolic carbon in $\delta^{13}C_{shell}$ as a proxy for metabolic rate. To calculate the fraction of metabolic carbon, we employed the following equation (McConnaughey et al., 1997):

$$\delta^{13}C_{shell} = \varepsilon + C_{meta} \times \delta^{13}C_{meta} + (1 - C_{meta}) \times \delta^{13}C_{DIC}, \quad (1)$$

where ε is the $\delta^{13}C$ fractionation between the shell and DIC (+2.7‰ ± 0.6‰ [aragonite], 1.0‰ ± 0.2‰ [calcite], dominated by HCO^{3-}) (Romanek et al., 1992), C_{meta} is the fraction of metabolic carbon incorporated into the shell, and $\delta^{13}C_{shell}$, $\delta^{13}C_{meta}$, and $\delta^{13}C_{DIC}$ are the $\delta^{13}C$ values corresponding to the shell, metabolic carbon, and seawater DIC, respectively.

We calculated C_{meta} in modern shell-bearing cephalopods using the same values of $\delta^{13}C_{meta}$ and $\delta^{13}C_{DIC}$ as Chung et al. (2021) (see the Supplemental Material for more details). Because no data on the $\delta^{13}C_{meta}$ of extinct cephalopods are available, we used −17‰, based on the value of siphuncular material in modern *Nautilus* (~−21‰ to −12‰; Crocker et al., 1985; Pape, 2016; see Tajika et al., 2022, for discussion). In addition, because direct measurements of $\delta^{13}C_{DIC}$ in ancient oceans are not possible, we calculated the average value of $\delta^{13}C_{DIC}$ using the $\delta^{13}C_{shell}$ of co-occurring bivalves. Following Tobin and Ward (2015), we assumed that the $\delta^{13}C_{meta}$ and C_{meta} of bivalves equal −19‰ and 10%, respectively. To test for a significant difference in C_{meta} among cephalopods, both for modern taxa and for fossil taxa from a single time interval, we performed an analysis of variance (Welch's ANOVA) for all taxa with sample sizes >10. This test was followed by a multiple comparisons test to determine which pair of taxa exhibited significant differences. The Welch's *t*-test was performed for the lower Maastrichtian taxa. All statistical tests were performed using the SciPy library within the Python 3.9.7 programming environment.

RESULTS

Modern Cephalopods

The calculated fraction of metabolic carbon (C_{meta}) in the $\delta^{13}C_{shell}$ of modern cephalopods is shown in Figure 2 and the Supplemental Material. The Welch's ANOVA for six species (*N. macromphalus*, *N. pompilius*, *A. argo*, *D. gigas*, *Sepia officinalis*, and *Spirula spirula*) reveals that there are significant differences among them ($p < 0.000001$). The two species of *Nautilus* exhibit values of C_{meta} (6%–35%) that are significantly lower than those of the other four species. The values of C_{meta} in *Nautilus* are followed by those of two internally shelled coleoids, *Spirula spirula* and *Sepia officinalis*

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[1] Supplemental Material. Raw data and additional information. Please visit https://doi.org/10.1130/GEOL.S.22654426 to access the supplemental material, and contact editing@geosociety.org with any questions.

