RESPONSE OF CRETACEOUS MARINE REPTILES TO PALEOCEANOGRAPHIC CHANGES: SEA LEVEL AND CLIMATE CHANGES AS DRIVERS OF ORIGINATION AND EXTINCTION

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ABSTRACT

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The Cretaceous Period was a time of great environmental volatility and most notably known for being one of the periods when dinosaurs existed. However, during this time the apex predators of the oceans were marine reptiles. These marine reptile groups included ichthyosaurs, plesiosaurs and mosasaurs. How these three marine reptile groups reacted to environmental volatility of the time during the Cretaceous was assessed in this study. Marine reptile occurrence data was compiled and used to calculate origination and extinction along with correlated with ocean temperature, ocean anoxia and sea level, proxies were used for both ocean temperature and ocean anoxia. Analyses included cross correlation along with multiple regression and random forest analysis. The results of these analyses showed that each marine reptile group were affected by the changing environment during the Cretaceous. Each marine reptile group were specifically affected the most by ocean anoxia with both ichthyosaur and plesiosaur diversity dropping due to anoxia but mosasaur diversity actually increased during times of anoxia. What was also interesting is that how volatile the environment was did not affect each marine reptile group strongly either positively or negatively. Overall each marine reptile group was affected by the changing environment of the Cretaceous but how volatile that environment was did not play any significance.

I would like to dedicate this to all of my friends and family who have supported me through this process, specifically my parents, Bill and Michele Vanderslice, and brother, Mark Vanderslice. I would also like to dedicate this to my late grandfather, Ronald Paradise, who loved all things science related and would have enjoyed this thesis immensely.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The Mesozoic Era includes the Triassic, Jurassic and Cretaceous Periods (Fig. 1). These three time periods are well known to the public because they were the time of the dinosaurs. However, during the same time the apex predators of the ocean were marine reptiles, including the ichthyosaurs, plesiosaurs and mosasaurs (Figs. 2, 3). Ichthyosaurs belong to the order Ichthyosauria and thrived during the Late Triassic and Early Jurassic, after which they eventually dwindled and became extinct in the Late Cretaceous, specifically around 95 Ma during the Cenomanian Age (Motani 2005). Plesiosaurs belong to the order Sauropterygia and arose in the Middle to Late Triassic. Plesiosaurs became the dominant marine predator in the Late Triassic, surpassing the ichthyosaurs during this time. Plesiosaurs eventually became extinct at the end of the Cretaceous (Motani 2009). Mosasaurs belong to the order Squamata, which also includes lizards and snakes, and first appeared in the Cretaceous. Mosasaurs eventually became the dominant marine predator group for most of the Late Cretaceous and were very successful until their extinction at the Cretaceous-Paleogene boundary (Polcyn et al. 2014). These three marine reptile groups varied quite a bit in terms of body plan and form; Figure 3 gives a generalized body plan that can be attributed to most members of each group. The three marine reptile groups fall generally into the class Reptilia but each group independently evolved aquatic locomotion and lifestyles (Fig. 4). Both ichthyosaur and plesiosaur clades died out entirely within or at the end of the Cretaceous, while mosasaurs were close relatives of modern lizards and snakes (Gauthier et al. 2012; Longrich et al. 2012).

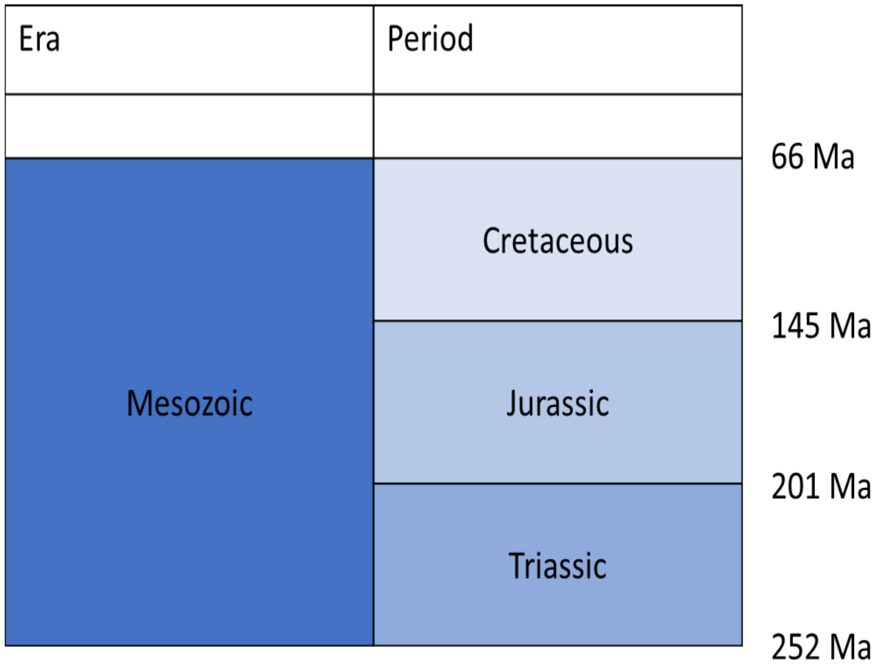

Fig. 1. Mesozoic Time Scale. Ichthyosaurs, mosasaurs and plesiosaurs lived during the Triassic, Jurassic and Cretaceous Periods. This study focuses on marine reptiles during the Cretaceous.

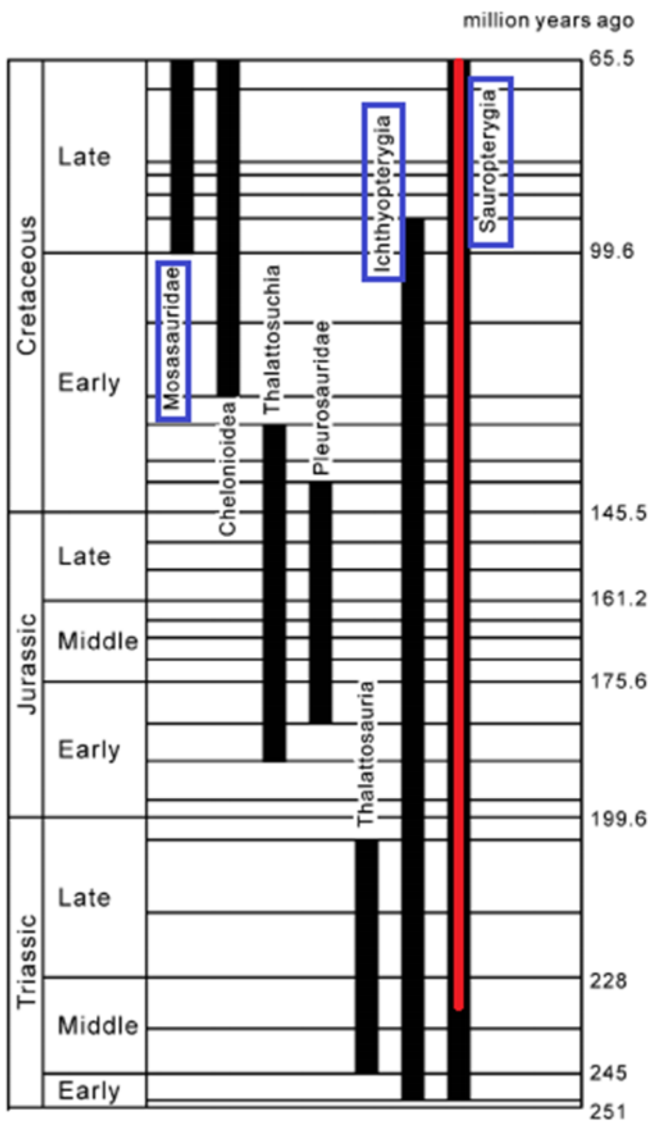

Fig. 2. Stratigraphic Ranges of Marine Reptile Groups. Timing of appearance and extinction of major marine reptile groups in the Mesozoic. The three groups that are the focus of this project are within the blue boxes, from left to right, Mosasauridae (mosasaurs), Ichthyopterygia (ichthyosaurs) and Sauropterygia (plesiosaurs). Since other groups fall within the order Sauropterygia the range shown is longer than for just plesiosaurs. The range of plesiosaurs is indicated by the red line overlying the line for Sauropterygia. (Modified from Motani 2009)

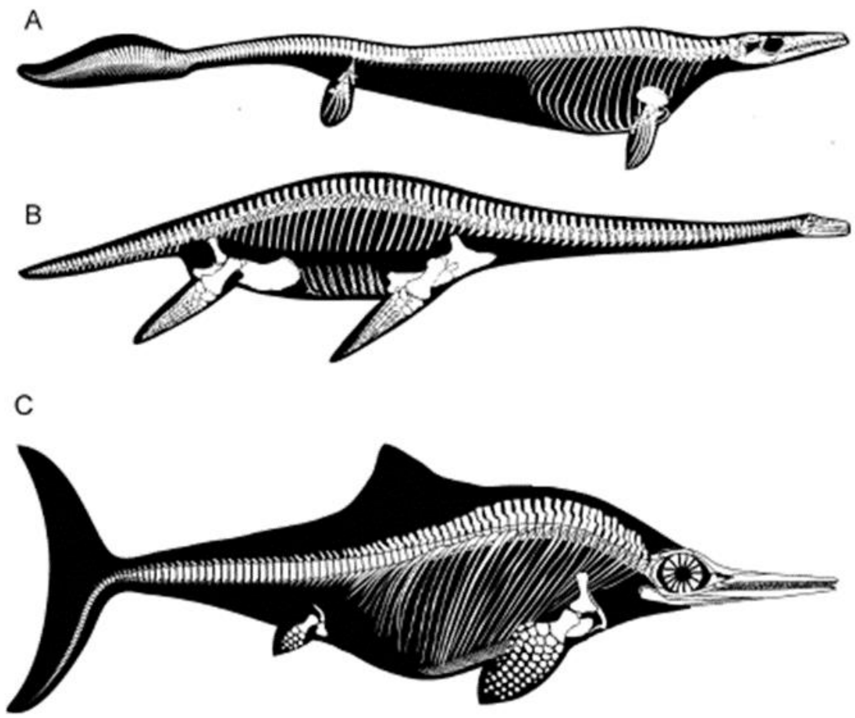

Fig. 3. Generalized Marine Reptile Body Plans. Body plans of the three Mesozoic marine reptile groups included in this study. (A) mosasaur, (B) plesiosaur and (C) ichthyosaur. Each group had a different body plans, which shows the independent evolution of bodies better suited for an aquatic lifestyle during the transition from a terrestrial to marine environment (Motani 2009).

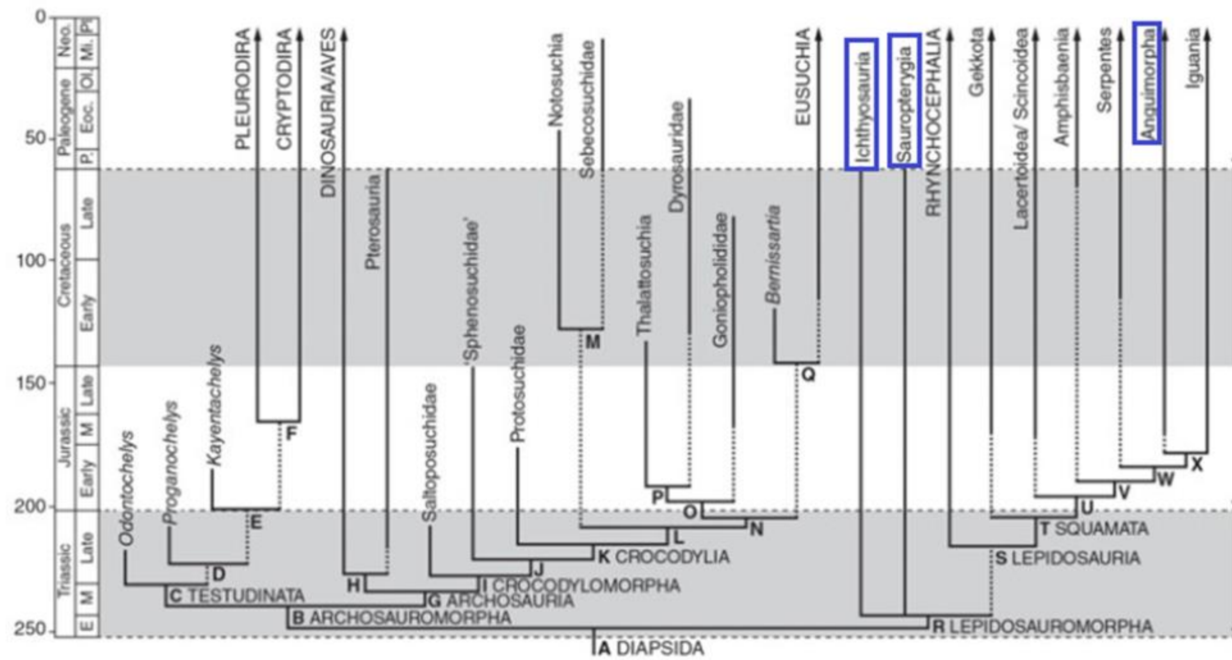

Fig. 4. Phylogenetic Tree of Diapsid Reptiles. Phylogenetic tree showing the relationships of ichthyosaurs, plesiosaurs and mosasaurs to each other along with other major diapsid groups. The three marine reptile groups, outlined in blue, are Ichthyosauria (ichthyosaurs), Sauropterygia (includes plesiosaurs) and Anguimorpha (includes mosasaurs). Mosasaurs belong to Squamata, which includes modern lizards and snakes, while ichthyosaurs and plesiosaurs were earlier off-shoots within Lepidosauromorpha. (Modified from Benton 2015).

The extinction of ichthyosaurs in the Cretaceous has been attributed to environmental factors. Fischer et al. (2016) investigated the possible drivers of ichthyosaur extinction. As mentioned previously, ichthyosaurs are different than the other two marine reptile groups in that they became extinct during the beginning of the Late Cretaceous, around the end of the Cenomanian stage. Fischer et al. (2016) proposed that by determining the mode of ichthyosaurs' extinction, new insights could be provided into the factors that would affect not only extinction but also diversity and evolution of marine reptiles during the Cretaceous. It is considered strange that ichthyosaurs died out so early in the Late Cretaceous as compared to their counterparts, the plesiosaurs and mosasaurs. The two main hypotheses that have previously been proposed have involved competition and resource limitation. The competition hypothesis asserts that ichthyosaurs were driven to extinction due to other marine reptiles out-competing them. However, Fischer et al. (2016) argued against the competition hypothesis by observing that other marine reptiles of a size that would compete with ichthyosaurs, in this case mosasaurs, did not start to appear until around 3 million years after the last appearance of ichthyosaurs. The other hypothesis is that resource limitations, specifically a mid-Cretaceous extinction event that killed off many cephalopods, which were their main diet, caused the extinction of ichthyosaurs. While this loss of prey may have caused a drop in ichthyosaur numbers, Fischer et al., (2016) argue that it did not constitute an event that would be great enough to cause the extinction of the entire clade. This is in part due to the fact that the last ichthyosaurs had morphologies suggesting they were generalist predators that could feed on multiple food sources and therefore would not be hugely impacted by one single food source dwindling. Fischer et al. (2016) concluded that ichthyosaurs, while highly diverse for much of the Mesozoic, were quite slow at evolving. This slow origination rate was coupled with the fact that the climate of this time was highly volatile, meaning that there were multiple ocean anoxic events along with multiple transgressive and regressive cycles; hence, Fischer et al. (2016) claimed that ichthyosaur extinction was driven by these fluctuating climate changes.

Sea level is often attributed as one of the driving factors that may have controlled marine reptile diversity and extinction. A recent study by Kelley et al. (2014) investigated this question by examining marine reptiles in the Triassic. They used strontium isotopes as a proxy for sea level change and defined two distinct ecomorphological groups of marine reptiles, “durophages”, taxa that exhibited specialized crushing tooth morphology indicating trophic links to the benthos, and “pelagic” taxa exhibiting specialized locomotory adaptations associated with open-water cruising. Occurrence data for the Triassic marine reptiles from all around the world were collected and divided into these two ecomorphological groups. Those data were used to calculate marine reptile diversity through time, which was correlated with sea level rises and falls as calculated from strontium isotopes. Kelley et al. (2014) found that while the different defined groups adapted in specific ways to the sea level change, there was an overarching decline in marine reptile diversity in the Late Triassic that can be attributed to sea level fall (Kelley et al. 2014).

