


An analysis of the impacts of Cretaceous oceanic anoxic events on global molluscan diversity dynamics

Nicholas A. Freymueller , Jason R. Moore, and Corinne E. Myers

Abstract.—Oceanic anoxic events (OAEs) are contemporaneous with 11 of the 18 largest Phanerozoic extinction events, but the magnitude and selectivity of their paleoecological impact remains disputed. OAEs are associated with abrupt, rapid warming and increased CO₂ flux to the atmosphere; thus, insights from this study may clarify the impact of current anthropogenic climate change on the biosphere. We investigated the influence of the Late Cretaceous Bonarelli event (OAE2; Cenomanian/Turonian stage boundary; ~94 Ma) on generic- and species-level molluscan diversity, extinction rates, and ecological turnover. Cenomanian/Turonian results were compared with changes across all Cretaceous stage boundaries, some of which are coincident with less severe OAEs. We found increased generic turnover, but not species-level turnover, associated with several Cretaceous OAEs. The absence of a species-level pattern may reflect species occurrence data that are too temporally coarse to robustly detect patterns. Five hypotheses of ecological selectivity relating anoxia to survivorship were tested across stage boundaries with respect to faunality, mobility, and diet using generalized linear models. Interestingly, benthic taxa were consistently selected against throughout the Cretaceous regardless of the presence or absence of OAEs. These results suggest that: (1) the Cenomanian/Turonian boundary (OAE2) was associated with a decline in molluscan diversity and increase in extinction rate that were significantly more severe than Cretaceous background levels; and (2) no differential ecological selectivity was associated with OAE-related diversity declines among the variables tested here.

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Introduction

Oceanic anoxic events (OAEs) occur when the oxygen minimum zone (OMZ)—a normal component of open-marine systems—expands, causing shallow continental shelf habitats to experience significant depletion in dissolved oxygen from the thermocline into the photic zone (Schlanger and Jenkyns 1976; Kuypers et al. 2004). OMZs form at several hundred meters depth where the balance between oxygen supply and organic decay results in low oxygen concentrations (Schlanger and Jenkyns 1976; Lalli and Parsons 1993). Today, OMZs may have oxygen concentrations as low as 10% of normal ocean conditions (Lalli and Parsons 1993). OMZ expansion can result from increased input of detrital organic matter (e.g., resulting from increased planktonic productivity) into the ocean system (Schlanger and Jenkyns 1976;

Skelton et al. 2006) and/or increased temperature, because warm water holds less dissolved oxygen (Falkowski et al. 2011).

Phanerozoic deoxygenation events brought on by OMZ expansion have been linked to external factors such as increased weathering, sediment, and nutrient flux to the ocean (Monteiro et al. 2012; Pogge von Strandmann et al. 2013; Owens et al. 2018). This is often attributed to increased seafloor spreading rates and the emplacement of Large Igneous Provinces (LIPs), both of which may cause increased CO₂ flux to the atmosphere and increased temperature (Leckie et al. 2002; Snow et al., 2005; Sageman et al. 2006; Jenkyns 2010; Barclay et al. 2010; van Bentum et al. 2012; Pogge von Strandmann et al. 2013; Owens et al. 2018). As a result, large swaths of the world's shallow oceans become severely oxygen depleted

(Schlanger and Jenkyns 1976). In the geologic record, OAEs are identified by a net sequestration of carbon, which may be observed as packages of organic-rich, laminated black shale deposits and abrupt $\delta^{13}\text{C}$ excursions (CIEs; up to $\pm 5\%$ depending on the source of CO_2 ; Erbacher et al. 1996; Sageman et al. 2006; Owens et al. 2018).

Due to their global extent and severity, OAEs have the potential to cause significant extinction, particularly in shallow coastal systems. For example, OAEs have been associated with higher rates of biotic turnover during the Permo-Triassic and Triassic–Jurassic mass extinctions (Wignall and Twitchett 1996; Kiesling et al. 2007; Kiessling and Aberhan 2007a, b). More specifically, significant foraminiferal turnover was observed coeval with several Cretaceous OAEs (Erba 1994; Leckie et al. 2002; Parente et al. 2008), and reef declines have also been connected with OAE activity (Arthur and Schlanger 1979; Grötsch et al. 1993; Föllmi et al. 1994; Weissert et al. 1998; Phelps et al. 2015).

However, there is also evidence that some OAEs are not associated with extinctions, or have only impacted select taxa; for example, the Toarcian OAE (~183 Ma) likely had little to no effect on belemnites (Ullmann et al. 2014). Beyond the effect of OAEs on raw diversity and extinction rates, there is additional uncertainty surrounding their ecological selectivity, especially regarding whether selectivity patterns were unique from background selection regimes (e.g., the differences between Kiesling et al. [2007] and Clapham and Payne [2011]). These discrepancies indicate that the precise influence of OAEs on marine fauna is not well known.

Mollusks are an important clade for testing the impact of OAEs; they are the most diverse invertebrate phylum (23% of all marine species; Sepkoski 1981; Appeltans et al. 2012) and the largest phylum represented in the fossil record, because they demonstrate relatively high and comparatively uniform preservation potential (Kidwell 2002, 2005). Thus, restricting analyses to mollusks minimizes biases surrounding rarity and taphonomy, while preserving sufficient sample sizes to facilitate statistical analyses. Moreover, of all marine invertebrate clades,

mollusks are the second-most tolerant to low-oxygen conditions, superseded only by foraminifera (Baker and Mann 1992; Moodley and Hess 1992; Ekau et al. 2010; Song et al. 2014).

The Cretaceous marine fossil record is particularly well sampled globally (Erbacher et al. 1996; Kuypers et al. 2004; Sageman et al. 2006; Forster et al. 2008; Elrick et al. 2009; Li et al. 2017), and consequently provides an ideal opportunity to test the influence of widespread anoxia on molluscan biodiversity, extinction, and ecological structure. There were as many as six OAEs during the Cretaceous Period: OAE1a (early Aptian; lasting ~1.0–1.3 Myr), OAE1b (Aptian/Albian; ~4.0 Myr), OAE1c (late Albian; <0.2 Myr), OAE1d (Albian/Cenomanian; ~0.5 Myr), OAE2 (Cenomanian/Turonian; ~0.82 Myr), and OAE3 (late Coniacian; ~1.1 Myr) (Schlanger and Jenkyns 1976; Leckie et al. 2002; Gröcke et al. 2006; Y. Li et al. 2008; Millán et al. 2014; Joo and Sageman 2014; X. Li et al. 2017). Of these, OAE1b and OAE2 were the most severe and/or widespread, each presenting a $>2\%$ positive CIE and extensive black shale deposition (Leckie et al. 2002; Monteiro et al. 2012; Joo and Sageman 2014). OAE3 shows the smallest CIE and is potentially a regional rather than a global event (Wagreich 2012; Lowery et al. 2017).