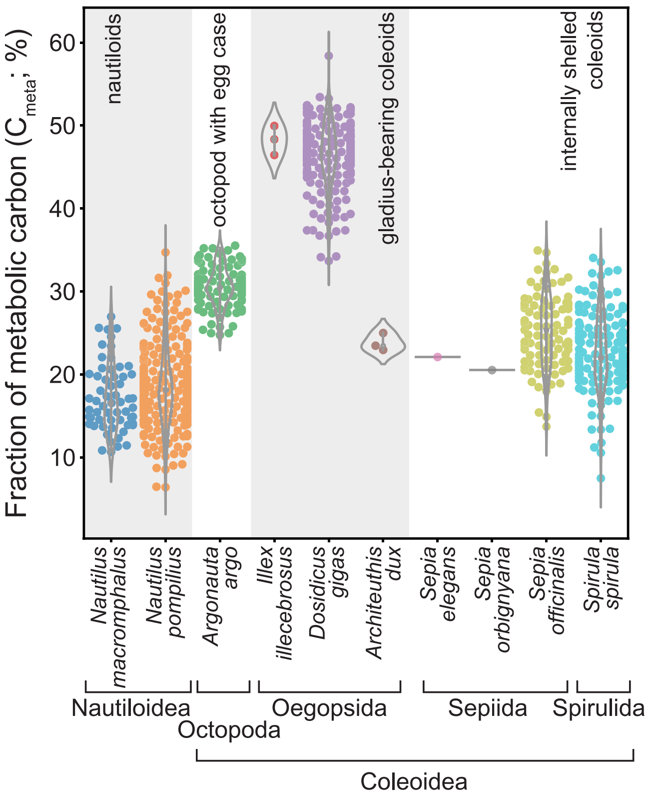

Figure 2. Violin and swarm plots of calculated fraction of metabolic carbon (C_{meta}) in modern cephalopods. Colored dots—data points plotted in a way that each data point will not overlap each other; gray dots—median value; curved lines—distribution of the data; straight lines—range of minimum and maximum values. Each point represents a single sample, not an average of multiple samples from one individual. Data for $\delta^{13}C_{shell}$ are from Bettencourt and Guerra (1999), Dance et al. (2014), Landman et al. (2004), Ohno et al. (2015), Price et al. (2009), Radtke (1983), Stevens et al. (2015), Tajika et al. (2022), and Trasviña-Carrillo et al. (2018).

(7%–35%); an octopod with an egg case, *A. argo* (25%–36%); and a gladius-bearing squid, *D. gigas* (34%–58%). The values within each group are significantly different from each other. Within any single taxon, the variation in C_{meta} is high. Additional details are reported in the Supplemental Material.

Fossil Ammonoids and Nautiloids

The calculated fractions of metabolic carbon in ammonoids and nautiloids from the three time-rock intervals are shown in Figure 3 and in the Supplemental Material. In the upper Maastrichtian *Discoscaphites iris* Zone of the Owl Creek Formation in Mississippi, the single data point for the nautiloid *Eutrephoceras* cf. *dekayi* falls at the lower end of the range for all ammonoid species (Fig. 3A). In the lower Maastrichtian *Baculites baculus–Baculites grandis* Zones of the Pierre Shale in Montana, there is a significant difference between the nautiloid *Eutrephoceras dekayi* (10%–23%) and all ammonoid species including *Hoploscaphites macer* and *Hoploscaphites criptonodosus* (7%–55%) (Fig. 3B). If we assume that the $\delta^{13}C_{DIC}$ we used to calculate the C_{meta} values for each time interval is correct, we can compare the fraction of metabolic carbon between taxa in each of these two time intervals. Our results reveal that the values for *E. dekayi* are significantly lower than those for all late Maastrichtian ammonoid species (Supplemental Material). In contrast, the values for the nautiloid *Cymatoceras* sp. from the lower Albian *D. mammillatum* Zone of the Ambarimaniga Formation in Madagascar are nearly the same as those for the co-occurring ammonoids (Fig. 3C; Supplemental Material).