Other work has shown that the times of greatest marine reptile diversity were during their initial movement back into the oceans during the Middle to Late Triassic (Stubbs and Benton 2016). Numerous locations for living and feeding were empty and available, allowing for a great increase in diversity and evolutionary innovation within the marine reptiles. However, Stubbs and Benton (2016) found that simply colonizing a new environment by itself does not necessarily serve as the starter for adaptive radiation and speciation. Rather, marine reptile diversity trends were driven very much by marine regression and transgression and the authors identified sea level highstands as times of elevated diversity. Left unexplained, however, is what other environmental changes related to sea level may have driven these diversity changes and by what mechanisms sea level related factors actually caused diversification or extinction (Stubbs and Benton 2016).

Much prior work has focused on the initial radiation of marine reptiles in the Triassic and/or has focused on a single marine reptile group. The Cretaceous was the period when mosasaurs first evolved and when all the different top marine reptile groups became extinct. It is also a time of significant global climate and oceanographic change, including major sea level rises and falls, pulses of global warming and cooling, several ocean anoxic events, and mass extinction events at the Cenomanian/Turonian and Cretaceous/Paleogene boundaries. The break-up of Pangea was a major driver for sea level rise along with changes in ocean circulation that allowed for different climatic shifts, all of which contributed to the overall environmental volatility of the Cretaceous (Skelton et al. 2003). The volatility of the Cretaceous can be seen in the multiple ocean anoxic events that occurred along with the changes in sea level (Fig. 5). There were two major ocean anoxic events (OAE) during the Cretaceous along with multiple smaller OAEs. The two major OAEs are OAE 1a, which occurred during the Aptian (120.5 Ma), and OAE 2, which occurred near the Cenomanian/Turonian boundary (93.5 Ma). Three smaller OAE events include OAE 1b (Aptian-Albian, 113-109 Ma), OAE 1c (Albian, 102 Ma) and OAE 1d (Cenomanian, 99.5 Ma) (Fig. 5, Table 1)

Sea level during this time was also shifting greatly as indicated by multiple transgressive and regressive cycles (Fig. 5). There was a major regressive cycle during the Valanginian, after which the general trend of sea level was rising with smaller transgressions and regressions within the larger trend. Another large regression occurred at the Turonian-Coniacian boundary and then sea level starts to generally trend towards falling until the end of the Cretaceous.

Climate varied through the Cretaceous. During the early Cretaceous the climate was generally cool with a warming trend occurring in the Aptian with some cool and wet phases occurring within that trend. The Cretaceous hit a temperature maximum around the Cenomanian-Turonian boundary with fluctuations occurring until the end of the Cretaceous (Skelton et al. 2003).

Global environmental variability during the Cretaceous makes this time interval an excellent target for rigorous investigation of the relationship between marine reptile diversity and several environmental parameters. Specifically, I addressed in this study the question of how changing environmental conditions, including sea level, oxygenation, and temperature, affected marine reptile diversity in the Cretaceous. I tested two hypotheses linking environmental changes and diversity: 1) that during times of lower sea level, ocean anoxia, and/or lower temperatures, marine reptile diversity decreased and 2) that times with faster rates of environmental change were associated with reductions in marine reptile diversity. I also tested the hypothesis 3) that these diversity decreases were associated with elevated extinction and/or decreased origination rates.

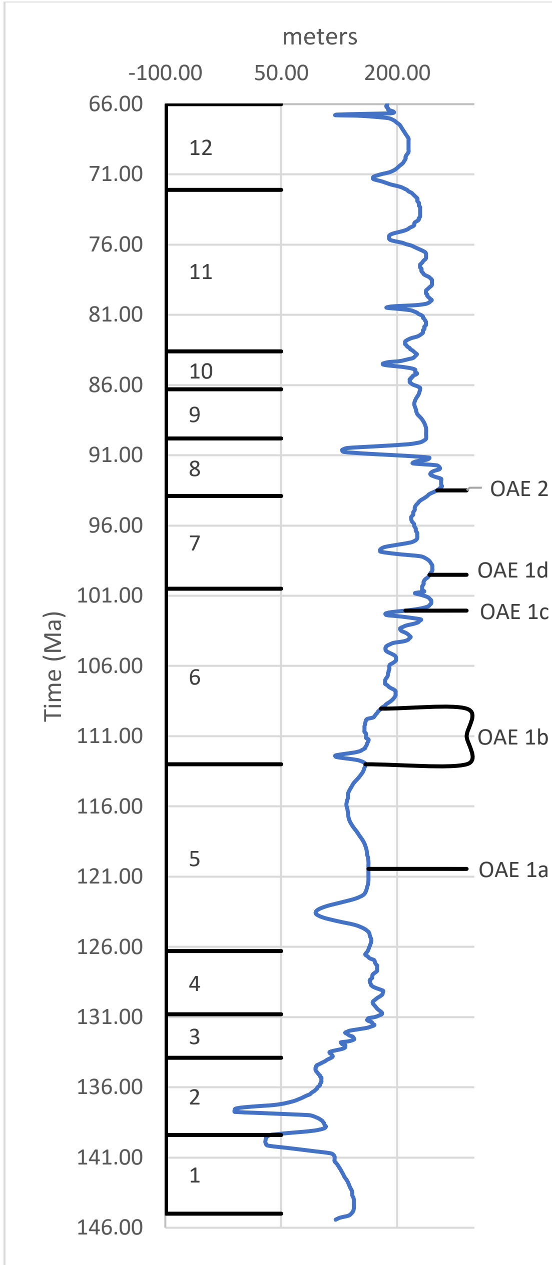

Fig. 5. Cretaceous Sea Level and Major OAEs. Eustatic sea level curve of Haq et al. (1987) marked with stage numbers for each stage in Cretaceous (Table 1 lists stages with corresponding numbers). Major and significant minor ocean anoxic events (OAEs) are marked.

Table 1. Cretaceous Time Scale with OAEs.

Epoch	**Age (Ma)**	**Stage No.**	**Stage**	**Ocean Anoxic Events (OAE)**
Late	72.1-66	12	Maastrichtian	
	83.6-72.1	11	Campanian	
	86.3-83.6	10	Santonian	
	89.8-86.3	9	Coniacian	
	93.9-89.8	8	Turonian	**OAE 2 (93.5 Ma)**
	100.5-93.9	7	Cenomanian	OAE 1d (99.5 Ma) OAE 1c (102 Ma)
Early	113-100.5	6	Albian	OAE 1b (113-109 Ma)
	126.3-113	5	Aptian	**OAE 1a (120.5)**
	130.8-126.3	4	Barremian	
	133.9-130.8	3	Hauterivian	
	139.4-133.9	2	Valanginian	
	145-139.4	1	Berriasian	

Exact dates of stages within the Cretaceous are shown along with their corresponding numbers. Major (in bold type) and significant minor ocean anoxic events are shown within each stage with the time at which they occurred.

METHODS

To test these three hypotheses, multiple data sets were compiled, including fossil occurrence data for Cretaceous marine reptiles and strontium, oxygen and carbon isotope data used as proxies for sea level, temperature and ocean oxygenation, respectively. Marine reptile species diversity, origination and extinction time series were generated and compared to isotopic proxy time series to assess the relationships between diversity dynamics and environmental changes.

Marine Reptile Occurrences

Occurrence data for marine reptiles were acquired from the Paleobiology Database (PBDB) (https://paleobiodb.org/). Three separate data sets were downloaded using the PBDB web interface, one for each marine reptile group, ichthyosaurs, mosasaurs and plesiosaurs, for occurrences from the Cretaceous. These were downloaded from the Paleobiology Database on 30 January, 2017, using the following parameters: time interval = Cretaceous, paleoenvironment = marine, Order = Ichthyosauria, Sauropterygia or Mosasauridae. Taxon and time period are required for PBDB searches, but other parameters can also be specified for inclusion in the downloaded data. For this study, the other parameters downloaded with the abundances were: the name of the species, the taxonomic rank (in this case species level), and the first and last interval of time from which fossils of the species were recovered, expressed both as named time intervals and as ages in millions of years ago (Ma). In many cases, the species had a duration of more than one stage during the Cretaceous. The references for each specimen were also downloaded, including the original paper reporting that specimen with the authors and year of publication. The family and genus of each specimen were included along with the abundance value (count) and abundance unit (specimen vs. individual vs. skeletal elements). Finally, the latitude and longitude of each fossil site, the paleolatitude and paleolongitude of the site, the lithologic description of the site, and the paleoenvironment of the site were included.

The fossil occurrence data from the PBDB were then cleaned to remove errors and unusable entries. This data set review included verifying that each fossil occurrence had a valid genus and species name and that these names were not misspelled or missing. In some cases, the genus name was present and valid, but stand in modifiers (sp., cf., aff.) were used for the species; these specimens were removed from the data set.

Once this cleaning up was performed, the total abundances (that is, number of occurrences) for each species and total abundances for each time interval for each marine reptile group were calculated (Table 2). Abundance data were binned by stratigraphic stage. To account for gaps in stratigraphic ranges, an abundance value of 1 was assigned for each stage in which a species was not recovered but during which it must have been extant (i.e., the range-through method). For example, if a particular species was found in the Santonian (10) and in the Maastrichtian (12), then that species must have also existed in the Campanian (11) even though there is no fossil occurrence for it in the data set. That species would therefore be marked conservatively as having an abundance of 1 in the Campanian.

Not every time interval contained at least 10 occurrences from the PBDB. To improve sample sizes, further literature review was performed to identify and add additional taxa to the data sets. Further occurrence data for ichthyosaur species were taken from Zammit (2012), including the species *Athabascasaurus bituminous*, *Maiaspondylus lindoei*, *Platypterygius americanus*, *Aegirosaurus leptospondylus*, *Platypterygius ochevi*, *Platypterygius hercynicus* and *Platypterygius sachicarum*. Once all the data were compiled and cleaned, the total number of occurrences (Table 2), species (Table 3) and genera (Table 4) were tallied for each group in each time interval. The complete set of Cretaceous marine reptile occurrences is available in supplementary Excel file 1; species and genus lists with stratigraphic ranges are in supplementary Excel file 2.

Table 2. Marine Reptile Occurrences.

Stage No.	Stage Name	Total Occurrences	Ichthyosaurs	Mosasaurs	Plesiosaurs
12	Maastrichtian	176		146	30
11	Campanian	254		168	86
10	Santonian	50		36	14
9	Coniacian	40		30	10
8	Turonian	44		14	30
7	Cenomanian	67	14	25	28
6	Albian	178	152		26
5	Aptian	54	17		37
4	Barremian	31	11		20
3	Hauterivian	26	15		11
2	Valanginian	20	10		10
1	Berriasian	22	12		10
Total Abundances		962	231	419	312

Total raw numbers of occurrences and ichthyosaur, mosasaur and plesiosaur occurrences for each stage of the Cretaceous. Note large values for ichthyosaurs during the Albian, large values for mosasaurs in the Maastrichtian and Campanian and large values for plesiosaurs during the Campanian.

Table 3. Marine Reptile Species Diversity.

Stage No.	**Stage Name**	**Ichthyosaurs**	**Mosasaurs**	**Plesiosaurs**
12	Maastrichtian		38	12
11	Campanian		37	25
10	Santonian		16	8
9	Coniacian		11	6
8	Turonian		10	14
7	Cenomanian	8	7	15
6	Albian	13		13
5	Aptian	11		13
4	Barremian	11		6
3	Hauterivian	13		6
2	Valanginian	6		3
1	Berriasian	7		7
Total Species		29	93	103

Number of ichthyosaur, mosasaur and plesiosaur species for each stage in the Cretaceous. Note high species diversity for mosasaurs in the Maastrichtian and Campanian and for plesiosaurs in the Campanian, which mirror high abundance values seen in Table 2.

Table 4. Marine Reptile Genus Diversity.

Stage No.	Stage Name	Ichthyosaurs	Mosasaurs	Plesiosaurs
12	Maastrichtian		16	10
11	Campanian		16	15
10	Santonian		12	11
9	Coniacian		9	10
8	Turonian		9	15
7	Cenomanian	2	5	13
6	Albian	6		10
5	Aptian	5		9
4	Barremian	8		6
3	Hauterivian	8		6
2	Valanginian	6		2
1	Berriasian	6		3
Total Genera		14	36	53

Number of ichthyosaur, mosasaur and plesiosaur genera for each stage in the Cretaceous. Genus-level diversity is similar for ichthyosaurs and Early Cretaceous plesiosaurs, with increasing diversity for mosasaurs and plesiosaurs later in the Cretaceous.

Marine Reptile Diversity, Origination and Extinction

Before biodiversity analyses could be performed, the raw diversity counts (Table 3) first needed to be rarefied to control for variations in sampling intensity in different time intervals. Rarefaction, which was done in the software package PAST 3.15 (Hammer et al. 2001), estimates how many taxa one would expect to find in a sample with a smaller number of individuals, allowing the comparison of diversity in samples of different size. Rarefaction was done for each individual marine reptile group. For ichthyosaurs and plesiosaurs, the Valanginian stage (2) was the time interval with the lowest number of occurrences (that is, the least sampled), while for mosasaurs, the Turonian stage (8) had the lowest number of occurrences. The rarefied diversity values for other time intervals were compiled (Table 5).

Table 5. Marine Reptile Rarefied Species Diversity.

		Rarefied			
Stage No.	**Stage Name**	**Diversity**	**Ichthyosaurs**	**Mosasaurs**	**Plesiosaurs**
12	Maastrichtian	10.36		8.66	5.36
11	Campanian	10.52		7.24	7.49
10	Santonian	11.32		9.07	6.27
9	Coniacian	9.57		7.18	6.00
8	Turonian	11.79		10.00	6.89
7	Cenomanian	10.82	4.25	5.39	6.87
6	Albian	6.15	3.07		7.93
5	Aptian	10.53	4.51		6.23
4	Barremian	9.77	6.00		4.03
3	Hauterivian	12.95	5.62		5.73
2	Valanginian	9.00	6.00		3.00
1	Berriasian	11.13	4.27		7.00

Rarefied species diversity values for all marine reptiles pooled and separately for ichthyosaurs, mosasaurs and plesiosaurs.

Rates of species-level origination and extinction were calculated following the method of Foote (2000). First, species were classified into four categories for each time interval based upon when their first and last appearances fall relative to that time bin. Taxa may be confined to the interval (FL), only cross the bottom boundary (bL), only cross the top boundary (Ft) or cross both the top and bottom boundaries (bt). Total raw diversity (N_{tot}) in a time interval is found by adding up the number (N) of taxa in each category:

$$N_{tot} = N_{FL} + N_{bL} + N_{Ft} + N_{bt}. \qquad (1)$$

Simple values for number of originations and extinctions were calculated with the equations:

$$\text{origination} = N_{FL} + N_{Ft} \qquad (2)$$

$$\text{extinction} = N_{FL} + N_{bL} \qquad (3)$$

The percentage of origination and extinction (Table 7) was calculated by dividing the number of originations or extinctions by the total number of species in each time interval (N_{tot}) and multiplying by 100.

Per-taxon rates for origination and extinction (Table 8) are calculated from the following equations:

$$\text{Origination} = (N_{FL} + N_{Ft}) / (N_{tot}) / \Delta t \qquad (4)$$

$$\text{Extinction} = (N_{FL} + N_{bL}) / (N_{tot}) / \Delta t. \qquad (5)$$

where Δt is the duration of that time interval. As seen above, per-taxon rates are calculated using the values of all taxa found within a specific time interval.

Estimated per-capita rates of origination (p) and extinction (q) (Table 9) were also calculated:

$$p = -\ln(N_{bt}/N_t) / \Delta t \qquad (6)$$

$$q = -\ln(N_{bt}/N_b) / \Delta t \qquad (7)$$

where $N_t = N_{Ft} + N_{bt}$, and $N_b = N_{Ft} + N_{bt}$. Estimated per-capita rates are different from per-taxon rates because rather than using all taxa found in a time interval, the singletons, taxon found only in a specific time interval, are excluded. Per-capita rates are used when the time interval is very long and any values calculated will be influenced heavily by the singletons. Therefore, for this study the percentages of originations and extinctions along with the per-capita rates of origination and extinction were used since the time intervals were not uniform and, in some instances, very long. (Foote 2000).