These OAEs occurred within the larger Cretaceous greenhouse climate system; gradual warming began at the Hauterivian/Barremian boundary (Frakes 1999; Fig. 1C) and continued until the middle Turonian (Clarke and Jenkyns 1999; Li and Keller 1999; Friedrich et al. 2012; Jarvis et al. 2011). Subsequent gradual cooling continued into the Paleocene, but included numerous relatively rapid warming/cooling events throughout (Clarke and Jenkyns 1999; Li and Keller 1999; Jarvis et al. 2011; Friedrich et al. 2012; O'Brien et al. 2017).

OAE2 (aka the Bonarelli event) is considered by far the most severe Cretaceous OAE (Erbacher et al. 1996; Kuypers et al. 2004; Sageman et al. 2006; Forster et al. 2008; Elrick et al. 2009; Baroni et al. 2014; Joo and Sageman 2014; Li et al. 2017; Owens et al. 2018). The abrupt CIE observed at this time ranges from +2.5 to 7‰, and averages around +3‰ globally (Owens et al. 2018). While the rate of seafloor spreading was high at this time, the

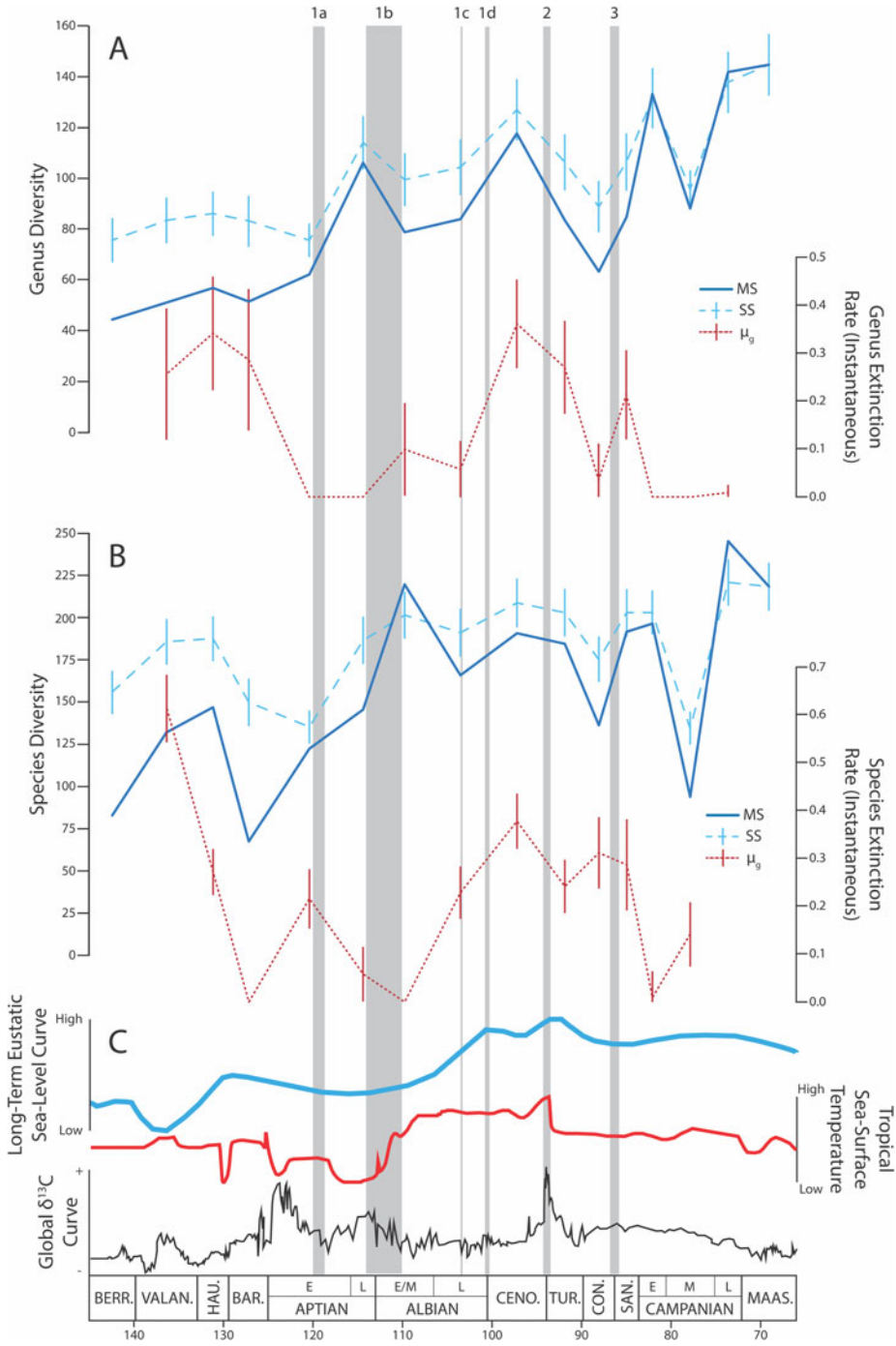


FIGURE 1. Timeline of diversity (including multiton subsampling [MS; Alroy 2017b] and sample-standardized [SS; for examples, see Bush et al. 2004; Kiessling et al. 2007] diversity estimates), instantaneous extinction rate (μ_g ; Alroy 2014), and environmental factors during the Cretaceous Period. Error bars on SS diversity show 2 SDs. OAEs are named and denoted with shaded gray bars according to their specific timing and duration. A, Genus-level diversity (MS and SS) and extinction rate (μ_g) patterns. B, Species-level diversity (MS and SS) and extinction rate (μ_g) patterns. C, Long-term eustatic sea-level curve (modified from Ogg et al. 2016), long-term tropical sea-surface temperature curve, and global $\delta^{13}C$ curve (both modified from the TimeScale Creator [Ogg et al. 2016]). BERR., Berriasian; VALAN., Valanginian; HAU., Hauterivian; BAR., Barremian; CENO., Cenomanian; TUR., Turonian; CON., Coniacian; SAN., Santonian; MAAS., Maastrichtian.

massive amount of warming and CO₂ flux is more likely associated emplacement of the Caribbean LIP, which is thought to have triggered the onset of rapid warming (Erba 1994; Leckie et al. 2002; Parente et al. 2008; Turgeon and Creaser 2008; Elrick et al. 2009; Barclay et al. 2010; although see Jarvis et al. [2011] for evidence of brief cooling—the Plenus cold event—just before the most severe anoxia).