DISCUSSION

Sensitivity of the Calculations of C_{meta} Based on $\delta^{13}C_{DIC}$

As noted above, calculation of the fraction of metabolic carbon (C_{meta}) is dependent on the value of $\delta^{13}C_{DIC}$. We calculated the $\delta^{13}C_{DIC}$ using co-occurring bivalves, assuming 10% contribution of metabolic carbon and −19‰ for $\delta^{13}C_{meta}$ (Tobin and Ward, 2015). However, ammonoids and nautiloids were nektobenthic, whereas bivalves lived on or in the substrate. Hence, for the upper Maastrichtian Owl Creek Formation, we used $\delta^{13}C$ data for planktic and benthic fora-

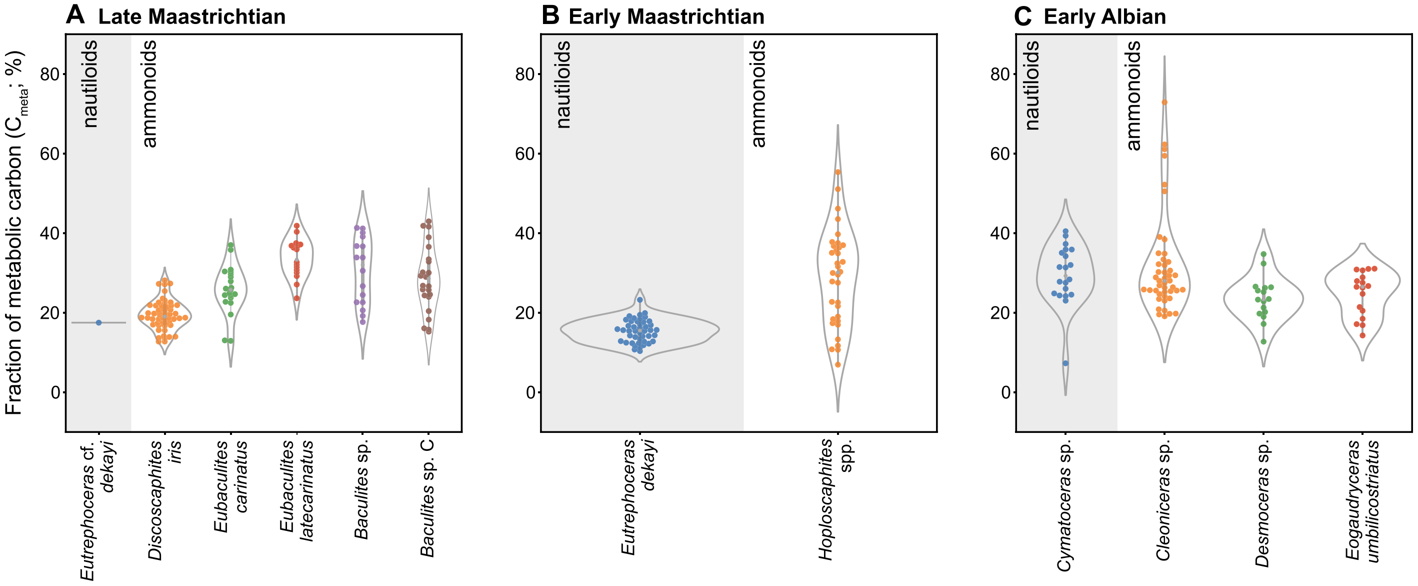

Figure 3. Violin and swarm plots of calculated fraction of metabolic carbon (C_{meta}) in fossil cephalopods. Symbols as in Figure 2. (A) Upper Maastrichtian *Discoscaphites iris* Zone, Owl Creek Formation, Mississippi, USA. (B) Lower Maastrichtian *Baculites baculus–Baculites grandis* Zones, Pierre Shale, Montana, USA. (C) Lower Albian *Douvilleiceras mammillatum* Zone, Ambarimaniga Formation, Madagascar. Data for $\delta^{13}C_{shell}$ are from Hoffmann et al. (2019), Landman et al. (2018), and Sessa et al. (2015). Additional data are in Supplemental Material (see text footnote 1).