Table 6. Marine Reptile Species Originations and Extinctions.

		Ichthyosaurs		Mosasaurs		Plesiosaurs	
Stage No.	**Stage Name**	**Originations**	**Extinctions**	**Originations**	**Extinctions**	**Originations**	**Extinctions**
12	Maastrichtian			25	38	10	12
11	Campanian			30	24	22	23
10	Santonian			15	10	6	5
9	Coniacian			8	8	6	4
8	Turonian			10	6	11	14
7	Cenomanian	3	8	7	6	12	12
6	Albian	5	8			8	10
5	Aptian	4	3			10	8
4	Barremian	10	4			4	3
3	Hauterivian	7	5			6	4
2	Valanginian	0	0			2	3
1	Berriasian	7	1			7	6

Ichthyosaurs show large numbers of species originating during the Barremian and no origination or extinction during the Valanginian. Mosasaurs show large numbers of origination and extinction during the Campanian and Maastrichtian while plesiosaurs show large values for origination and extinction during the Campanian.

Table 7. Marine Reptile Species Origination and Extinction Percentages.

		Ichthyosaurs		Mosasaurs		Plesiosaurs	
Stage No.	**Stage Name**	**% originate**	**% extinct**	**% originate**	**% extinct**	**% originate**	**% extinct**
12	Maastrichtian			65.79	100.00	83.33	100.00
11	Campanian			81.08	64.86	88.00	92.00
10	Santonian			83.33	55.56	75.00	62.50
9	Coniacian			66.67	66.67	100.00	66.67
8	Turonian			90.91	54.55	78.57	100.00
7	Cenomanian	37.50	100.00	100.00	85.71	80.00	80.00
6	Albian	38.46	61.54			61.54	76.92
5	Aptian	36.36	27.27			76.92	61.54
4	Barremian	90.91	36.36			66.67	50.00
3	Hauterivian	53.85	38.46			100.00	66.67
2	Valanginian	0.00	0.00			66.67	100.00
1	Berriasian	100.00	14.29			100.00	85.71

Initial values of 100% origination reflect the start of the data sets and should not be treated as meaningful. Peak origination percentage for ichthyosaurs in the Barremian is not matched by a large extinction percentage. Mosasaurs have high origination percentages in the Turonian, Santonian and Campanian while the extinction percentages are lower and less variable. Plesiosaur values include apparent complete turnovers across the Valanginian/Hauterivian and Turonian/Coniacian boundaries.

Table 8. Marine Reptile Per-Taxon Rates of Species Origination and Extinction.

		Ichthyosaurs		**Mosasaurs**		**Plesiosaurs**	
Stage No.	**Stage Name**	**Origination**	**Extinction**	**Origination**	**Extinction**	**Origination**	**Extinction**
12	Maastrichtian			0.108	0.164	0.137	0.164
11	Campanian			0.097	0.077	0.077	0.080
10	Santonian			0.309	0.206	0.278	0.231
9	Coniacian			0.190	0.190	0.286	0.190
8	Turonian			0.222	0.133	0.192	0.244
7	Cenomanian	0.057	0.152	0.152	0.130	0.121	0.121
6	Albian	0.031	0.049			0.049	0.062
5	Aptian	0.027	0.021			0.058	0.046
4	Barremian	0.202	0.081			0.148	0.111
3	Hauterivian	0.174	0.124			0.323	0.215
2	Valanginian	0.000	0.000			0.121	0.182
1	Berriasian	0.179	0.026			0.179	0.153

Note large values for origination in ichthyosaurs in the Barremian, Hauterivian and Berriasian along with larger values for extinction in Cenomanian and Hauterivian. Mosasaurs show larger origination rates for the Santonian and Turonian while also showing larger extinction rates for Santonian and Coniacian. Plesiosaurs origination per-taxon rates are higher in the Santonian, Coniacian and Turonian while extinction per-taxon rates are higher in Santonian, Turonian and Hauterivian.

Table 9. Marine Reptile Per-Capita Rates of Species Origination and Extinction.

		Ichthyosaurs		**Mosasaurs**		**Plesiosaurs**	
Stage No.	**Stage Name**	**p**	**q**	**P**	**q**	**p**	**q**
12	Maastrichtian			no data	no data	no data	no data
11	Campanian			0.163	0.109	no data	no data
10	Santonian			0.513	0.150	0.150	0.000
9	Coniacian			0.396	0.396	no data	no data
8	Turonian			0.393	0.000	no data	no data
7	Cenomanian	no data	no data	no data	no data	0.166	0.166
6	Albian	0.041	0.078			0.032	0.073
5	Aptian	0.022	0.012			0.038	0.000
4	Barremian	no data	no data			0.244	0.154
3	Hauterivian	0.093	0.000			no data	no data
2	Valanginian	0.000	0.000			no data	no data
1	Berriasian	no data	no data			no data	no data

No data indicates a situation where the rate could not be calculated, e.g., when values for N_b or N_t are 0. Ichthyosaurs show highest per-capita rates for origination (p) during the Hauterivian and for extinction (q) during the Albian. Mosasaurs have higher per-capita rates for p during the Santonian and for q during the Coniacian. Plesiosaurs have larger per-capita rates for p during the Barremian and Cenomanian while the q rates are high during Cenomanian and Barremian as well.

Environmental Proxies

Stable isotope values and sea level data were used as proxies to assess environmental change over time. Temperature is reflected in $\delta^{18}O$ values of carbonates and biominerals, with higher values indicating cooler temperatures. Enhanced burial of organic carbon, associated with ocean anoxia, is indicated by positive excursions in $\delta^{13}C$ in marine carbonates and organic-rich mudstones. The ratio of $^{87}Sr/^{86}Sr$ in carbonates can be used as a proxy for sea level. This relationship reflects the input of strontium to the ocean from continental weathering (^{87}Sr) versus from mantle input via submarine volcanism (^{86}Sr). The change in strontium from the mantle through time is due to increases and decreases in the production of oceanic crust. Hence, the changing levels of strontium isotopes can be used as a proxy for production of oceanic lithosphere, and then taking that relationship further, sea level change, since high seafloor spreading rates lead to higher sea levels, and higher sea levels reduce the flux of continental weathering products into the ocean. Hence, high $^{87}Sr/^{86}Sr$ indicates times of sea level fall while low $^{87}Sr/^{86}Sr$ indicates times of sea level rise.

Prokoph et al. (2008) compiled comprehensive, high resolution isotope data for oxygen, carbon and strontium from marine low-Mg calcite shells spanning much of the Phanerozoic. The compilation of data is free to access, and spans through the time period of interest, the Cretaceous. Prokoph and colleagues transformed their data into continuous time series using a Gaussian filter that takes into account the estimated stratigraphic uncertainty of each sample. For the Cretaceous, Prokoph et al.'s (2008) isotope time series generally have a temporal resolution of 1 million years or better.

While the Prokoph et al. (2008) isotope data are relatively high-resolution, this is not the case for the marine reptile occurrences. The PBDB data have a temporal resolution of a few million years, that is, the individual stages of the Cretaceous. To correlate the isotope time series with the diversity time series derived from the PBDB, the isotope values were rebinned by averaging all of the isotope values that fell into the time range of each stage (Tables 10-12). In some cases, there were no isotope values for a specific stage. The resolution for this problem was to interpolate a value for that missing stage based on the stages bracketing it.

As an independent metric of global sea level change, the Haq et al. (1987) eustatic sea level curve, derived from sequence stratigraphic analyses, was included in the analyses. The Haq et al. (1987) sea level data had fine temporal resolution similar to the Prokoph et al. (2008) isotope data, so once again, values were averaged for each Cretaceous stage (Table 12).

Prokoph et al. (2008) split the oxygen and carbon isotope values into those derived from tropical, temperate, arctic and deep sea samples (Tables 10, 11). In order to better constrain the $\delta^{18}O$ and $\delta^{13}C$ values for the purposes of this study, the fossil occurrences for each marine reptile group were similarly grouped based upon the paleolatitude of the site in which the fossil was found to create a percentage of fossil specimens located in tropical, temperate and arctic settings (Table 13). Tropical was defined as within 30° of the equator while temperate was defined as between 30°-60° from the equator and arctic was 60° or higher.

Table 10. Cretaceous $\delta^{18}O$ Values.

Stage No.	Stage Name	Tropical δ18O (‰)	Temperate δ18O (‰)	Arctic δ18O (‰)	Deep Sea δ18O (‰)
12	Maastrichtian	-1.27	-0.76	0.05	0.509
11	Campanian	-1.52	-1.52	-0.42	-0.3
10	Santonian	-1.89	-2.44	-0.91	-0.91
9	Coniacian	-2.26	-2.53	-1.4	-1.07
8	Turonian	-1.95	-2.77	-1.203	-1.08
7	Cenomanian	-2.58	-2.32	-1.006	-0.7
6	Albian	-2.14	-0.75	-0.81	-0.37
5	Aptian	0.27	-0.83	0.59	0.18
4	Barremian	-0.16	-0.41	1.04	
3	Hauterivian	-0.21	0.37	0.705	
2	Valanginian	-0.08	-0.04	0.37	
1	Berriasian	-0.6	-1.1	-0.59	

$\delta^{18}O$ values in ‰ for different latitude zones. More negative values indicate warmer temperatures while more positive values indicate colder temperatures. Isotope data from Prokoph et al. (2008).

Table 11. Cretaceous $\delta^{13}C$ Values.

Stage No.	Stage Name	Tropical δ13C (‰)	Temperate δ13C (‰)	Arctic δ13C (‰)	Deep Sea δ13C (‰)
12	Maastrichtian	2.39	2.26	2.09	1.083
11	Campanian	2.37	2.47	1.67	0.92
10	Santonian	2.2	2.5	1.64	0.43
9	Coniacian	2.02	2.72	1.6	0.84
8	Turonian	2.94	2.85	0.817	1.6
7	Cenomanian	2.33	2.95	0.034	1.12
6	Albian	2.15	1.96	-0.75	1.26
5	Aptian	2.84	2.38	1.9	2.21
4	Barremian	-0.17	1.02	2.55	
3	Hauterivian	-0.08	1.2	2.14	
2	Valanginian	-0.08	0.52	1.73	
1	Berriasian	-1.13	0.42	0.53	

$\delta^{13}C$ vales in ‰ for different latitude zones. More positive values indicate enhanced burial of carbon associated with anoxic events. Isotope data from Prokoph et al. (2008).

Table 12. Cretaceous $^{87}Sr/^{86}Sr$ Ratios and Sea Level.

Stage No.	Stage Name	87Sr/86Sr	Sea Level (m)
12	Maastrichtian	0.707744	194.67
11	Campanian	0.707585	226.33
10	Santonian	0.707466	215.7
9	Coniacian	0.707352	230.35
8	Turonian	0.707356	227.46
7	Cenomanian	0.707447	225.3
6	Albian	0.707413	189.37
5	Aptian	0.707319	147.62
4	Barremian	0.707477	171.12
3	Hauterivian	0.707440	142.92
2	Valanginian	0.707370	81.85
1	Berriasian	0.707278	114.7

$^{87}Sr/^{86}Sr$ ratios used as proxies for sea level compared to estimated eustatic sea level values (in meters above modern) for the stages in the Cretaceous. High $^{87}Sr/^{86}Sr$ is interpreted as a time of sea level fall while low $^{87}Sr/^{86}Sr$ is interpreted as a time of sea level rise. Isotope data from Prokoph et al. (2008) and sea level data form Haq et al. (1987).

Table 13. Marine Reptile Occurrences in Each Latitude Zone.

	%arctic	%temperate	%tropical
Ichthyosaurs	26.1	69.6	4.4
Mosasaurs	2.0	72.8	25.3
Plesiosaurs	19.4	74.6	6.0

Percentage of occurrences for the three marine reptile groups in the three latitude zones used in $\delta^{18}O$ and $\delta^{13}C$. Ichthyosaur and plesiosaur specimens are found mostly in the temperate zone with some in the arctic. Most mosasaur specimens are also found in the temperate zone, but many others are tropical, with few in the arctic.

Stages during which the environmental proxies were changing rapidly and/or to a large degree were considered to be volatile. The times of highest environmental volatility for all the proxies were during stages 4-6. Diversity, origination and extinction were viewed at these three stages to determine whether times with faster rates of environmental change were associated with reductions in marine reptile diversity (Hypothesis 2) and whether these diversity deccreases were associated with elevated extinction and/or decreased origination rates (Hypothesis 3).

Quantitative Analyses

To assess the correlations among the marine reptile diversity, origination and extinction time series and the environmental proxy time series, time series analyses were performed using the software package PAST 3.15 (Hammer et al. 2001). Specifically, the autocorrelation of each species diversity time series was calculated to assess potential periodicity and cross-correlations were calculated between each species diversity time series and each environmental proxy time series, in order to test whether marine reptile diversity decreased during times of lower temperature, increased anoxia, or lower sea level (Hypothesis 1).

Autocorrelation identifies any correlations between elements of a series and other elements from the same series at given intervals. The output of each autocorrelation analysis includes a plot of correlation versus lag size. Time series with strong periodicity will show high positive or negative correlation at lags equivalent to one and one-half the period of the signal, respectively. Autocorrelation analyses were conducted on both raw and rarefied diversity time series along with origination and extinction time series and the environmental proxies.

Cross-correlation identifies correlations between two different time series. As with autocorrelation, the output includes a plot of correlation versus lag size. Two time series that move in sync with each other will show a strong correlation at lag = 0; if the time series have similar periodicity, correlation will also be high at a lag equivalent to the period of the signal. When one time series changes in response to the other, the peak correlation will be at a lag equal to the size of the temporal offset or response time. Cross-correlations were computed in PAST for the four rarefied species diversity time series (all taxa pooled and each of the three marine reptile groups) along with the origination and extinction time series versus each of the four environmental proxy time series ($\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$, eustatic sea level).

As an independent test of whether marine reptile diversity is influenced by environmental factors multiple linear regression and random forest analysis were performed. Multiple regression was performed with the PAST program and using the R program while random forest regression was performed using the R program (R Core Team 2013). Multiple regression was performed in both PAST and R due to R having the versatility to allow for better outputs, such as AIC values, PAST was used due to the small sample sizes for both ichthyosaurs and mosasaurs. Multiple regression involves using a set of independent variables to predict a dependent variable. In this study the dependent variable was the rarefied species diversity, species origination and extinction and species per-capita origination and extinction rates for all taxa pooled and separately for ichthyosaurs, mosasaurs and plesiosaurs (12 analyses in total. Per-capita rates were used as the best representation of origination and extinction, however, in many cases there were no data values for stages; therefore, origination and extinction percentages were also used as a more complete time series. The independent variables in each case were the different environmental proxies, including tropical, temperate and arctic $\delta^{18}O$ and tropical, temperate and arctic $\delta^{13}C$ along with $^{87}Sr/^{86}Sr$ and eustatic sea level. The important outputs of the multiple regression analysis are the p, R and R^2 values. The p values represent significance for or against the null hypothesis of no correlation, with a small p value indicating strong evidence against the null hypothesis. The R values represents the direction of correlation with a negative R value indicating a negative correlation and a positive R value indicating a positive correlation. Finally, the R^2 value indicates how close the data are to the regression line or how predictable the dependent variable is from the independent variables. The Akaike information criterion (AIC) is an estimate of the relative quality of statistical models for a given set of data. Essentially the AIC values are used to weigh/score the independent variables.

Random forest analysis is a machine learning approach that generates multiple decision trees (in this study, 10,000) to determine how dependent values are influenced by the independent values. Each decision tree in the "forest" is given a classification and that tree votes for that class and then the forest chooses the classification that has the most votes over all of the trees in the forest. The random forest analyses performed in this study each used 10,000 trees and 3 nodes to determine importance values with the nodes being the amount of times the tree will split and make a classification. The importance values from these analyses indicate the independent variables that most strongly predict the dependent value, based on how many times the independent variable occurs within the multiple decision trees (Breiman 2001). An independent value that has the highest importance value is considered the most important and therefore is the variable most likely to influence the dependent variable.

RESULTS

Marine Reptile Diversity, Origination and Extinction

A comparison of graphs of raw (Fig. 6) and rarefied (Fig. 7) species abundances through time shows that the large spikes at stage 6 for both overall diversity and ichthyosaurs in the raw values are not present in the rarefied values. The spikes in the raw data are therefore likely due to sampling bias, specifically oversampling of Albian ichthyosaurs from certain regions within the data set. Similarly, the large number of Campanian occurrences for mosasaurs and plesiosaurs likely also reflect more intensive sampling.