Paleobiologically, OAE2 is coincident with the 10th largest extinction event during the Phanerozoic (Raup and Sepkoski 1984; Bambach et al. 2004; Bambach 2006). Approximately 25% of all marine genera and 33–53% of all marine species went extinct; this represents ~2.5 times the average background-extinction percentage for genera at the time (Bambach 2006). Several studies have shown that microfauna such as foraminifera show considerable turnover across OAE2 (e.g., Erba 1994; Leckie et al. 2002; Parente et al. 2008).

This investigation tests the influence of OAE2 on molluscan biodiversity, extinction, and ecological structure using a quantitative occurrence-based approach made possible by the Paleobiology Database (PBDB; <http://www.paleobiodb.org>). Previous studies of molluscan diversity at this time provide contradictory results. Some have shown that only a regional loss of ammonite species diversity occurred across OAE2 and that the loss was primarily due to a decrease in origination rates (e.g., Monnet and Bucher 2007; Monnet 2009). Others suggest upward of a 60% decrease in global ammonite generic diversity (Elder 1989; Harries and Little 1999; Hirano et al. 2000; Bambach 2006; Jagt-Yazykova 2011, 2012). There is also debate regarding the timing of molluscan turnover, that is, whether extinctions were directly tied to OAE2 (Harries and Little 1999; Bambach 2006) or whether the extinction largely predated the Bonarelli event (Fisher 2006; Monnet and Bucher 2007; Monnet 2009; Kaiho et al. 2014). Notably, many of these studies compared data gathered from select sites at the local/regional scale; whereas the analyses described here estimate diversity and extinction patterns at the global scale with stage-level temporal resolution (comparable to other diversity studies at different time intervals; e.g., Sepkoski 1981; Raup and Sepkoski

1982, 1984, 1986; Jablonski 1986; Foote 2000; Alroy et al. 2001; Bush et al. 2004; Kiessling and Aberhan 2007a,b; Kiessling et al. 2007; Alroy 2008, 2010a; Clapham and Payne 2011).

Methods

All analyses for this study were performed in R (v. 3.2.4; R Core Development Team 2017). MS code was provided by Alroy (2017a).

Taxonomic Sampling

Global occurrence data for marine molluscan taxa were downloaded from the PBDB on 6 August 2018. These data spanned the Tithonian (latest Jurassic) through the Danian (earliest Paleogene) stages. The data were filtered to include: only genera whose taxonomy was included in Sepkoski's (2002) compendium, as it is considered to be the most comprehensive and most broadly accepted consensus of fossil marine animal genera; taxa that were identified to the species level (for species–genera comparisons); and individual occurrences that could be stratigraphically constrained to the geologic stage level (~5 Myr each). Binning occurrence data at this temporal resolution (4–6 Myr) has previously been shown to reveal meaningful changes in both ecology and diversity (Kiessling et al. 2007; Kiessling and Aberhan 2007a,b; Clapham and Payne 2011; Supplementary Table S1).

Because some Cretaceous stages (Aptian, Albian, and Campanian) are approximately twice this duration (~12 Myr), these stages were split into substages (early Aptian, late Aptian, early/middle Albian, late Albian, early Campanian, middle Campanian, and late Campanian) to reduce bias from variable temporal bin sizes. Finer temporal resolution (i.e., substage level) is not consistently reported in the occurrence data available through the PBDB. Thus, the analyses were limited to ~5 Myr temporal bins. This resulted in diversity, extinction, and ecological analysis across 16 Cretaceous time bins (Table 1).

Stratigraphic singletons were removed to reduce the uncertainty in distinguishing rare taxa from those subject to taphonomic or sampling biases (Foote 1997, 2000; Lenat and Resh 2001). Stratigraphic singletons were defined as

TABLE 1. Results of the multitaxon subsampling (MS) and sample-standardized (SS) estimates for all 16 Cretaceous time bins at both the genus and species levels. SS diversities include mean diversity of 999 replicates \pm 2 SDs.

Stage	Occurrences	Duration (Myr)	MS genus diversity	SS genus diversity	MS species diversity	SS species diversity
Berriasian	1300	5.2	44	76 \pm 8.71	83	157 \pm 12.82
Valanginian	2086	6.9	51	83 \pm 9.00	132	185 \pm 13.51
Hauterivian	1402	3.5	57	86 \pm 8.69	146	186 \pm 13.22
Barremian	1192	4.4	51	83 \pm 10.05	68	149 \pm 13.95
Early Aptian	316	10	62	75 \pm 6.58	121	135 \pm 9.74
Late Aptian	791	3	106	114 \pm 10.57	145	173 \pm 13.96
Early–middle Albian	1303	6	79	99 \pm 10.44	218	200 \pm 13.79
Late Albian	1591	6.5	84	104 \pm 10.98	166	191 \pm 14.15
Cenomanian	5504	6.6	117	127 \pm 12.08	191	207 \pm 14.45
Turonian	3015	4.1	83	106 \pm 11.02	188	205 \pm 14.09
Conician	940	3.5	63	89 \pm 10.08	137	175 \pm 13.44
Santonian	1788	2.7	85	106 \pm 11.29	190	202 \pm 13.94
Early Campanian	1509	3	133	131 \pm 11.84	196	202 \pm 12.95
Middle Campanian	371	5.4	88	96 \pm 7.43	94	135 \pm 9.73
Late Campanian	2926	3.1	142	138 \pm 12.04	245	219 \pm 13.70
Maastrichtian	17,950	6.1	145	125 \pm 12.15	217	217 \pm 14.18

taxa that did not have at least one occurrence in any preceding and following geologic stage (e.g., occurred in the Cenomanian, but not in the Albian or Turonian; for additional examples, see Sepkoski 1997; Alroy 2000; Alroy et al. 2001; Kiessling et al. 2007). We used the Tithonian and Danian stages to determine the presence of singletons for the Berriasian and Maastrichtian, respectively; Tithonian and Danian occurrences were not independently analyzed for changes in diversity or ecology. Even data treated in this manner have the potential to contain edge effects; however, the OAE-bounded intervals that we focused on are in the middle of our time series, rendering these edge effects unlikely to influence impacts of OAEs on diversity patterns. The resulting data set included 1029 genera, 11,599 species, and 53,084 molluscan occurrences (see Supplementary Table S1 for raw PBDB data and Supplementary Table S2 for the cleaned data set).