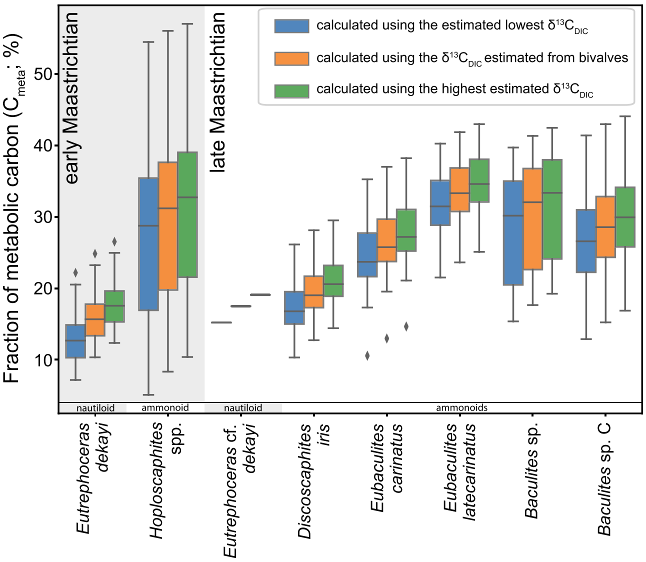

Figure 4. Box plot of calculated fraction of metabolic carbon (C_{meta}) using different $\delta^{13}C_{DIC}$ (DIC—dissolved inorganic carbon) values in early and late Maastrichtian cephalopods. Diamond symbols mark outliers. Estimated lowest and highest values of $\delta^{13}C_{DIC}$ for early Maastrichtian cephalopods are −1.97‰ and −1.05‰, respectively. Estimated lowest and highest values for $\delta^{13}C_{DIC}$ for late Maastrichtian cephalopods are 0.76‰ and 1.61‰, respectively.

minifera (Sessa et al., 2015) to assess the effect of water-column variation in $\delta^{13}C_{DIC}$ on our results. We hypothesized that the $\delta^{13}C$ of planktic and benthic foraminifera is comparable to the $\delta^{13}C_{DIC}$ of surface and bottom water, respectively, and used the average and median values of $\delta^{13}C$ to calculate the maximum possible range of $\delta^{13}C_{DIC}$ of the water column (0.76‰–1.61‰).

This approach cannot be applied to the early Maastrichtian because data on foraminifera are unavailable. Indeed, the bivalve-based $\delta^{13}C_{DIC}$ for the early Maastrichtian (∼−1.4‰) is lower than that for the late Maastrichtian. We attribute this difference to the proximity of the study area to the Sheridan Delta and the likelihood of freshwater input into the seaway, thus lowering the $\delta^{13}C_{DIC}$ (for further discussion, see Cai et al., 2020). However, assuming that the range of $\delta^{13}C_{DIC}$ in the early Maastrichtian is similar to that of the late Maastrichtian, the range of $\delta^{13}C_{DIC}$ is −1.05‰ to −1.94‰, respectively. Figure 4 shows the comparison between early and late Maastrichtian cephalopods, incorporating the potential variation in $\delta^{13}C_{DIC}$. These results suggest that the variation in $\delta^{13}C_{DIC}$ does not significantly affect the comparative results.

The early Albian site from Madagascar represents a deeper-water setting than the two Maastrichtian sites. For example, Hoffmann et al. (2019) estimated that the nautiloid *Cymatoceras* sp. inhabited a maximum water depth of 250 m and that the ammonoids *Cleoniceras* and *Desmoceras* inhabited a maximum water depth of 450–500 m. Thus, all these cephalopods lived in a deeper-water habitat and may have universally experienced a lower metabolic rate compared to those at the Maastrichtian sites. In addition, the spatial variation of $\delta^{13}C_{DIC}$ over ∼200 m (the difference in habitat depth between the nautiloids and ammonoids) may further mask the actual difference in metabolic rates between the two groups.