Some of the occurrence (Fig. 8) and rarefied diversity (Fig. 9) time series were autocorrelated. Specifically, overall marine reptile abundance showed a strong positive autocorrelation at a lag size of 5 (reflecting the two peaks at stage 6 and stage 11; Figs. 6A and 8A), while mosasaur abundance showed positive autocorrelations at lag sizes of 1 and 2 stages (perhaps due to the high values in stages 11 and 12; Figs. 6C and 8C). Ichthyosaur and plesiosaur abundance time series did not show strong autocorrelations. These patterns changed when considering the rarified species diversity time series (Fig. 9) Here, mosasaur diversity showed very strong negative autocorrelation at a lag size of 1 and positive autocorrelation at a lag size of 2 (Fig. 9C). This pattern makes sense, as the mosasaur diversity curve fluctuates up and down with each stage (Fig. 7C). The plesiosaur diversity time series showed a negative correlation at a lag size of 4 (Fig. 9D), which appears to reflect longer-scale fluctuations in diversity, especially in the Early Cretaceous (stages 1-6; Fig. 7D). The pooled marine reptile (Fig. 9A) and ichthyosaur (Fig. 9B) diversity time series did not show significant autocorrelation.

Originations and extinctions for each of the three marine reptile groups (Figs. 10-12) show fluctuations throughout the Cretaceous. Ichthyosaur originations peaked in the Barremian (stage 4) before declining (Fig. 10A), while extinctions were notably low in the first part of the Early Cretaceous (stages 1-5) before climbing in the Albian (stage 6) and Cenomanian (stage 7) to the clade’s final extinction (Fig. 10B). Mosasaurs experienced increasing numbers of originations and extinctions through most of the Late Cretaceous; in the Maastrichtian, extinctions remained high while originations dropped off (Fig. 11). Plesiosaur origination and extinction time series are generally similar, with large spikes in the Campanian (stage 11) followed by declines in numbers of both originations and extinctions in the Maastrichtian (stage 12); Fig. 12).

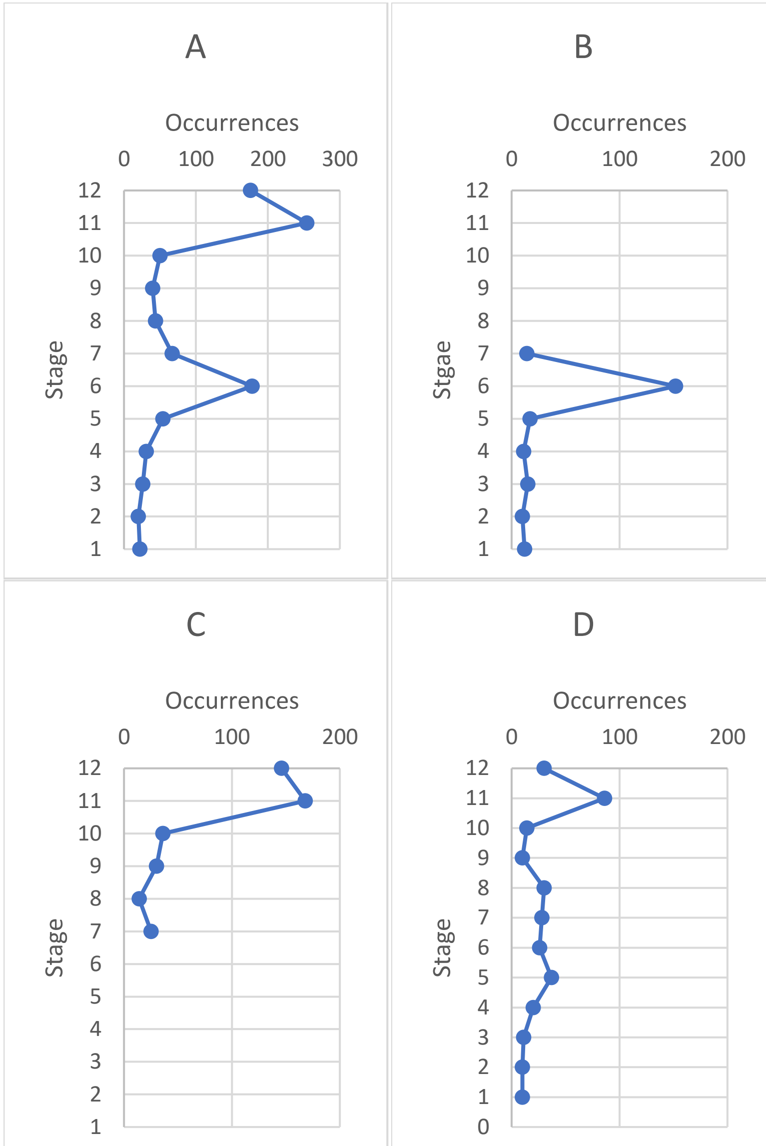

Fig. 6. Raw Marine Reptile Occurrences. Raw counts for overall occurrences (A), ichthyosaurs (B), mosasaurs (C) and plesiosaurs (D). Note large spikes for overall occurrences and ichthyosaurs at stage 6 (Albian) and spikes for mosasaurs and plesiosaurs at stage 11 (Campanian).

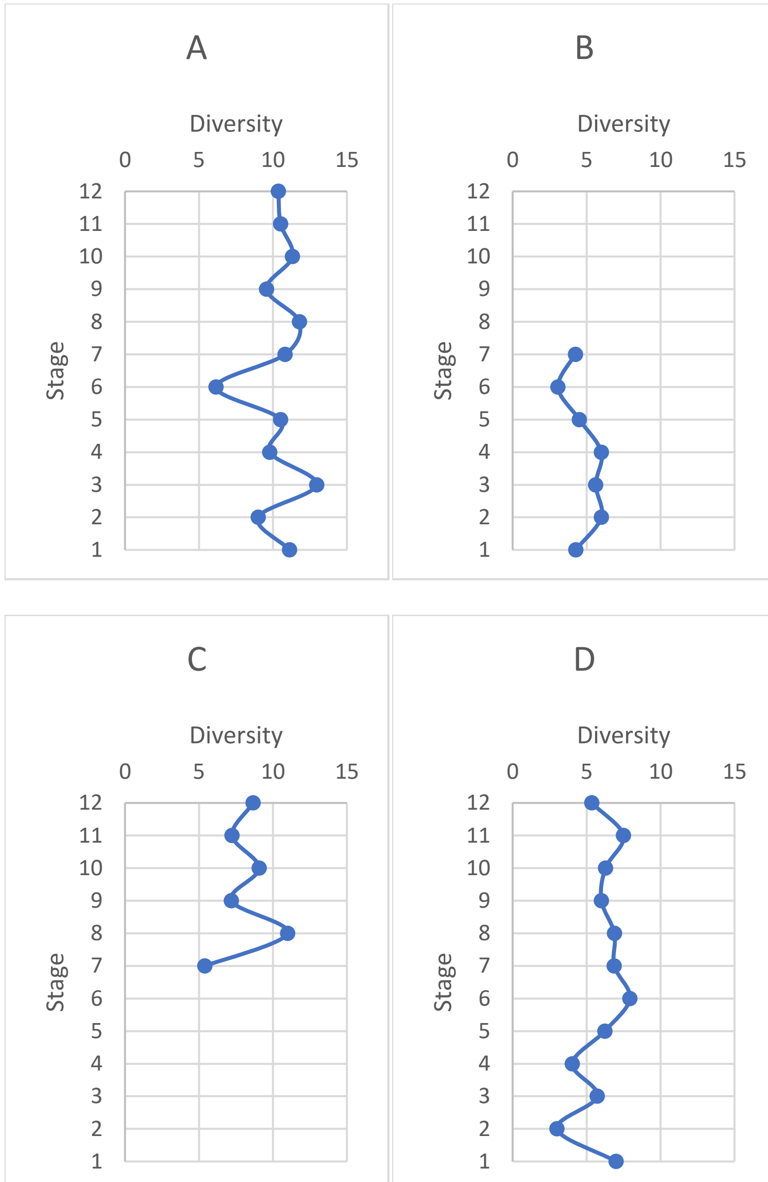

Fig. 7. Rarefied Marine Reptile Diversity. Rarefied species richness values for all marine reptiles (A), ichthyosaurs (B), mosasaurs (C) and plesiosaurs (D).

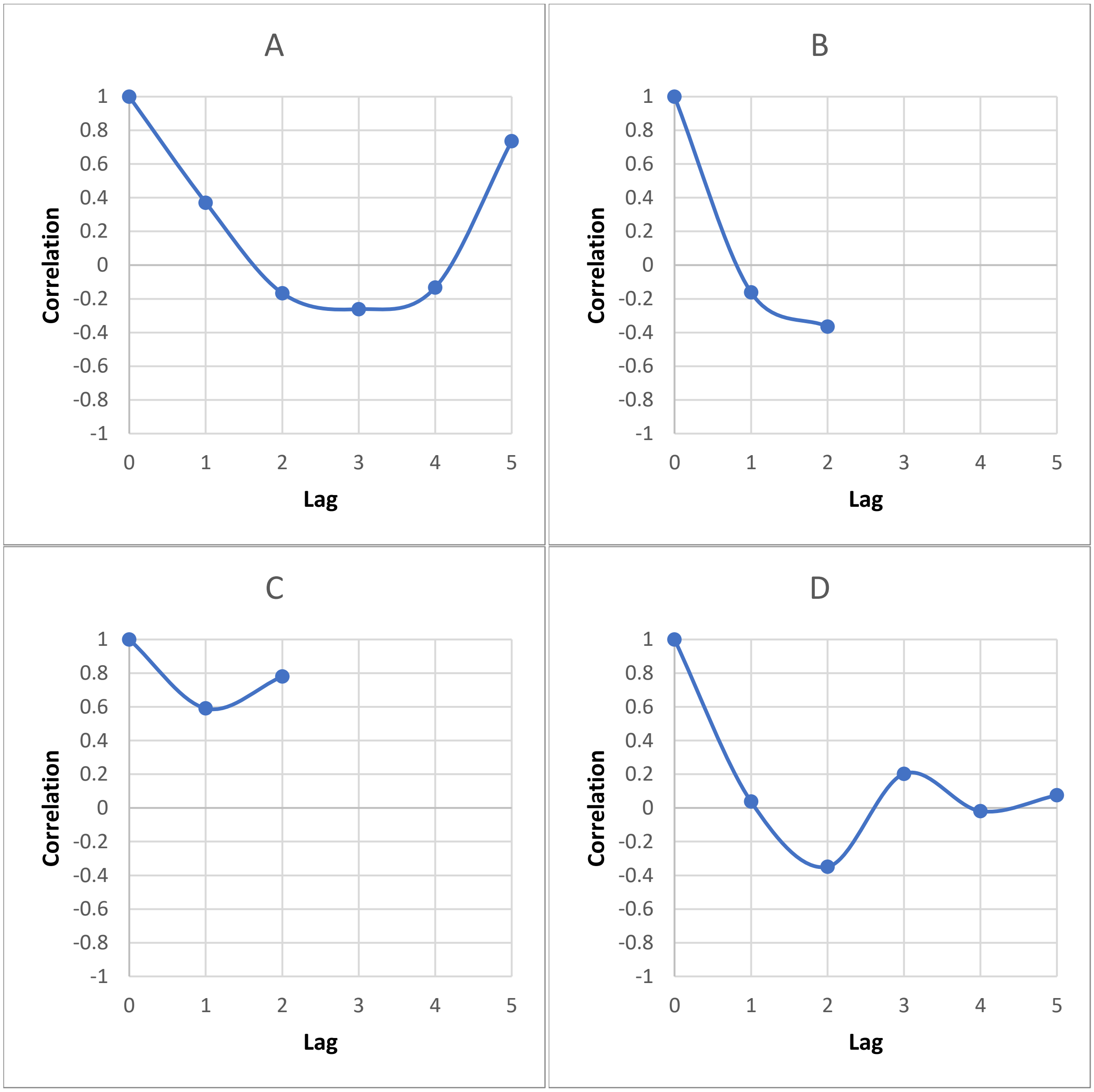

Fig. 8. Raw Species Occurrences Autocorrelation. Autocorrelation graphs for raw overall occurrences (A), ichthyosaurs (B), mosasaurs (C) and plesiosaurs (D) occurrences.

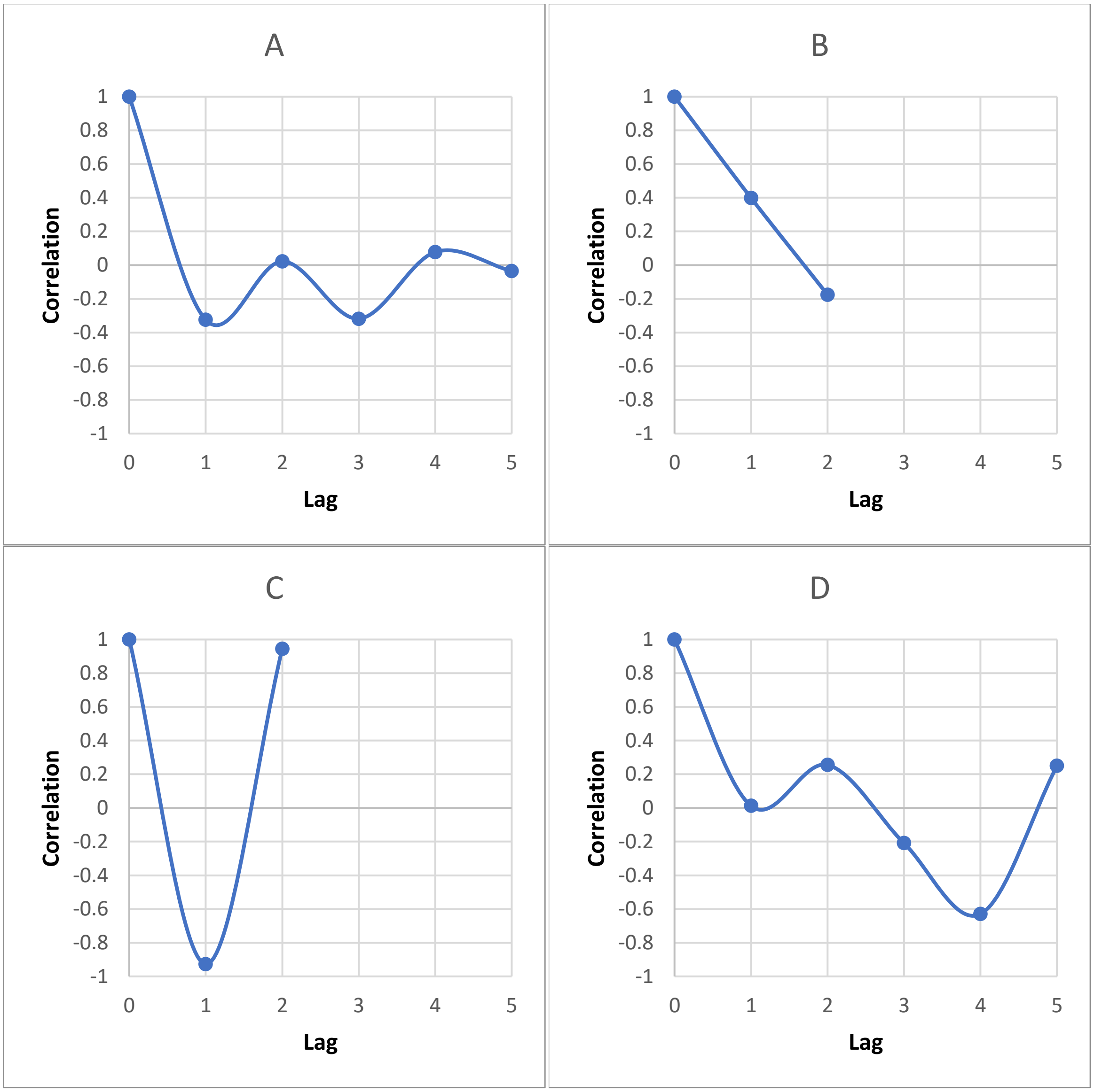

Fig. 9. Rarefied Species Diversity Autocorrelation. Autocorrelation graphs for rarefied overall diversity (A), ichthyosaur (B), mosasaur (C) and plesiosaur (D) occurrences.