A significant proportion of large-scale paleobiological studies are conducted on genus-level taxonomic data (e.g., Simpson 1961; Allmon 1992; Sepkoski 1998). This is in part because species-level identifications are often considered less robust than those binned within genera (Raup and Sepkoski 1982; Wheeler and Meier 2000). However, given the potential for higher-level taxonomy to dilute or even obscure species-level patterns (Hendricks et al. 2014), we evaluated the difference

between generic and species data sets explicitly by performing analyses at both taxonomic levels. This resulted in 32 data sets for diversity and ecological analysis: 16 time bins for each of two taxonomic levels.

Taxonomic Diversity

Taxonomic diversity was calculated using multitaxon subsampling (MS) on all 32 data sets (Alroy 2017a,b). In comparison studies, MS has been shown to be a more robust method of estimating diversity than previous methods of fair/coverage-based sampling (e.g., shareholder quorum subsampling or extrapolation methods; Alroy 2010a,b, 2017a,b). MS also performs better than more traditional methods of sample-standardized (SS) diversity estimates, because it avoids issues such as flattening of diversity curves (Alroy 2010a,b, 2017b), although we also estimated diversity using the SS method for comparison. We calculated diversity using both MS and SS methods for all Cretaceous time bins at both the genus and species levels (see the Methods Appendix in the Supplementary Material for a more detailed explanation).

Extinction Rates

Extinction rates were calculated on the genus- and species-level data sets using two different techniques: the Alroy (2008) three-timer rate (μ_3) and the Alroy (2014) gap-filler

rate (μ_G). To calculate confidence intervals on our extinction rates, we rarefied both our genus- and species-level data sets 999 times, selecting one-third of each data set with replacement in every repetition, and then calculated the μ_3 and μ_G extinction rates (see the Methods Appendix in the Supplementary Material for a more detailed explanation).

Ecology

To estimate ecological selectivity of diversity patterns across each time bin, we tested the relationship between taxon survivorship and taxon ecology using generalized linear models (GLMs) for single and multiple logistic regression. Logistic regression is ideal for extinction-related studies, as the outcome of selectivity is binary (i.e., the species either went extinct or survived; for additional examples, see Clapham and Payne 2011; Payne et al. 2016a,b). Taxa were classified into broad ecological categories according to clade membership, faunality, mobility, and feeding strategy, based on PBDB descriptions that are broadly determined by prior morphological analysis (Supplementary Table S1). Clade membership was assigned at the class level: Bivalvia, Cephalopoda, and Gastropoda. Scaphopoda and Polyplacophora were represented by a combined three genera for the entire occurrence data set; thus, they were used for diversity and extinction calculations, but not for ecological analysis. Clade membership and feeding strategies were considered categorical variables (ranked either 0 or 1 for each subcategory), whereas faunality and mobility were treated as ordinal variables. Feeding strategies were categorized as: filter feeding, suspension feeding, detritivorous, carnivorous, and grazing. Omnivores and chemosymbionts were present but rare; these taxa were also retained for investigating diversity and extinction patterns but removed for the ecological analyses. Faunality was assigned to each taxon along an increasingly bottom-dwelling to pelagic gradient as either infaunal (1), semi-infaunal (2), epifaunal (3), or nektonic/nektobenthic (4). Mobility was classified as stationary (1), facultatively mobile (2), or actively mobile (3). Survivorship was categorized as extant (1) in the time bin of the taxon's first occurrence until the time bin of

last occurrence, even if the taxon did not occur in an intermediate time bin; the taxon was labeled extinct (0) in the time bin of its last occurrence and not present (NA) in all bins before its first occurrence and following its last occurrence. Thus, Lazarus taxa were categorized as extant in time bins where they failed to occur. Because there were no intra-generic differences in assigned ecological traits in the PBDB, we performed this analysis using the generic data sets only.

The majority of ecological classifications from the PBDB are made at the genus or the family level. However, some are made at the class or ordinal level. Across our 32 data sets approximately 10% of genera were assigned ecological classifications at the genus level. Approximately 62% and 28% of taxa were classified at the family/subfamily and class/order levels, respectively. Because this may bias genus-level analyses of ecological selectivity, we performed two sets of sensitivity analyses that tested for ecological selectivity among: (1) only those taxa with ecological classifications at the genus level and (2) only those taxa with ecological classifications at the family level and below. Sensitivity analyses provided results identical to those for the full data sets, and therefore these results are not reported separately.

To better understand the causal relationships between survivorship and combinations of ecological traits, we examined five GLM models testing specific hypotheses of OAE ecological selectivity. These hypotheses were generated a priori based on the current best understanding of molluscan responses to environmental change to avoid introducing biases from data dredging/*p*-hacking. All models included the impact of molluscan clade membership (i.e., Bivalvia, Cephalopoda, and Gastropoda) on survivorship to test for phylogenetic independence.

The first model represented a "full model" (model 1), which tested the hypothesis that survivorship depended on the interactions of all measured ecological characteristics (clade membership, faunality, mobility, and all feeding categories: detritivores, carnivores, suspension feeders, and grazers). Four subsets of the full model tested hypotheses with existing theoretical or empirical support as drivers of

survivorship given the low oxygen conditions associated with OAEs. Faunality was included in all models, as OAEs are characterized by severely reduced oxygen in the shallow shelf environments preferred by mollusks. For example, Clapham and Payne (2011) found that infaunal taxa were more likely to go extinct than epifaunal taxa at the end-Permian—when there was severe anoxia—as OMZ expansion onto the shallow shelf should affect the benthos before the rest of the water column (Schlanger and Jenkyns 1976; Clapham and Payne 2011). Thus, model 2 tested the hypothesized effects of clade membership and faunality in controlling survivorship.