Impact of Metabolic Rate on the Evolution of Ammonoids and Nautiloids

The metabolic rate of modern *Nautilus* is significantly lower than that of all the coleoids studied, based on the stable carbon isotope proxy. This result agrees well with the estimates of metabolic rates based on oxygen consumption experiments, summarized by O'Dor and Webber (1991). There is no difference in the fraction of metabolic carbon among different species of *Nautilus*. The metabolic rate of the Maastrichtian nautiloid *Eutrephoceras* is also lower than that of all the co-occurring ammonoids examined. Intraspecific variation of the metabolic rate in ammonoids appears as high as (or higher than) that in modern coleoids. It is noteworthy that the metabolic rate is significantly different even among species within a single ammonoid genus such as *Eubaculites* (Fig. 3).

A higher metabolic rate entails a higher energy requirement per time unit to sustain minimal life activities. Therefore, a higher rate can be a disadvantage during a drastic food shortage. At the end of the Cretaceous, the Chicxulub asteroid impact as well as the Deccan Traps eruptions may have produced a transient episode of surface-water acidification (Henehan et al., 2019). This may have resulted in the decline of primary producers and planktic organisms, a likely food source for many ammonoids (see Kruta et al., 2011). Nautiloids may have been able to survive such a food-impoverished environment due to their lower metabolic rate and broader diet (for a discussion about the scavenging diet of modern nautilus, see Ward and Wicksten, 1980). The difference in egg size between the two groups is also linked to the availability of food resources. The larger embryonic size (∼10 mm) of Maastrichtian nautiloids versus those of ammonoids (∼1 mm) guaranteed an abundant supply of nourishment during the embryonic stage, preparing the postembryonic organism for the reality of a harsh, new world.

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REFERENCES CITED

Alegret, L., Thomas, E., and Lohmann, K.C., 2012, End-Cretaceous marine mass extinction not caused by productivity collapse: Proceedings of the National Academy of Sciences of the United States of America, v. 109, p. 728–732, https://doi.org/10.1073/pnas.1110601109.

Bettencourt, V., and Guerra, A., 1999, Carbon- and oxygen-isotope composition of the cuttlebone of *Sepia officinalis*: A tool for predicting ecological information?: Marine Biology, v. 133, p. 651–657, https://doi.org/10.1007/s002270050505.

Cai, Y.H., You, C.F., Wu, S.F., Cai, W.J., and Guo, L.D., 2020, Seasonal variations in strontium and carbon isotope systematics in the Lower Mississippi River: Implications for chemical weathering: Chemical Geology, v. 553, https://doi.org/10.1016/j.chemgeo.2020.119810.

Chung, M.T., Chen, C.Y., Shiao, J.C., Shirai, K., and Wang, C.H., 2021, Metabolic proxy for cephalopods: Stable carbon isotope values recorded in different biogenic carbonates: Methods in Ecology and Evolution, v. 12, p. 1648–1657, https://doi.org/10.1111/2041-210X.13630.

Cochran, J.K., Kallenberg, K., Landman, N.H., Harries, P.J., Weinreb, D., Turekian, K.K., Beck, A.J., and Cobban, W.A., 2010, Effect of diagenesis on the Sr, O, and C isotope composition of late Cretaceous mollusks from the Western Interior Seaway of North America: American Journal of Science, v. 310, p. 69–88, https://doi.org/10.2475/02.2010.01.

Crocker, K.C., DeNiro, M.J., and Ward, P.D., 1985, Stable isotopic investigations of early development in extant and fossil chambered cephalopods I. Oxygen isotopic composition of eggwater and carbon isotopic composition of siphuncle organic matter in *Nautilus*: Geochimica et Cosmochimica Acta, v. 49, p. 2527–2532, https://doi.org/10.1016/0016-7037(85)90120-6.

Dance, M.A., Bello, G., Furey, N.B., and Rooker, J.R., 2014, Species-specific variation in cuttlebone $\delta^{13}C$ and $\delta^{18}O$ for three species of Mediterranean cuttlefish: Marine Biology, v. 161, p. 489–494, https://doi.org/10.1007/s00227-013-2346-x.