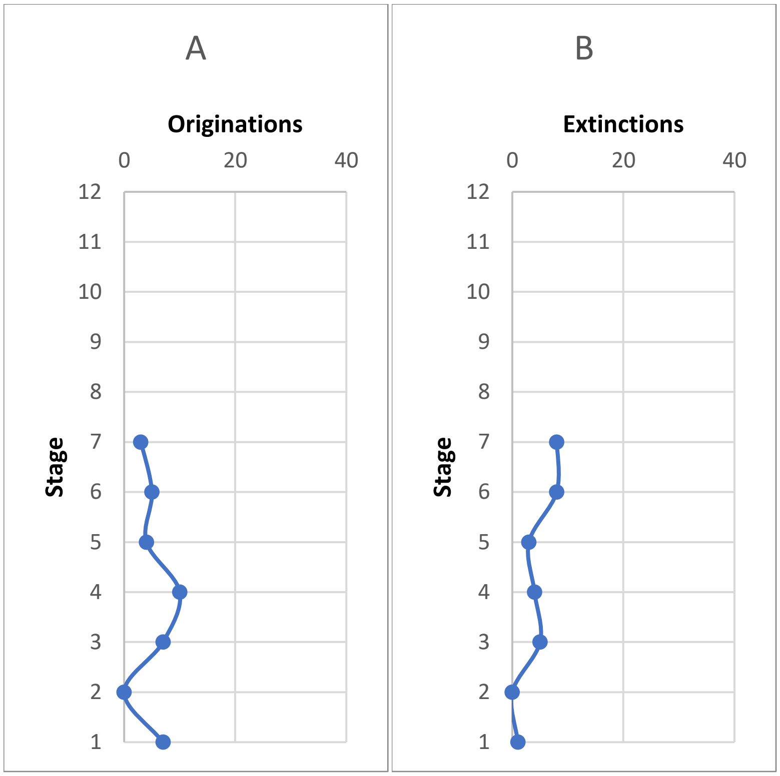

Fig. 10. Ichthyosaur Species Originations and Extinctions. Ichthyosaur originations (A) show a dip at stage 2 with a high at stage 4 and then a general decline. Ichthyosaur extinctions (B) show a general increasing trend with some small fluctuations.

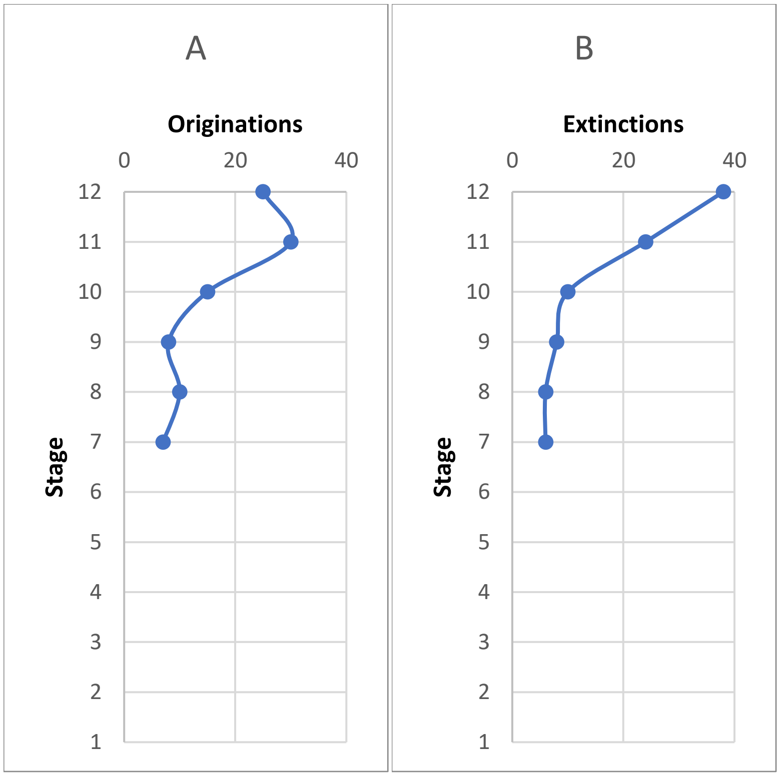

Fig. 11. Mosasaur Species Originations and Extinctions. Mosasaur originations (A) show a large increase from stage 9 to stage 11 with a decrease at the end of the Cretaceous. Mosasaur extinctions (B) showing a sharp increase from stage 10 until the end of the Cretaceous.

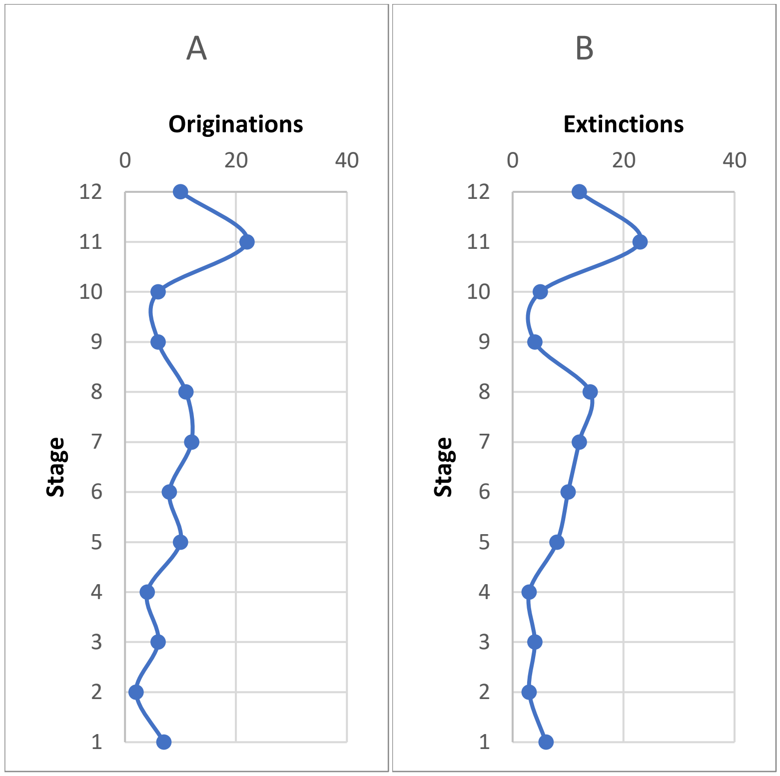

Fig. 12. Plesiosaur Species Originations and Extinctions. Plesiosaur originations (A) show general fluctuations throughout the Cretaceous with a sharp increase in stage 11. Plesiosaur extinctions (B) show a similar trend to originations.

To further evaluate Hypothesis 3 (that diversity drops are associated with elevated extinction and/or decreased origination), times of decreased diversity were compared to origination and extinction rates (Table 14). Ichthyosaurs showed increased origination and extinction for stages 5-6 and decreased origination and extinction for stages 4-5. Mosasaurs had overall increased extinction during times of diversity decrease with origination showing both increases and decreases. Plesiosaurs show mostly decreases in both origination and extinction rates during stages of diversity reduction.

Table 14. Marine Reptile Origination and Extinction Compared to Diversity Decreases.

Ichthyosaurs		
Diversity Decrease Stages	Origination	Extinction
5-6	Increase	Increase
4-5	Decrease	Decrease

Mosasaurs		
Diversity Decrease Stages	Origination	Extinction
10-11	Increase	Increase
8-9	Decrease	Increase

Plesiosaurs		
Diversity Decrease Stages	Origination	Extinction
11-12	Decrease	Decrease
8-9	Decrease	Decrease
6-7	Increase	Increase
3-4	Decrease	Decrease
1-2	Decrease	Decrease

For stages during which diversity was decreasing, the direction of change in origination and extinction rates for each marine reptile group are compiled. Origination and extinction values mirror each other for both ichthyosaurs and plesiosaurs, while mosasaurs overall had increases in both origination and extinction except for when origination increased during one decrease stage.

Environmental Proxies

All $\delta^{18}O$ graphs show an increase in values into stages 3 and 4, which indicates cooling, followed by a decline that lasts until stage 10, which indicates some warming, and finally increasing (cooling) until the end of the Cretaceous. It is notable that $\delta^{18}O$ values are generally higher in the Early Cretaceous (stages 1-6), even though significant global warming is known to have taken place in the early Late Cretaceous (stages 7-8). Tropical and temperate $\delta^{13}C$ values trend generally towards positive values, with some decline occurring through stages 7-12, indicating enhanced rates of organic matter burial through the Cretaceous (Fig. 14). Arctic $\delta^{13}C$ also has a general trend towards positive but with a sharp decline from stage 5 to 6, meaning a lower rate of carbon burial. The ocean anoxia events OAE1a (stage 5) and OAE2 (stages 7-8) are marked by high $\delta^{13}C$ values, especially in the tropical and deep sea records. There is a difference between the $^{87}Sr/^{86}Sr$ and sea level curves (Fig. 15), which would be predicted to be mirror images of each other (high $^{87}Sr/^{86}Sr$ = low sea level), especially in the Early Cretaceous (stages 1-6). It is likely that $^{87}Sr/^{86}Sr$ ratios during the Cretaceous are not a precise indicator of sea level but are influenced by a variety of factors.

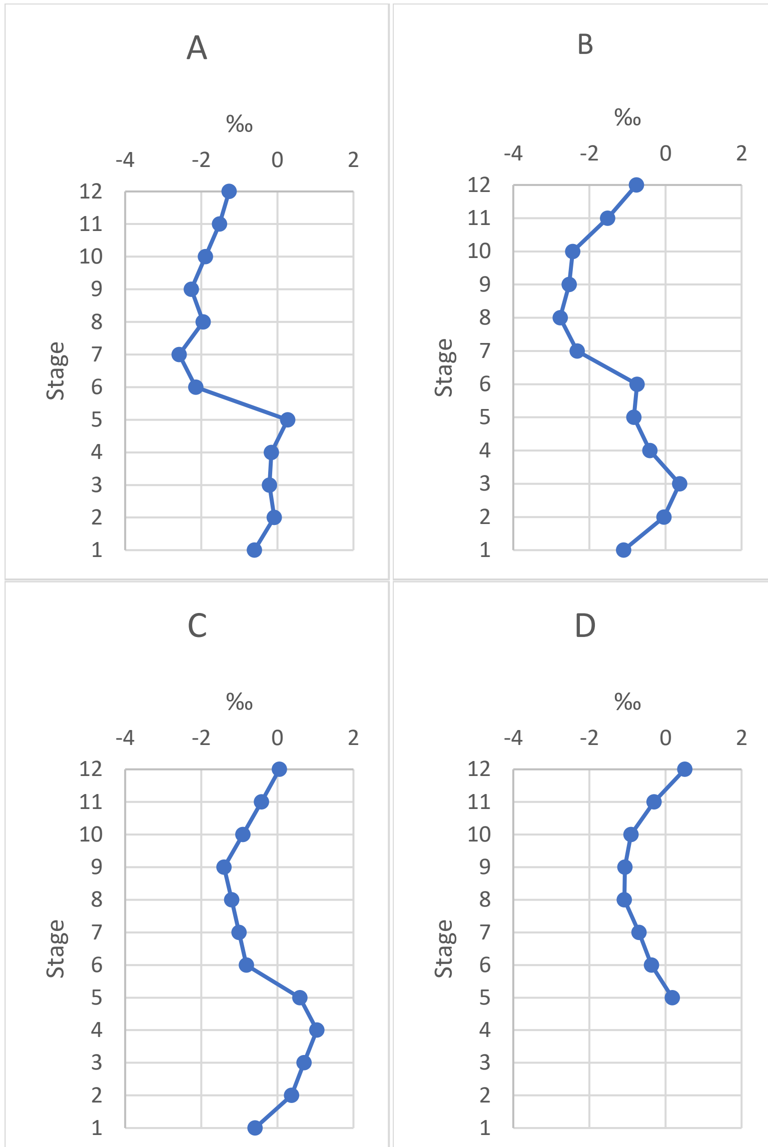

Fig. 13. $\delta^{18}O$ in the Cretaceous. Tropical (A), temperate (B), arctic (C) and deep sea (D) data. Curves are similar overall.

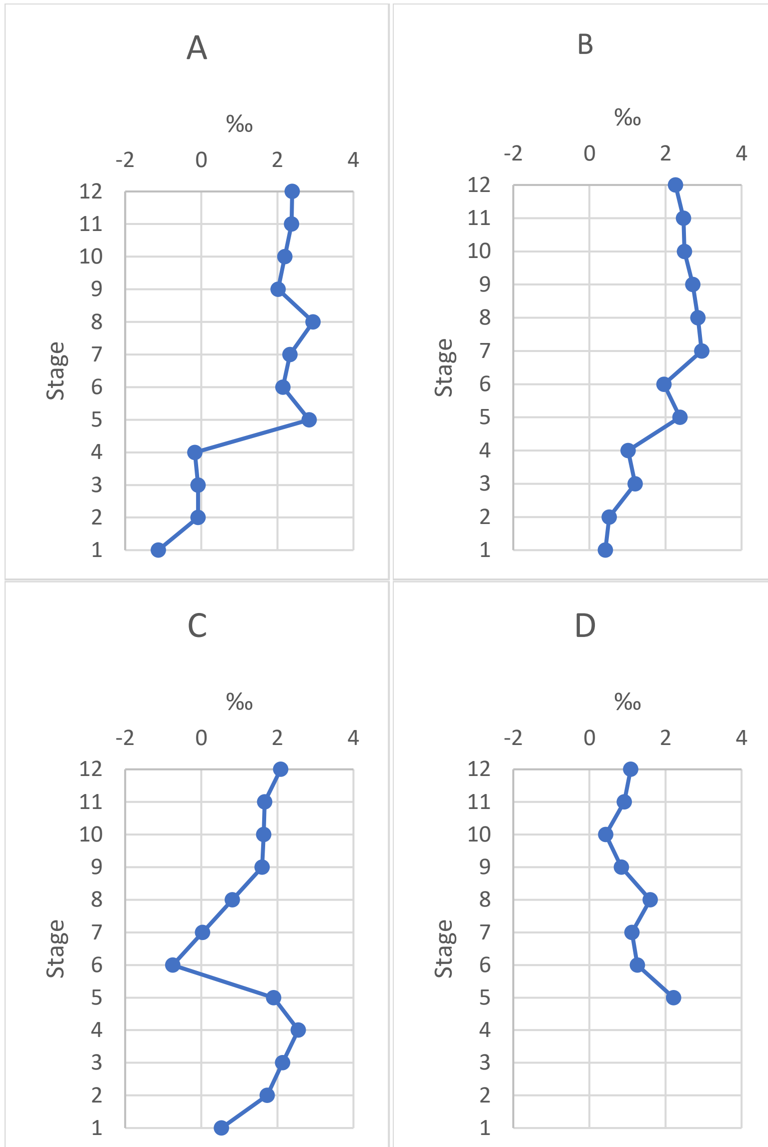

Fig. 14. $\delta^{13}C$ in the Cretaceous. Tropical (A), temperate (B), arctic (C) and deep sea (D) data. Most of the graphs show a similar trend to slightly more positive values towards the end of the Cretaceous, while they diverge from each other between stages 4 and 8.