Model 3 tested the influence of clade membership, feeding strategy, and faunality on patterns of survivorship. We hypothesized that suspension feeders and detritivores would demonstrate increased survivorship relative to carnivores and grazers across time bins that contained/were bound by an OAE due to the large increase in detrital organic matter resulting from increased anoxia-driven mortality. Aberhan and Baumiller (2003) note that after the Triassic–Jurassic mass extinction (which includes the influence of an OAE), the bivalve community was nearly devoid of infaunal suspension feeders. Furthermore, grazers were found to be negatively impacted across the Permo-Triassic mass extinction (Xie et al. 2010), potentially due to the emergence of cyanobacteria as the dominant primary producers at the time (Ohkouchi et al. 2006; Kashiyama et al. 2008; Paul 2008). We hypothesized carnivores to decrease in diversity due to increased prey mortality resulting from anoxia and because carnivory has been shown to require higher oxygen concentrations for both prey capture and metabolism (Sperling et al. 2013).

Model 4 tested for the effects of clade membership, faunality, plus only detritivory and suspension feeding on survivorship. This model represented the combination of the two feeding strategies hypothesized to perform well (suspension feeders and detritivores) relative to the two feeding strategies we hypothesized to show increased extinction (grazers and carnivores). Model 5 tested for the relationship between clade membership, faunality,

mobility, detritivory, suspension feeding, and survivorship. The inclusion of mobility tested the prediction that actively mobile taxa may be more likely to access surface waters, which would have had the highest dissolved oxygen content.

The likelihood of the hypotheses associated with each model was estimated using the Akaike information criterion (AIC values) and associated Akaike weights (w_i ; Akaike 1974); models with more support have lower AIC values and higher w_i values. Models within two AIC of each other are similarly well supported by the data (Burnham and Anderson 2002), hence all models within two AIC of the model with the lowest AIC should be considered good explanatory candidates. Absolute model explanatory power was assessed by comparison of null and residual deviances (Anderson and Burnham 2002; Burnham and Anderson 2002).

Results

Diversity Dynamics and Extinction Rates

The pattern of Cretaceous diversity recovered in these analyses is similar across both methodologies for subsampling (MS and SS) and both taxonomic levels (genus and species; Fig. 1). MS recovers significant generic diversity declines across four time bins: the late Aptian/early–middle Albian, Cenomanian/Turonian, Turonian/Coniacian, and early Campanian/middle Campanian boundaries. We primarily interpret MS-derived diversity and gap-filler extinction rates (μ_G), as these are the preferred methods for unbiased diversity and extinction rate estimation and are not subject to the biases of flattened diversity estimates and “un-fair” methods of sampling (Alroy 2010a,b, 2014, 2017b; see Supplementary Table 1 for a direct comparison between μ_3 and μ_G extinction rate estimations).

Figure 1 and Table 1 provide results of molluscan diversity and extinction rate estimates for the entire Cretaceous. The genus-level analysis supports the hypothesis that OAE2 resulted in substantially increased extinction rates and decreases in diversity (Fig. 1A; Leckie et al. 2002; Kuhnt et al. 2011; Joo and Sageman 2014). OAE1b also shows a decreased diversity

in the early–middle Albian, but this is not supported by increased extinction rates (Fig. 1A). In addition to significant diversity decreases, three pulses of diversity increase were recovered through the middle part of the Cretaceous: across the early Aptian/late Aptian, the late Albian/Cenomanian, and Coniacian through early Campanian boundaries. These intervals were not associated with decreases in extinction rates.

Ecology

Table 2 provides the results of the GLMs quantitatively testing the relationships between taxon survivorship and specific combinations of ecological traits. Of the five hypotheses tested, the faunality-only model (model 2) was determined the most likely model to explain survivorship for 10 of the 14 stages analyzed (the GLM algorithm failed to converge for the Barremian and middle Campanian data sets, reducing the number of time bins tested from 16 to 14; this did not affect any time bins associated with an OAE). The faunality, suspension-feeding, and detritivory model (model 3) was commonly the second most likely model (Table 2). All models indicated a stronger selection against taxa that were increasingly benthic. Whereas these results support ecological selectivity associated with survivorship patterns during the Cretaceous in general, there is no signal of a change in selectivity patterns between OAE-influenced and non-OAE influenced time bins.

Discussion

Cretaceous Diversity and Extinction Trends

Two of the four observed declines in Cretaceous molluscan genus diversity are associated with OAE events (OAE1b: late Aptian/early–middle Albian; and OAE2: Cenomanian/Turonian). There was no global OAE during the Turonian/Coniacian diversity decline. The fourth decline (early Campanian/middle Campanian) is likely an artifact of sample size. This interval is marked by a substantial decrease in taxon occurrences, 371 occurrences compared with 1509 and 2926 occurrences in the adjacent bins (Table 1). The remaining less severe OAEs (OAE1a, c, d, and OAE3), do not

show a consistent pattern with respect to changing generic diversity or extinction rates. Thus, all observed substantial diversity declining trends in the Cretaceous are associated with OAEs; the most substantial occurred during the Cenomanian to Coniacian interval that experienced OAE2.

A conservative interpretation of these data supports primarily minor changes in generic diversity throughout the Cretaceous and no clear impact of OAEs in general or OAE2 in particular (Fig. 1A). However, SS analyses are known to artificially flatten diversity curves versus the less biased MS (Alroy 2010a,b, 2017b), potentially explaining the differences in observed significance of diversity declines in SS compared with MS estimates. Therefore, we suggest that the substantial MS diversity declines observed across OAE1b and OAE2 are more likely to reflect real patterns of Cretaceous molluscan diversity, which supports our initial hypothesis.

Species-level diversity analyses using both MS and SS methods do not consistently match the patterns observed among genera (Fig. 1B). OAE-associated diversity declines are only observed across the OAE1c interval and OAE3, two of the more minor OAEs (Leckie et al. 2002; Joo and Sageman 2014). Differences between the species- and genus-level diversity data sets may be expected given that species have relatively short average life spans (a few million years) compared with the temporal bin length in this study (~5 Myr; Raup 1978). That is, high species-level turnover may reflect background-extinction rates summed over long time bins and not inform hypotheses of OAE environmental perturbation. If this is the case, then the genus-level data set may more accurately reflect faunal responses to OAEs in general.

The highest estimated generic extinction rate during the Cretaceous occurs across the Cenomanian/Turonian boundary, concurrent with OAE2. This supports the hypothesis that OAE2 may have contributed to significantly higher extinction than background extinction. However, there is no consistent pattern of increased extinction rates at any of the other OAEs (Fig. 1).