Gallagher, W.B., 1991, Selective extinction and survival across the Cretaceous/Tertiary boundary in the northern Atlantic Coastal Plain: Geology, v. 19, p. 967–970, https://doi.org/10.1130/0091-7613(1991)019<0967:SEASAT>2.3.CO;2.

Henehan, M.J., et al., 2019, Rapid ocean acidification and protracted Earth system recovery followed the end-Cretaceous Chicxulub impact: Proceedings of the National Academy of Sciences of the United States of America, v. 116, p. 22,500–22,504, https://doi.org/10.1073/pnas.1905989116.

Hoffmann, R., Riechelmann, S., Ritterbush, K.A., Koelen, J., Lübke, N., Joachimski, M.M., Lehmann, J., and Immenhauser, A., 2019, A novel multiproxy approach to reconstruct the paleoecology of extinct cephalopods: Gondwana Research, v. 67, p. 64–81, https://doi.org/10.1016/j.gr.2018.10.011.

Kruta, I., Landman, N., Rouget, I., Cecca, F., and Tafforeau, P., 2011, The role of ammonites in the Mesozoic marine food web revealed by jaw preservation: Science, v. 331, p. 70–72, https://doi.org/10.1126/science.1198793.

Landman, N.H., Cochran, J.K., Cerrato, R., Mak, J., Roper, C.F.E., and Lu, C.C., 2004, Habitat and age of the giant squid (*Architeuthis sanctipauli*) inferred from isotopic analyses: Marine Biology, v. 144, p. 685–691, https://doi.org/10.1007/s00227-003-1245-y.

Landman, N.H., Goolaerts, S., Jagt, J.W.M., Jagt-Yazykova, E.A., Machalski, M., and Yacobucci, M.M., 2014, Ammonite extinction and nautilid survival at the end of the Cretaceous: Geology, v. 42, p. 707–710, https://doi.org/10.1130/G35776.1.

Landman, N.H., Grier, J.W., Cochran, J.K., Grier, J.C., Petersen, J.G., and Towbin, W.H., 2018, Nautilid nurseries: Hatchlings and juveniles of *Eutrephoceras dekayi* from the lower Maastrichtian (Upper Cretaceous) Pierre Shale of east-central Montana: Lethaia, v. 51, p. 48–74, https://doi.org/10.1111/let.12222.

Landman, N.H., Kennedy, W.J., Grier, J., Larson, N.L., Grier, J.W., Linn, T., Tackett, L., and Jicha, B.R., 2020, Large scaphitid ammonites (*Hoploscaphites*) from the Upper Cretaceous (upper Campanian–lower Maastrichtian) of North America: Endless variation on a single theme: Bulletin of the American Museum of Natural History, v. 441, p. 1–131, https://doi.org/10.1206/0003-0090.441.1.1.

McConnaughey, T.A., Burdett, J., Whelan, J.F., and Paull, C.K., 1997, Carbon isotopes in biological carbonates: Respiration and photosynthesis: Geochimica et Cosmochimica Acta, v. 61, p. 611–622, https://doi.org/10.1016/S0016-7037(96)00361-4.

O'Dor, R.K., and Webber, D.M., 1991, Invertebrate athletes: Trade-offs between transport efficiency and power density in cephalopod evolution: Journal of Experimental Biology, v. 160, p. 93–112, https://doi.org/10.1242/jeb.160.1.93.

Ohno, A., Miyaji, T., and Wani, R., 2015, Inconsistent oxygen isotopic values between contemporary secreted septa and outer shell walls in modern *Nautilus*: Lethaia, v. 48, p. 332–340, https://doi.org/10.1111/let.12109.

Pape, E., 2016, Biogeochemical evidence for chemosymbiosis in the fossil record [Ph.D. thesis]: Leeds, UK, University of Leeds, 285 p.