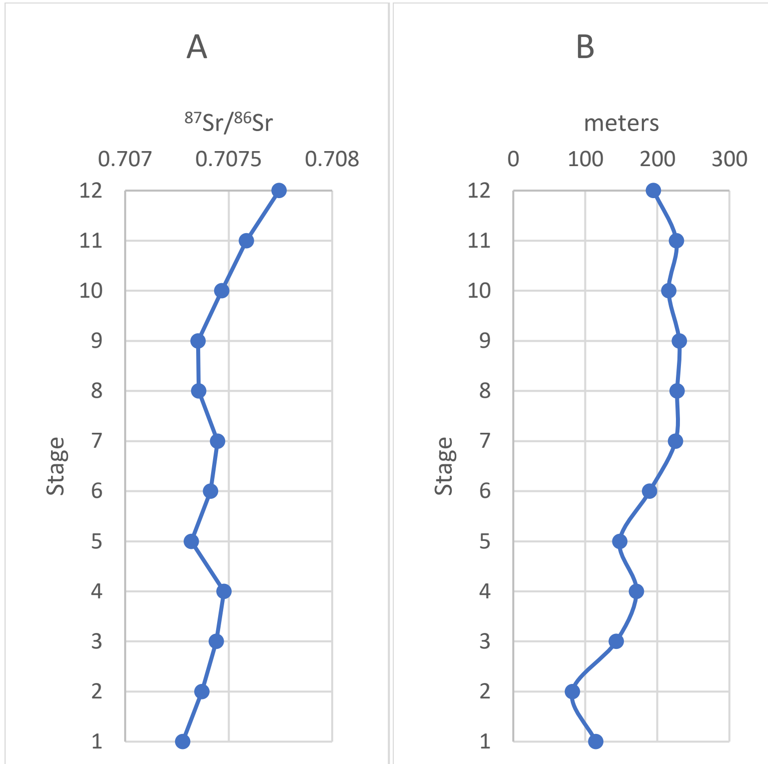

Fig. 15. Cretaceous $^{87}Sr/^{86}Sr$ and Sea Level. Note that $^{87}Sr/^{86}Sr$ (A) is not a close proxy for sea level (B), likely due to multiple drivers of isotopic composition, including climate changes and ocean volcanism.

Environmental volatility for the Cretaceous is shown as being the most pronounced during stages 4-6. During these stages marine reptile diversity, origination and extinction were therefore observed to see if they showed high or low values during these times of rapid environmental change (Table 15). Mosasaurs did not occur during these stages where environmental volatility was high and therefore are not discussed here. For diversity, as well as origination and extinction, values that fell within the 3 highest values were considered high while values that fell within the 3 lowest were considered low. For ichthyosaurs, diversity was relatively high during stage 4 but low during stage 6, origination was high during stage 4 and extinction was low during stage 5. Plesiosaurs have low values for diversity, origination and extinction during stage 4 with diversity also being high during stage 6.

Table 15. Environmental Volatility Compared to Marine Reptile Diversity Metrics.

	Ichthyosaurs			Plesiosaurs		
Stage	Diversity	Origination	Extinction	Diversity	Origination	Extinction
6	Low	-	-	High	-	-
5	-	-	Low	-	-	-
4	High	High	-	Low	Low	Low

Stages 4-6 experienced the highest environmental volatility during the Cretaceous. Diversity, origination and extinction rates were categorized as "low", "high" or neither for stages 4, 5, and 6, as listed in the table. Note the lack of similarity in ichthyosaur versus plesiosaur diversity dynamics during these intervals.

Relationships between Diversity Dynamics and Environmental Change

Cross-correlations were used to assess the relationship between diversity, origination, and extinction and the environmental proxies. For correlation graphs, values that are ±0.8 or higher are considered to be a strong correlation, while any values that occur at the end lag sizes, ±6, are not considered significant, due to edge effects. The lag size indicates how much temporal offset exists between the two signals; a positive lag indicates the environmental proxy changed before the diversity or turnover metric did, while a negative lag indicates that the diversity or turnover metric changed before the proxy did. Since here the goal is to test proxies as drivers of diversity and turnover, positive lags will be of particular interest. A summary of all cross-correlation results is provided in Table 16.

Diversity Cross-Correlations

The diversity time series were cross-correlated with the isotope values to better understand if diversity dynamics correlate with environmental change. The $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and sea level time series were cross-correlated with the overall rarified species diversity of all the marine reptiles in the Cretaceous (Figs. 16, 17, 18). The overall marine reptile species diversity time series is strongly correlated with both deep sea $\delta^{18}O$ and deep sea $\delta^{13}C$ at a lag of +5; the latter also shows negative correlations at lags of +1 and +4.

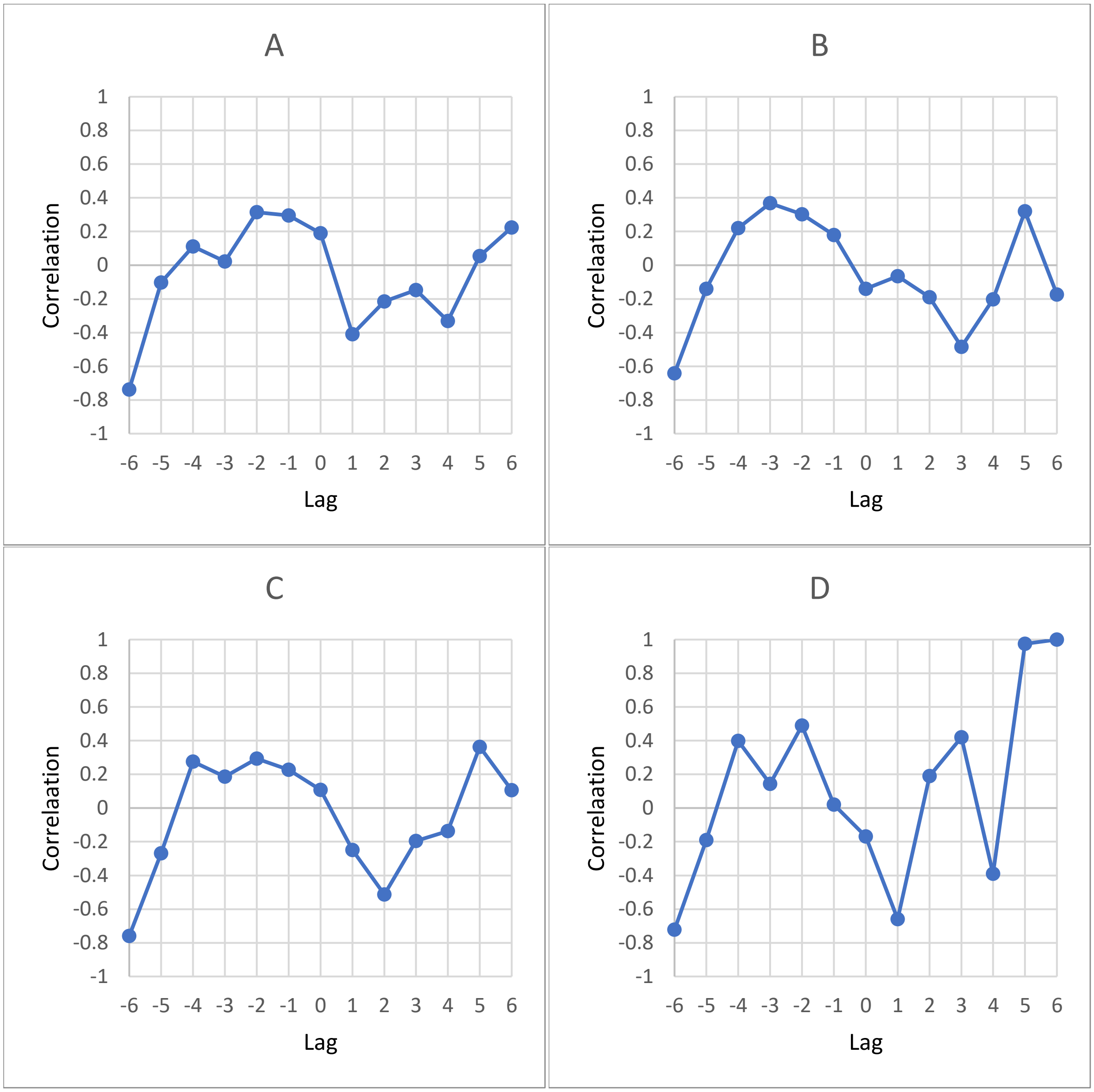

Fig. 16. Rarefied Species Diversity Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note the strong correlation at lag +5 for the deep sea record.

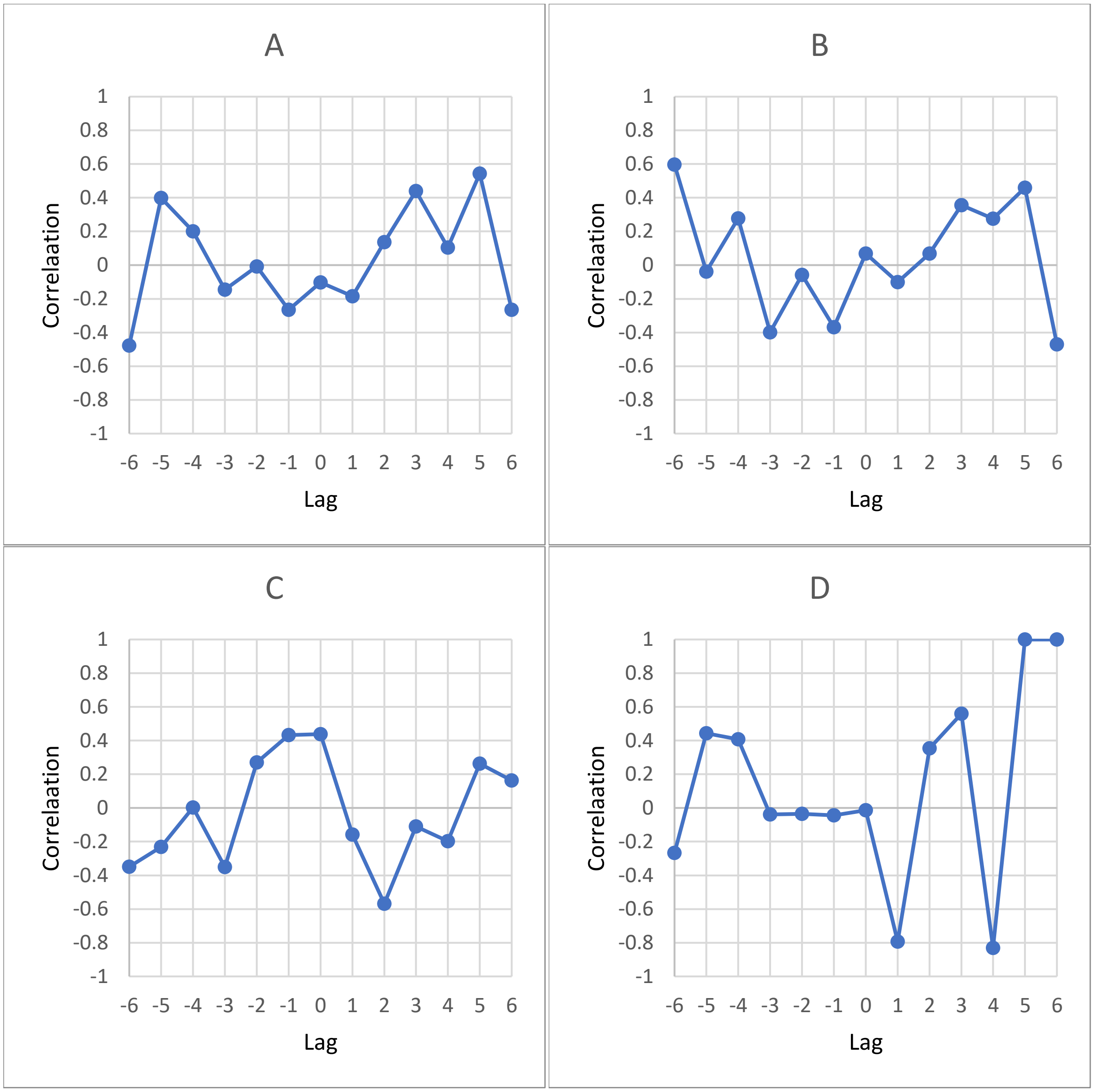

Fig. 17. Rarefied Species Diversity Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D) zones. Note the strong positive correlation at a lag of +5 and strong negative correlations at +1 and +4 for the deep sea record.

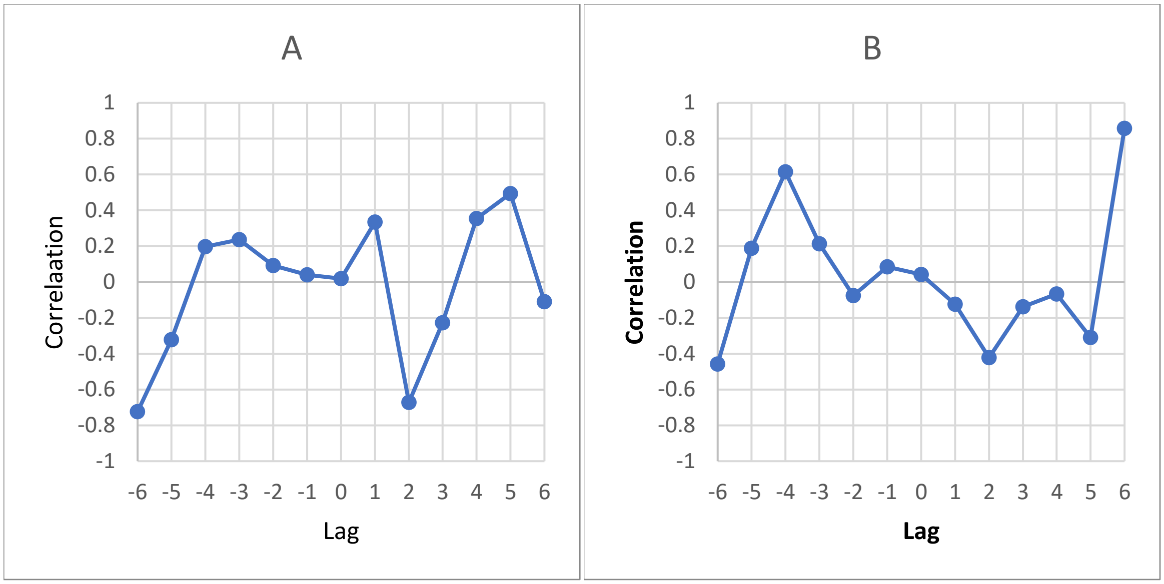

Fig. 18. Rarefied Species Diversity Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. $^{87}Sr/^{86}Sr$ ratios (A) and sea level (B), as with other environmental proxies, show no strong correlations with marine reptile diversity.

The ichthyosaur rarified species diversity time series was cross-correlated with $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and sea level time series (Figs. 19-21). The ichthyosaur diversity has a strong negative correlation with tropical, temperate, arctic and deep sea $\delta^{18}O$ at lags of -1 and 0. A strong negative correlation indicates that as ichthyosaur diversity decreases the $\delta^{18}O$ value increases. The negative lag indicates that the ichthyosaur diversity is changing before the $\delta^{18}O$ changes. Strong positive correlations are seen in the tropical, temperate, and arctic records at a lag of -5, in the tropical record at +4, in the arctic record at lags of +4 and +5, and in the deep sea record at lags of +3 and +4. Ichthyosaur diversity has a strong negative correlation with tropical, temperate, arctic and deep sea $\delta^{13}C$ at lags of -2, -5 and +3, +1 and -2, respectively. This indicates that ichthyosaur diversity decreases precede increases in tropical, temperate, and deep sea $\delta^{13}C$ at lags of 2, 5 and 2 stages, respectively. Alternatively, ichthyosaur diversity decreases one stage before arctic $\delta^{13}C$ increases.