The species-level data set supports high extinction rates across the Cenomanian/

TABLE 2. Results of the generalized linear model (GLM) analysis. Columns include: time bin, model name, residual deviance, residual degrees of freedom (df), difference between null and residual deviance (Δ deviance), p -value, Akaike information criterion (AIC) value, Δi , and Akaike weight (w_i). The null deviances and null degrees of freedom (null df) are included for every set of models. The most likely model in each time bin is denoted with bold and italics. Model 1 = clade membership (Bivalvia, Cephalopoda, and Gastropoda) + faunality + mobility + all feeding strategies (detritivores, carnivores, suspension feeders, and grazers); model 2 = clade membership + faunality; model 3 = clade membership + faunality + all feeding strategies; model 4 = clade membership + faunality + mobility + detritivory + suspension feeding; model 5 = clade membership + faunality + mobility + detritivory + suspension feeding.

Time bin	Model	Residual deviance	df	Δ deviance	p -value	AIC	Δi	w_i	Null deviance	Null df
Berriasian	1	90.60	106	8.848	0.264	106.60	7.32	0.02	99.45	113
	2	91.28	110	8.164	0.043	99.28	0	0.77		
	3	90.75	107	8.695	0.191	104.75	5.47	0.05		
	4	90.95	108	8.493	0.131	102.95	3.67	0.12		
	5	91.42	107	8.025	0.236	105.42	6.14	0.04		
Valanginian	1	74.79	129	16.018	0.067	94.79	8.07	0.01	90.81	138
	2	76.72	134	14.091	0.007	86.72	0	0.75		
	3	75.85	131	14.962	0.036	91.85	5.13	0.06		
	4	76.45	132	14.358	0.026	90.45	3.73	0.12		
	5	75.49	131	15.32	0.032	91.49	4.77	0.07		
Hauterivian	1	87.55	117	22.711	0.004	105.55	7.13	0.02	110.27	125
	2	90.42	122	19.844	< 0.001	98.42	0	0.68		
	3	89.23	118	21.031	0.004	105.23	6.81	0.02		
	4	89.25	120	21.016	0.001	101.25	2.83	0.16		
	5	87.89	119	22.372	0.001	101.89	3.47	0.12		
Barremian	1									
	2									
	3									
	4									
	5									
GLM algorithm failed to converge										
Early Aptian	1	35.71	63	14.52	0.069	53.71	5.89	0.02	50.23	71
	2	40.94	68	9.297	0.026	48.94	1.11	0.27		
	3	35.82	64	14.41	0.044	51.82	4.00	0.06		
	4	35.82	66	14.41	0.013	47.82	0	0.47		
	5	35.71	65	14.52	0.024	49.71	1.89	0.18		
Late Aptian	1	101.32	148	22.23	0.005	119.32	2.84	0.11	123.55	156
	2	108.48	153	15.07	0.002	116.48	0	0.47		
	3	101.36	149	22.19	0.002	117.36	0.88	0.30		
	4	107.80	151	15.75	0.008	119.80	3.32	0.09		
	5	107.80	150	15.75	0.015	121.80	5.32	0.03		
Early–middle Albian	1	179.33	335	33.59	< 0.001	197.33	1.00	0.34	212.92	343
	2	192.42	340	20.5	< 0.001	200.42	4.09	0.07		
	3	188.93	336	23.99	0.001	204.93	8.60	0.01		
	4	190.73	338	22.19	< 0.001	202.73	6.40	0.02		
	5	182.33	337	30.59	< 0.001	196.33	0	0.56		
Late Albian	1	138.02	199	6.63	0.577	156.02	4.77	0.04	144.65	207
	2	143.25	204	1.4	0.706	151.25	0	0.39		
	3	138.02	200	6.63	0.468	154.02	2.77	0.10		
	4	139.53	202	5.12	0.401	151.53	0.28	0.34		
	5	139.51	201	5.14	0.526	153.51	2.26	0.13		
Cenomanian	1	239.19	299	23.96	0.002	257.19	6.51	0.02	263.15	307
	2	242.68	304	20.47	< 0.001	250.68	0	0.49		
	3	239.37	300	23.78	0.001	255.37	4.69	0.05		
	4	239.58	302	23.57	< 0.001	251.58	0.90	0.31		
	5	239.43	301	23.72	0.001	253.43	2.75	0.12		
Turonian	1	181.10	225	29.76	< 0.001	199.10	3.56	0.08	210.86	233
	2	187.54	230	23.32	< 0.001	195.54	0	0.46		
	3	181.88	226	28.98	< 0.001	197.88	2.34	0.14		
	4	185.08	228	25.78	< 0.001	197.08	1.54	0.21		
	5	184.61	227	26.25	< 0.001	198.61	3.07	0.10		
Coniacian	1	69.45	122	23.777	0.003	87.45	4.73	0.05	93.23	130
	2	77.53	127	15.701	0.001	85.53	2.81	0.12		
	3	69.98	123	23.247	0.002	85.98	3.26	0.10		
	4	70.72	125	22.508	< 0.001	82.72	0	0.51		
	5	70.37	124	22.857	0.001	84.37	1.65	0.22		

TABLE 2. *Continued.*

Time bin	Model	Residual deviance	df	Δ deviance	<i>p</i> -value	AIC	Δ <i>i</i>	<i>w_i</i>	Null deviance	Null df
Santonian	1	118.75	189	10.86	0.210	136.75	8.00	0.01	129.61	197
	2	120.75	194	8.86	0.031	128.75	0	0.74		
	3	119.14	190	10.47	0.163	135.14	6.39	0.03		
	4	119.85	192	9.76	0.082	131.85	3.10	0.16		
	5	119.84	191	9.77	0.135	133.84	5.09	0.06		
Early Campanian	1	81.26	213	28.541	< 0.001	99.26	6.98	0.02	109.80	221
	2	84.29	218	25.517	< 0.001	92.29	0	0.73		
	3	82.38	214	27.418	< 0.001	98.38	6.10	0.03		
	4	83.57	216	26.229	< 0.001	95.57	3.29	0.14		
	5	82.75	215	27.054	< 0.001	96.75	4.46	0.08		
Middle Campanian	1									
	2									
	3									
	4									
	5									
GLM algorithm failed to converge										
Late Campanian	1	73.81	283	13.324	0.101	91.81	4.90	0.04	87.14	291
	2	78.92	288	8.22	0.042	86.92	0	0.50		
	3	76.20	284	10.942	0.141	92.20	5.28	0.04		
	4	76.61	286	10.531	0.062	88.61	1.69	0.22		
	5	74.73	285	12.404	0.054	88.73	1.82	0.20		
Maastrichtian	1	568.20	457	49.64	< 0.001	586.20	1.94	0.23	617.84	465
	2	580.69	462	37.15	< 0.001	588.69	4.43	0.07		
	3	568.26	458	49.58	< 0.001	584.26	0	0.60		
	4	576.23	460	41.61	< 0.001	588.23	3.97	0.08		
	5	576.23	459	41.61	< 0.001	590.23	5.97	0.03		

Turonian and Santonian/early Campanian boundaries, but also shows high extinction in the Early Cretaceous and elevated extinction rates for a protracted period in the middle Cretaceous (Fig. 1B). As noted earlier, we are inclined to trust the generic-level over the species-level extinction rate estimates, given the potential confounding issues of species durations compared with temporal bin sizes (Raup and Sepkoski 1982; Wheeler and Meier 2000).