Price, G.D., Twitchett, R.J., Smale, C., and Marks, V., 2009, Isotopic analysis of the life history of the enigmatic squid *Spirula spirula*, with implications for studies of fossil cephalopods: Palaios, v. 24, p. 273–279, https://doi.org/10.2110/palo.2008.p08-067r.

Radtke, R.L., 1983, Chemical and structural characteristics of statoliths from the short-finned squid *Illex illecebrosus*: Marine Biology, v. 76, p. 47–54, https://doi.org/10.1007/BF00393054.

Romanek, C.S., Grossman, E.L., and Morse, J.W., 1992, Carbon isotopic fractionation in synthetic aragonite and calcite: Effects of temperature and precipitation rate: Geochimica et Cosmochimica Acta, v. 56, p. 419–430, https://doi.org/10.1016/0016-7037(92)90142-6.

Schulte, P., et al., 2010, The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary: Science, v. 327, p. 1214–1218, https://doi.org/10.1126/science.1177265.

Sessa, J.A., Larina, E., Knoll, K., Garb, M., Cochran, J.K., Huber, B.T., MacLeod, K.G., and Landman, N.H., 2015, Ammonite habitat revealed via isotopic composition and comparisons with co-occurring benthic and planktonic organisms: Proceedings of the National Academy of Sciences of the United States of America, v. 112, p. 15,562–15,567, https://doi.org/10.1073/pnas.1507554112.

Stevens, K., Iba, Y., Suzuki, A., and Mutterlose, J., 2015, Biological and environmental signals recorded in shells of *Argonauta argo* (Cephalopoda, Octobrachia) from the Sea of Japan: Marine Biology, v. 162, p. 2203–2215, https://doi.org/10.1007/s00227-015-2750-5.

Tajika, A., Landman, N.H., Hoffmann, R., Lemanis, R., Morimoto, N., Ifrim, C., and Klug, C., 2020, Chamber volume development, metabolic rates, and selective extinction in cephalopods: Scientific Reports, v. 10, 2950, https://doi.org/10.1038/s41598-020-59748-z.

Tajika, A., Landman, N.H., Cochran, J.K., Goiran, C., and Le Bouteiller, A., 2022, Isotopic evidence concerning the habitat of *Nautilus macromphalus* in New Caledonia: PLoS One, v. 17, e0271235, https://doi.org/10.1371/journal.pone.0271235.

Tajika, A., Nützel, A., and Klug, C., 2018, The old and the new plankton: Ecological replacement of associations of mollusc plankton and giant filter feeders after the Cretaceous?: PeerJ, v. 6, e4219, https://doi.org/10.7717/peerj.4219.

Tobin, T.S., and Ward, P.D., 2015, Carbon isotope ($\delta^{13}C$) differences between Late Cretaceous ammonites and benthic mollusks from Antarctica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 428, p. 50–57, https://doi.org/10.1016/j.palaeo.2015.03.034.

Trasviña-Carrillo, L.D., Hernández-Herrera, A., Torres-Rojas, Y.E., Galván-Magaña, F., Sánchez-González, A., and Aguíñiga-García, S., 2018, Spatial and trophic preferences of jumbo squid *Dosidicus gigas* (D'Orbigny, 1835) in the central Gulf of California: Ecological inferences using stable isotopes: Rapid Communications in Mass Spectrometry, v. 32, p. 1225–1236, https://doi.org/10.1002/rcm.8147.

Ward, P., and Wicksten, M.K., 1980, Food sources and feeding behavior of *Nautilus macromphalus*: The Veliger, v. 23, p. 119–124.

Zakharov, Y.D., Tanabe, K., Shigeta, Y., Safronov, P.P., Smyshlyaeva, O.P., and Dril, S.I., 2016, Early Albian marine environments in Madagascar: An integrated approach based on oxygen, carbon and strontium isotopic data: Cretaceous Research, v. 58, p. 29–41, https://doi.org/10.1016/j.cretres.2015.08.014.

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