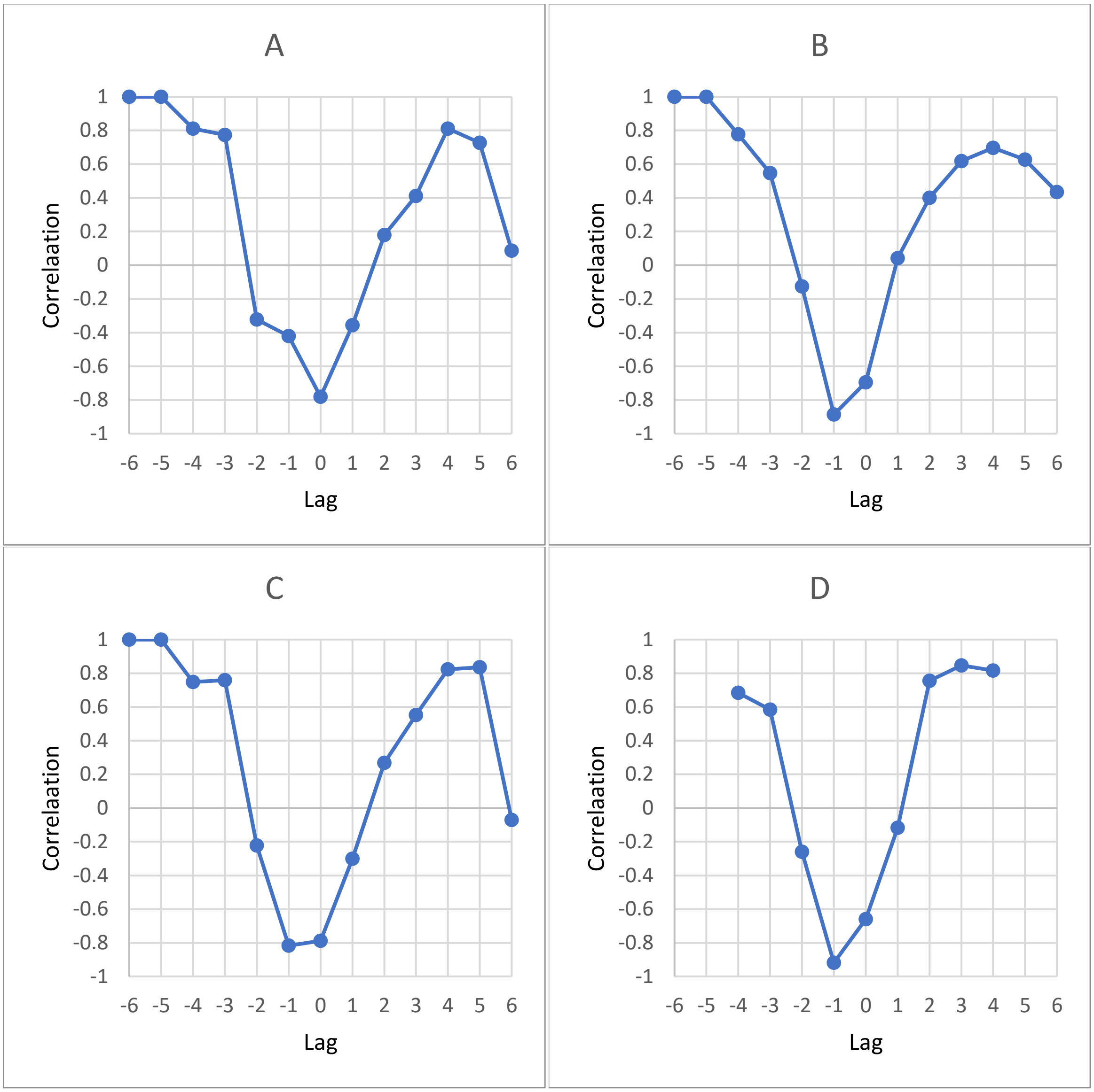

Fig. 19. Rarefied Ichthyosaur Species Diversity Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note very strong negative correlation for all graphs at a lag of -1 and/or 0, and positive correlations at lags of -5 (tropical, temperate, arctic), +3 (deep sea), +4 (tropical, arctic, deep sea), and +5 (arctic).

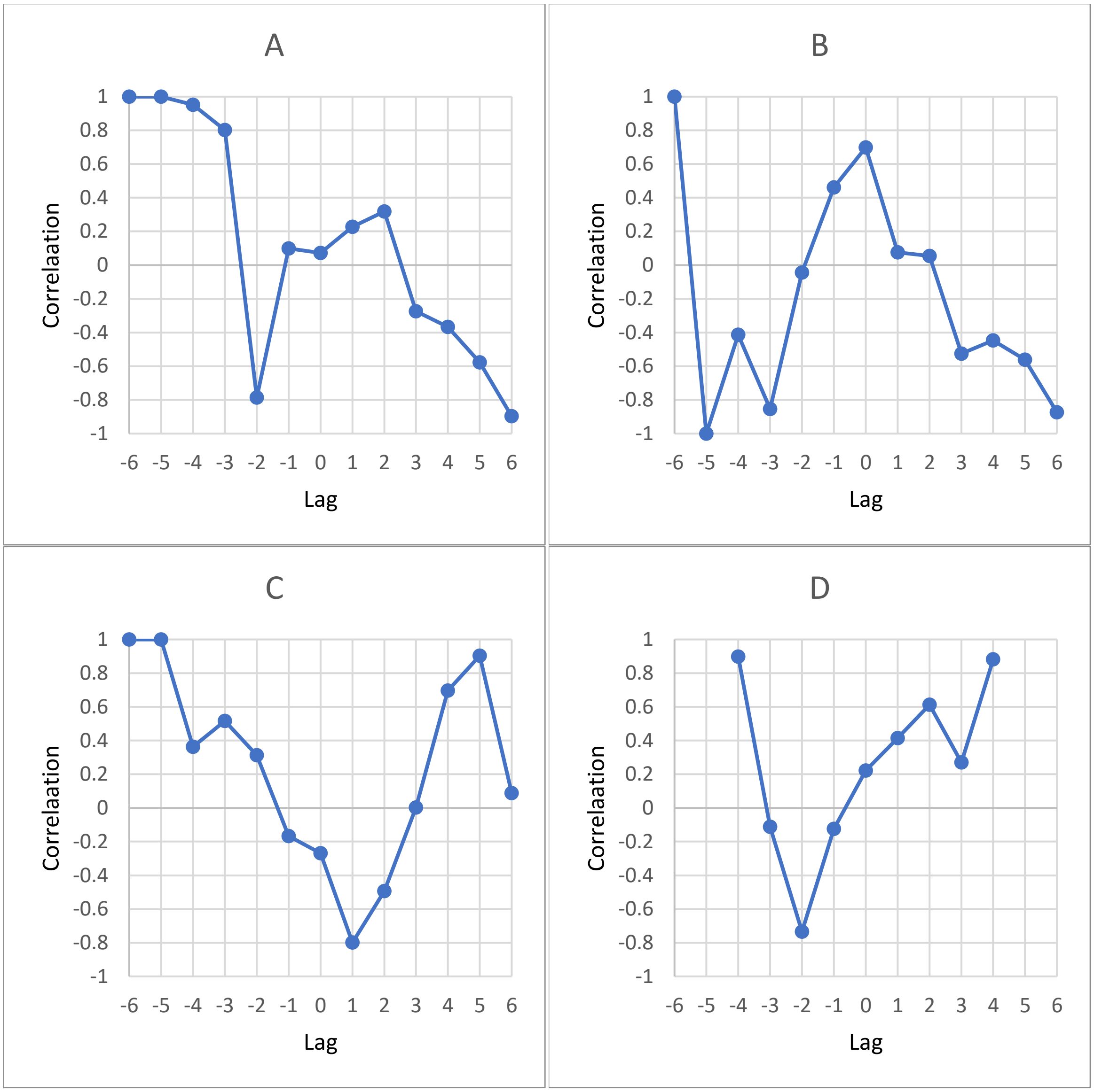

Fig. 20. Rarefied Ichthyosaur Species Diversity Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). All graphs are different from each other and show strong negative correlations between ichthyosaur diversity and tropical, temperate, and arctic $\delta^{13}C$ at lags of -2, at -5 and -3, and at +1, respectively.

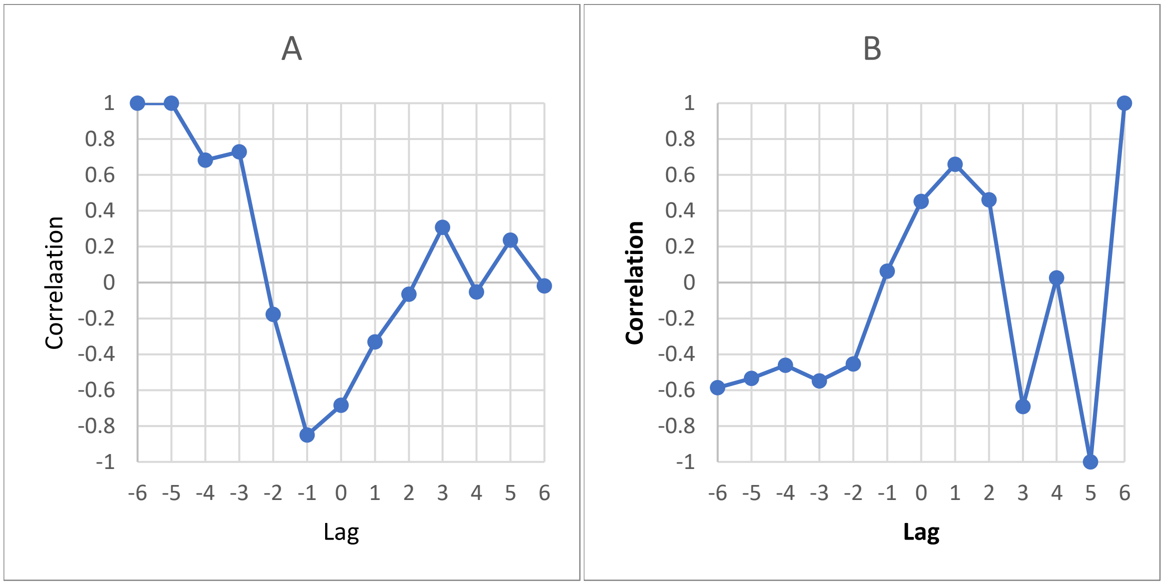

Fig. 21. Ichthyosaur Species Diversity Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. $^{87}Sr/^{86}Sr$ ratios (A) show a negative correlation at a lag of -1, and generally a very similar shape to that of ichthyosaur diversity cross-correlated with arctic carbon (Fig. 13C). Sea level (B) shows a negative correlation at a lag of 5.

The mosasaur diversity time series was cross correlated with $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and sea level time series (Figs. 22-24). Mosasaur diversity has a strong positive correlation at lags of -5 and -4 for tropical, temperate, and arctic $\delta^{18}O$. This indicates that mosasaur diversity increased first at 5-4 stages before $\delta^{18}O$ increased. Mosasaur diversity shows a similar response for tropical, temperate, and arctic $\delta^{13}C$ and for $^{87}Sr/^{86}Sr$.

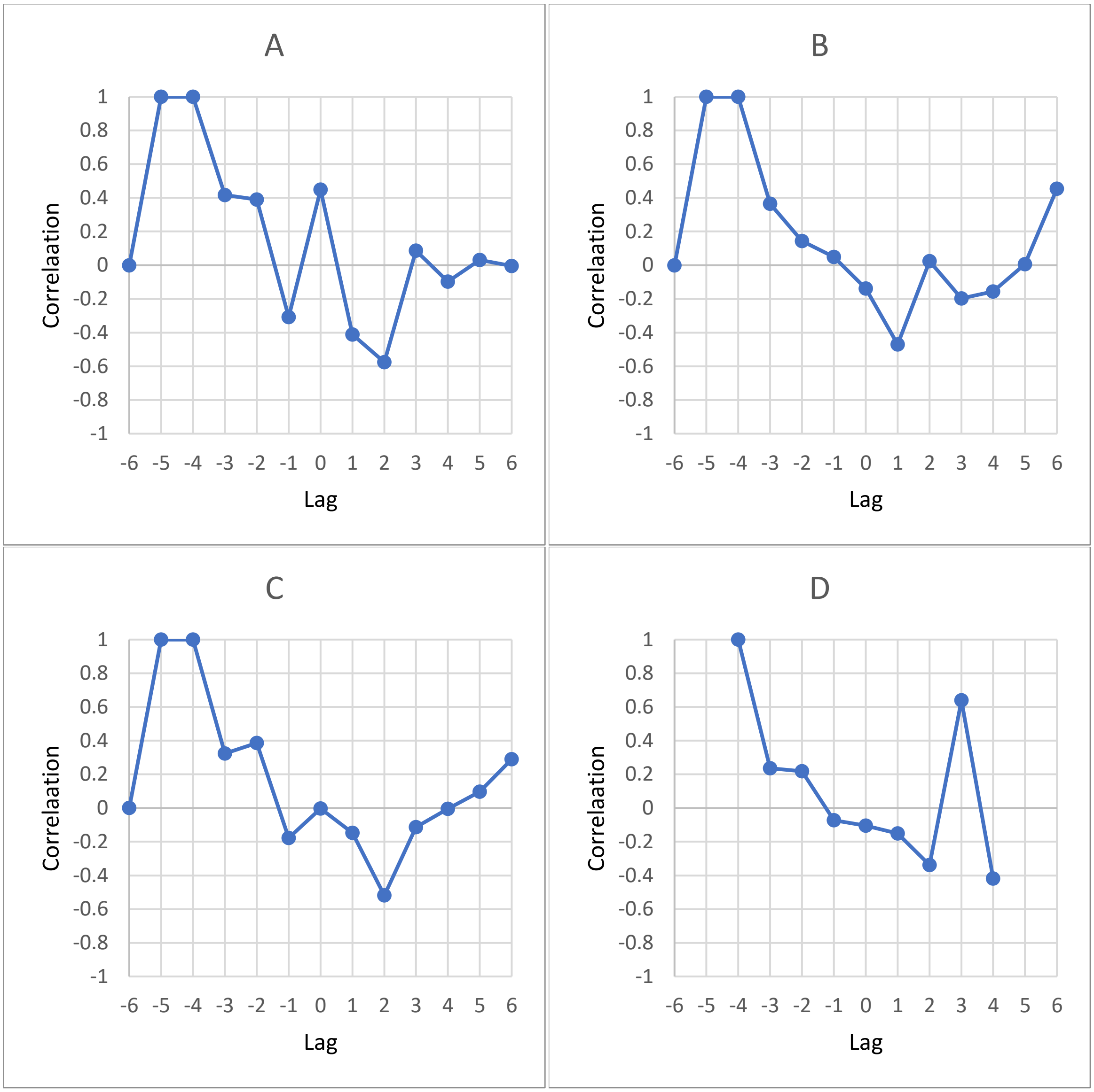

Fig. 22. Rarefied Mosasaur Species Diversity Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). All of the graphs except for deep sea (D) show a strong positive correlation at lags of -5 and -4.

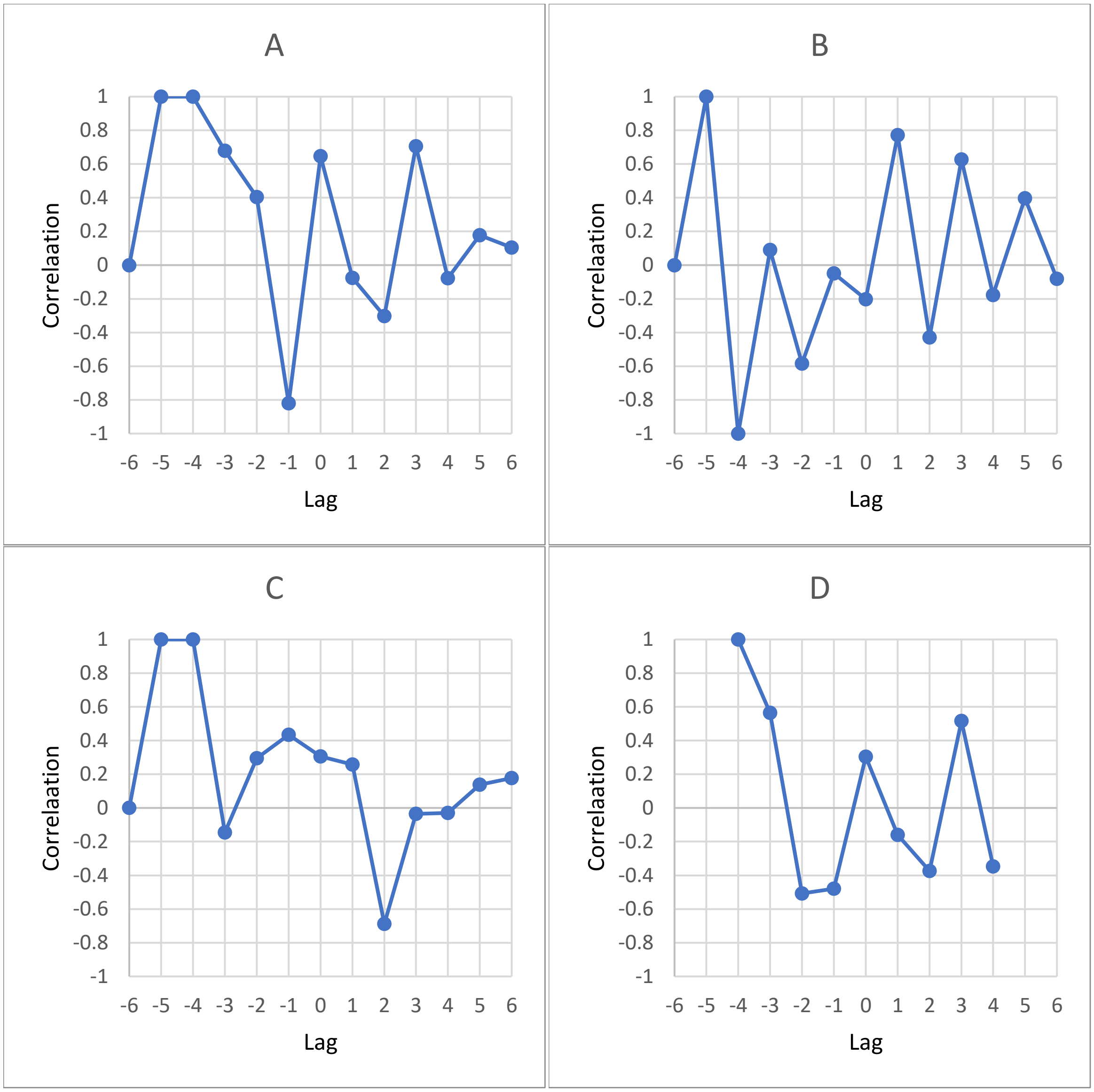

Fig. 23. Rarefied Mosasaur Species Diversity Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Both tropical (A) and arctic (C) graphs show a strong positive correlation at lags of -5 and -4, similar to the correlations of mosasaur abundance with tropical, temperate and arctic oxygen values (Fig. 16A, B & C). Temperate carbon (B) also shows a strong positive correlation at lag of -5 but not at -4, which instead corresponds to a negative correlation.