Influence of OAE2

Our analyses are consistent with previous work that has demonstrated significant extinctions in a broad set of marine macro- and micro-invertebrate taxa across the Cenomanian/Turonian at higher taxonomic levels (Raup and Sepkoski 1984; Leckie et al. 2002; Bambach 2006; Parente et al. 2008). At face value, the significant loss of molluscan diversity across the Cenomanian/Turonian supports the hypothesis that the Bonarelli event (OAE2) had a marked negative impact on mollusk biodiversity and potentially contributed to significant turnover at multiple taxonomic levels. The

apparent diversity decreases after OAE1b provide some further support for this hypothesis. However, the broad temporal resolution of the data available for this study prevents conclusive attribution of these diversity patterns to OAEs. Detailed, temporally constrained studies focused stratigraphically around these events would provide a further test of the hypothesis supported here.

Ecological Selectivity in the Cretaceous

GLM analysis of the entire Cretaceous supports relatively uniform ecological selectivity against taxa with more benthic habitats (Table 2). We hypothesized that OAE2 (and OAEs generally) should more negatively impact the infauna than other ecological lifestyles. However, faunality was shown to be a predictor of extinction risk whether or not a time bin was associated with an OAE, that is, turnover among taxa toward the infaunal end of the depth gradient was uniformly higher than turnover in taxa living in the water column across the entire Cretaceous. These results argue against our initial hypotheses (Table 2) of OAEs as the most dominant factors

controlling diversity change across this interval. However, our results do not rule out the role of OAEs in driving extinctions, particularly given that low-oxygen environments likely dominated the sediment–water interface throughout the Cretaceous, with OAEs potentially intensifying these pressures over shorter intervals. Further, unique environmental circumstances associated with each Cretaceous OAE may have modified selection regimes to produce the results reported here (OAE1a was preceded by a *negative* CIE, OAE1b was associated with three pulses of black shale deposition in addition to positive CIEs, etc.).

Ecological selectivity has been identified at other times in the Phanerozoic when widespread ocean anoxia is the hypothesized kill mechanism (e.g., Kiessling et al. 2007; Clapham and Payne 2011). These investigations also confirm that ecological selectivity can be observed when using ~5 Myr time bins, despite the most severe anoxia spanning a shorter interval (e.g., ~800 kyr in Kiessling et al. [2007]), albeit using different taxa or ecological characteristics. Alternative explanations for the selectivity patterns observed here include: (1) the factors causing OAE-driven extinction are not those that are often hypothesized; (2) the Cenomanian/Turonian diversity decline was not driven by the Bonarelli event; (3) the magnitude of extinctions caused by OAE2 was not severe enough to overwhelm background-extinction selectivity patterns.

Different Ecological/Abiotic Variables.—Traits such as geographic-range size, tropical versus nontropical habitat, dispersal ability, and substrate type have been found to be significant predictors of survivorship at other times of elevated extinction (e.g., Jablonski 1986; Jablonski and Hunt 2006; Kiessling et al. 2007; Clapham and Payne 2011). We note, however that these studies focused on cnidaria, foraminifera, and other marine invertebrate clades, which may respond to anoxia in fundamentally different ways compared with mollusks due to differences in circulatory/respiratory systems and physiology (Baker and Mann 1992; Moodley and Hess 1992; Knoll et al. 1996, 2007; Childress and Seibel 1998; Kiessling et al. 2007; Ekau et al. 2010; Song et al. 2014).

Alternatively, extinction potential across the Cenomanian/Turonian may be more

influenced directly by changing temperatures as opposed to concomitant anoxic conditions (or the interactions between these factors). Atlantic equatorial sea-surface temperature (SST) warmed rapidly during OAE2 and reached up to 36–43°C (Forster et al. 2007; van Bentum et al. 2012). High latitudes also experienced abrupt warming, with SSTs reaching up to 20°C in the Arctic Ocean (Jenkyns et al. 2004). These peaks culminated at the end of a temperature rise of ~3°C in ~50 kyr (Jenkyns et al. 2004; Forster et al. 2007; van Bentum et al. 2012). Song et al. (2014; Fig. 1B) showed that the median maximum thermal limits of cephalopods, bivalves, and gastropods are ~32°C, ~33°C, and ~36°C, respectively (see also Baker and Mann 1992; Moodley and Hess 1992; Ekau et al. 2010). Song et al. (2014) also demonstrated that a combination of anoxia and extremely high temperatures best accounted for ecologically selective extinctions at the Permo-Triassic mass extinction.

Given that the Cenomanian/Turonian has been characterized as the warmest interval of the Cretaceous greenhouse climate (Leckie et al. 2002), it is plausible that high temperatures may have acted in conjunction with anoxia to dramatically reduce biodiversity. A paleoenvironmental test of this hypothesis is challenging given that the geologic and geochemical evidence of higher temperature is tightly associated with that for anoxic conditions (Fig. 1C). However, if temperature had a strong direct effect on molluscan extinction, then selectivity may be better reflected in physiological temperature tolerances, geographic-range size, or abiotic niche breadth variation among clades as opposed to the ecological factors tested here. In qualitative support of this, previous research has identified differences in regional clade-level extinction percentages during the Cenomanian/Turonian within the Mollusca (Elder 1987, 1989; Harries and Little 1999). These may reflect differences in physiological temperature limits, which would result in first cephalopod, then bivalve, then gastropod species experiencing high rates of mortality and extinction as global SSTs exceeded their thermal limits (Song et al. 2014).

Extinction Not a Result of the OAE.—Although we observe significant diversity loss

associated with OAE2, the actual turnover observed may not be directly caused by the anoxic event. Some previous work at regional spatial scales (e.g., Elder 1989; Monnet and Bucher 2007; Parente et al. 2008; Monnet 2009) has suggested that much of the faunal loss from the Cenomanian to the Turonian occurred before the onset of OAE2. These extinctions are attributed to the mid-Cenomanian event (MCE). Elder (1989) found a gradual, stepwise decrease in both ammonites and bivalve diversity throughout the late Cenomanian in the Western Interior Seaway. Monnet and Bucher (2007) and Monnet (2009) found increased ammonite losses only in Europe, where there are pulses of extinction, with the first pulse coeval with a positive CIE in the mid-Cenomanian (Coccioni and Galeotti 2003). The second pulse begins in the late Cenomanian, but predates the expansion of OAE2 anoxia by ~ 0.75 Myr (Monnet and Bucher 2007; Monnet 2009). Parente et al. (2008) also found evidence of stepwise extinctions during the Cenomanian, with OAE2 representing the final decrease. In this view, OAE2 ensued in the wake of multiple extinction events rather than acting as the cause of them.

Notably, Coccioni and Galeotti (2003) previously identified the MCE as a minor OAE associated with the beginning of black shale deposition ~ 2 Myr before OAE2. The MCE is posited to have represented the “point of no return” of increasing CO_2 and ocean temperatures during the Cenomanian (Coccioni and Galeotti 2003). Thus, even if extinctions began in the middle Cretaceous, ocean anoxia is still an important potential mechanism causing diversity declines. However, under this scenario, OAEs create a stepwise extinction beginning in the middle Cenomanian and continuing into OAE2 at the Cenomanian/Turonian boundary. Stepwise extinction could explain the apparent lack of differential ecological selectivity observed here. If ecologically sensitive taxa became extinct during the MCE, with more resistant taxa lost during the most extreme anoxia of OAE2, then the overall time-averaged pattern of diversity change may obscure ecological selectivity unique to each extinction pulse.

As Bambach (2006) noted, extinction occurs over ecological timescales (10^1 to 10^3 years),

and the time averaging of paleontological samples over geologic timescales (10^4 to 10^7 years; our study is $\sim 3\text{--}6$ Myr) can obscure ecological signals. However, although the temporal resolution of this study prevented an explicit test of stepwise extinction timing, other research has identified ecological selectivity associated with OAEs with similar resolution (e.g., Kiesling et al. 2007). Further systematic analyses at a finer temporal scale than what is commonly reported in the PBDB would better illuminate the explicit timing of extinctions, and whether they predated OAE2.

Bad, but Not Bad Enough.—A third explanation for the lack of observed differential ecological selectivity is that OAE2 did not modify background selectivity patterns. For example, mass extinctions often demonstrate different ecological selectivity patterns relative to background extinction (Droser et al. 2000; McGhee et al. 2004, 2012a,b; Krug and Patzkowsky 2015). Whereas background processes impart a selectivity against taxa deeper in the water column and sediment, it is possible that OAE-driven processes either positively reinforced or were not sufficiently severe to overwhelm this signal at the Cenomanian/Turonian boundary. The lack of unique OAE selectivity lends some additional support that diversity declines at this time were lower magnitude than those during mass extinctions. Thus, it seems prudent to explore alternative ecological variables (geographic range, mineralogy, tropicality, etc.) before concluding that OAE2 was too mild to overwhelm background ecological selectivity patterns.

It is worth noting that explanations surrounding the “different variables” and “not the OAE” hypotheses above operate on different spatio-temporal scales. Many of the alternative factors associated with selectivity at other times operate at large spatiotemporal (and even taxonomic) scales. For example, geographic range has been associated with increased survivorship across major extinction events on a regional to global spatial scale and on the order of millions of years, but only at the clade level (e.g., Jablonski 1986, 1987). In contrast, the “not the OAE” hypothesis is based on evidence at the local to regional scale at temporal resolutions associated with ecological communities (years to thousands of years). As a consequence,

these explanations are not necessarily mutually exclusive, and a better understanding the ecological change associated with molluscan decline across the Cenomanian/Turonian requires additional data at both resolutions.

This research ultimately establishes that the OAE associated with the Cenomanian/Turonian is correlated with higher extinction rates and a significant global decline in molluscan diversity. The observed lack of OAE-related ecological selectivity demonstrates that further inquiry into both global- and community-level ecology at this time would be fruitful.

Conclusions

We observe a marked decrease in molluscan generic diversity and increase in extinction rates concurrent with OAE2 at the resolution of the geologic stage. When interpreted within the broader context of diversity change across the entire Cretaceous, including multiple global OAEs, generic diversity is also observed to markedly decrease during the other more severe Cretaceous OAE (OAE1b). Therefore, these results also support the potential for OAEs in general to significantly impact molluscan diversity.

Multiple logistic regression analysis identifies faunality as a strong predictor of survivorship patterns in the Cretaceous. However, no differential influence of ecology was observed affecting likelihood of survivorship across OAE intervals relative to this background. It is plausible that ecological/abiotic selectivity exists in traits not tested here, the observed declines in diversity are not OAE derived, or OAEs only enhance extinction pressure on taxa without imparting a unique ecological signal. Further analysis at higher temporal resolution (e.g., the outcrop and/or biozone scale) would likely improve the discrimination ability between ecological traits and extinction selectivity throughout this interval.

Although not a direct analogue, as a greenhouse climate, the Late Cretaceous provides a comparison of how oceanic environments may respond to globally warmer conditions over long timescales (Spicer and Corfield 1992; Hayward et al. 2011; Myers et al. 2013). In support of this, deoxygenation rates are remarkably similar between those of OAE2 and recent

observations in modern oceans (Owens et al. 2013; Ostrander et al. 2017). Ocean systems are already feeling effects of modern climate change, including mass coral bleaching (Ainsworth et al. 2016), acidification (Hoegh-Guldberg et al. 2007), and deoxygenation (Stramma et al. 2010; Keeling et al. 2010; Falkowski et al. 2011; Ito et al. 2017; Breitburg et al. 2018). These circumstances may be facilitating an emerging modern mass extinction (Barnosky et al. 2011; Ceballos et al. 2015; Payne et al. 2016b; Rothman 2017). Thus, research that attempts to disentangle the relationship between biodiversity and the geologic record of OAEs provides important insight and boundary conditions for predicting how modern species may respond to current and future environmental changes. Investigations into the long-term response of molluscan species to environmental perturbations are warranted to ensure that the diversity declines observed in the Cretaceous, particularly across the Cenomanian/Turonian boundary, are not replicated in the Anthropocene.

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