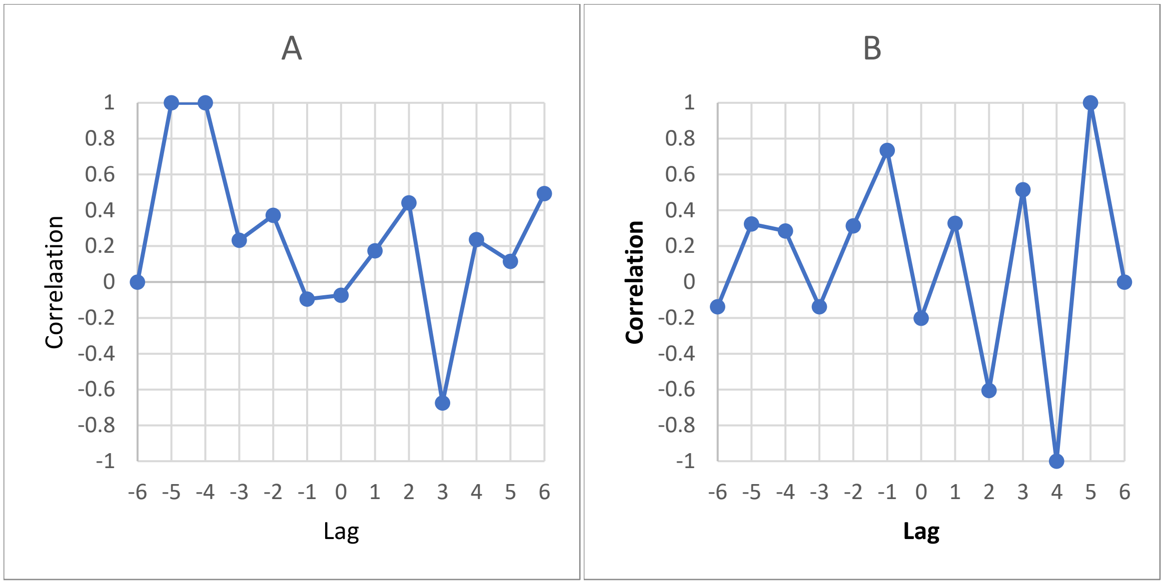

Fig. 24. Mosasaur Species Diversity Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. $^{87}Sr/^{86}Sr$ ratios (A) show a strong positive correlation at lags of -5 and -4, similar to those seen for oxygen and carbon time series (Fig. 16 & 17). Sea level (B) shows a strong negative correlation at a lag of 4 and then a strong positive correlation immediately following at lag 5.

The plesiosaur diversity time series was cross correlated with $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and sea level time series (Fig. 25-27). Plesiosaur diversity has a strong positive correlation with tropical $\delta^{18}O$ at a lag of -5, indicating that plesiosaur diversity increased five stages before $\delta^{18}O$ increased. Plesiosaur diversity has a strong positive correlation with arctic $\delta^{13}C$ at a lag of -5 along with a positive correlation with deep sea $\delta^{13}C$ at a lag of 3. This indicates that plesiosaur diversity was increasing five stages before arctic $\delta^{13}C$ was increasing and plesiosaur diversity was increasing three stages after deep sea $\delta^{13}C$ increased. Finally, there were no strong correlations between plesiosaur diversity and $^{87}Sr/^{86}Sr$ or sea level.

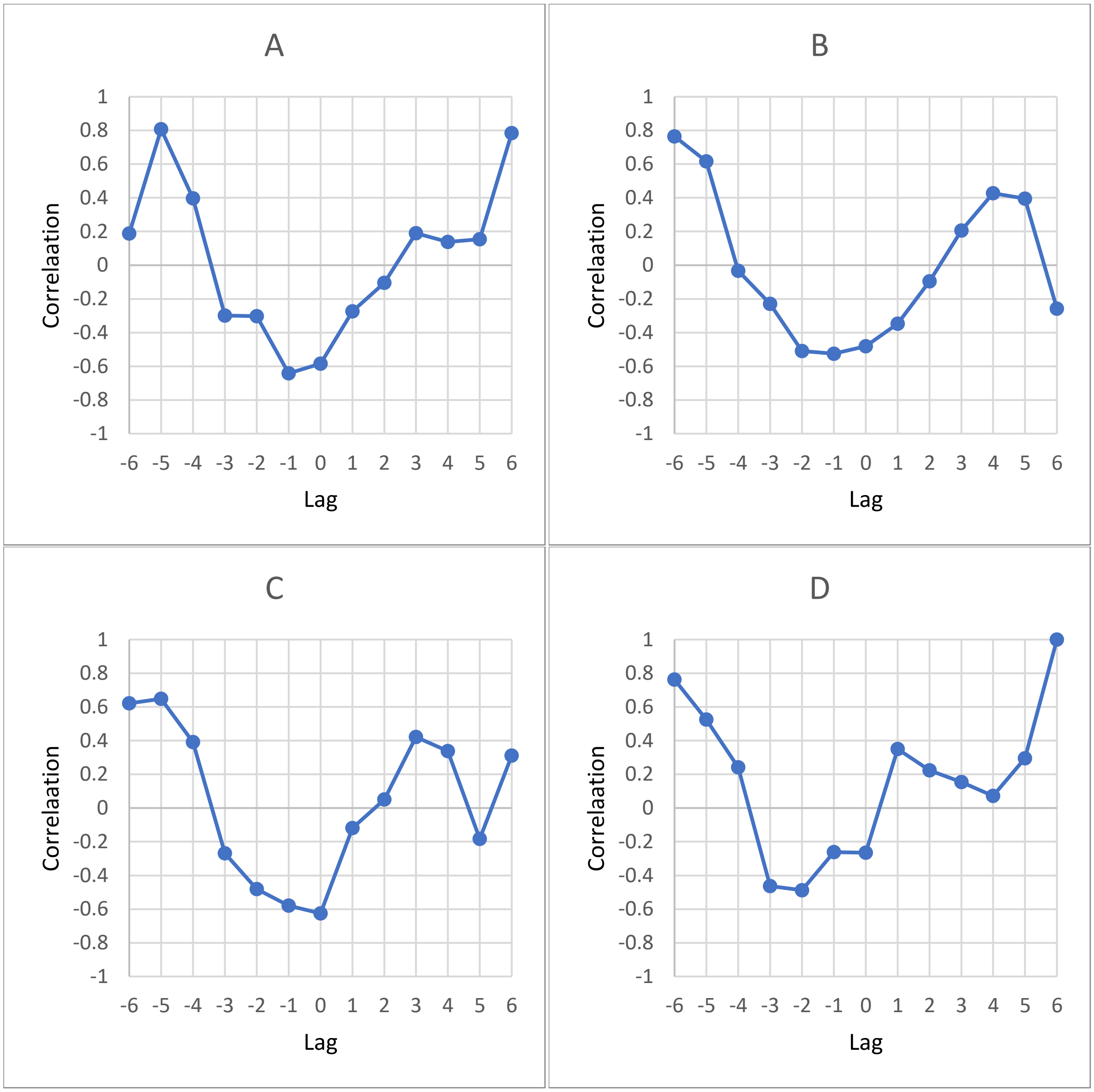

Fig. 25. Rarefied Plesiosaur Species Diversity Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). The only strong correlation observed is with the tropical record at a lag of -5.

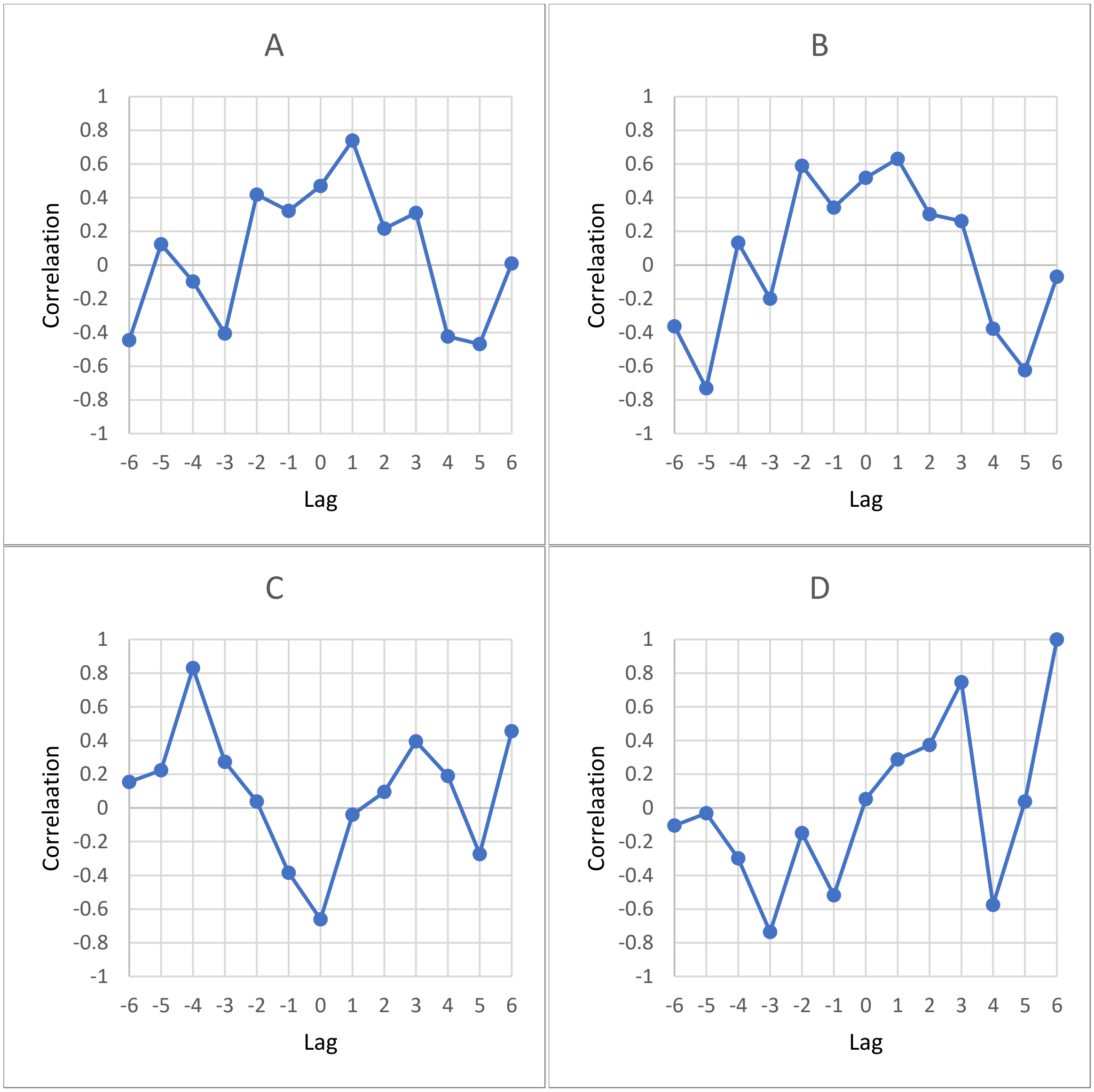

Fig. 26. Rarefied Plesiosaur Species Diversity Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). There are no strong correlations except for the arctic $\delta^{13}C$ record, which shows a positive correlation with species diversity at a lag of -4.

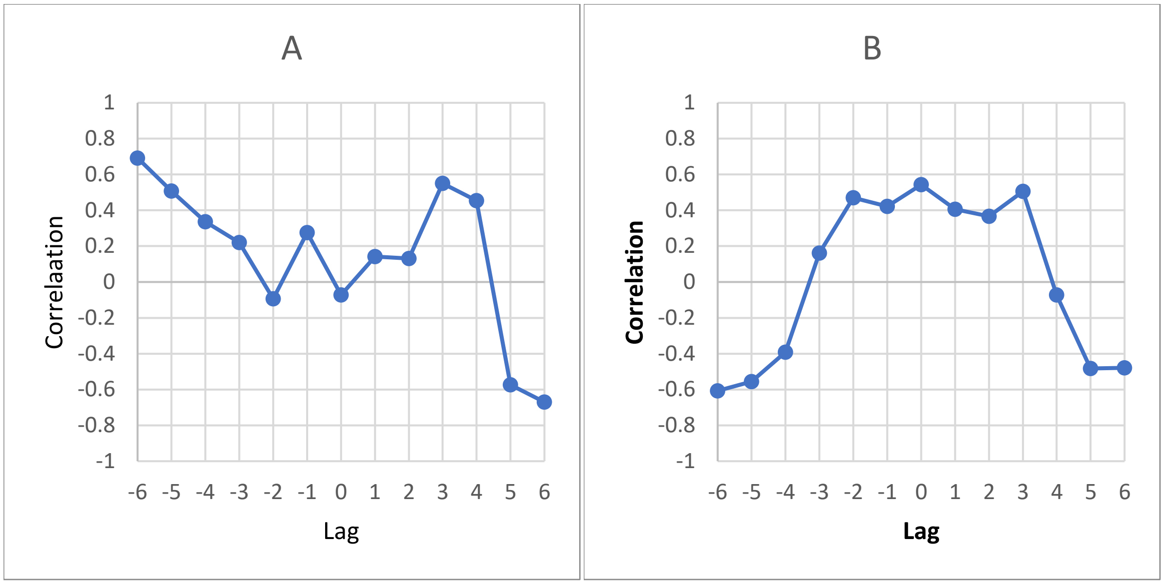

Fig. 27. Plesiosaur Species Diversity Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. $^{87}Sr/^{86}Sr$ ratios (A) with no strong correlations. Sea level (B) also has no strong correlations.

Origination and Extinction Cross-Correlations

Origination and extinction time series for ichthyosaurs were cross correlated with $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and sea level (Figs. 28-33). For origination, strong negative correlations occur at lags of +5 for tropical, temperate and arctic $\delta^{18}O$, with tropical (lags of +1 and +5), arctic (+5), and deep sea (+1) $\delta^{13}C$, with $^{87}Sr/^{86}Sr$ (+5), and sea level (+4). Positive correlations are observed with the temperate (+5) and deep sea (+3) $\delta^{13}C$ records and with sea level (+5). The extinction time series shows a similar response, with strong negative correlations for tropical, temperate and arctic $\delta^{18}O$ at lag +5 (also at -4 for the temperate $\delta^{18}O$ record), and positive correlations for tropical (0) and temperate (+3) records. Negative correlations are observed for tropical and arctic $\delta^{13}C$ at lag +5, temperate $\delta^{13}C$ at lags +1 and +4, and deep sea $\delta^{13}C$ at lag -2. Positive correlations with $\delta^{13}C$ are seen at lag +4 (arctic), lag +5 (temperate) and -3 (tropical). The ichthyosaur extinction time series is negatively correlated with $^{87}Sr/^{86}Sr$ at lags -3 and +5 and sea level at lag +4, while it is positively correlated with $^{87}Sr/^{86}Sr$ at lags +4 and sea level at lags -5, -4, and +5.

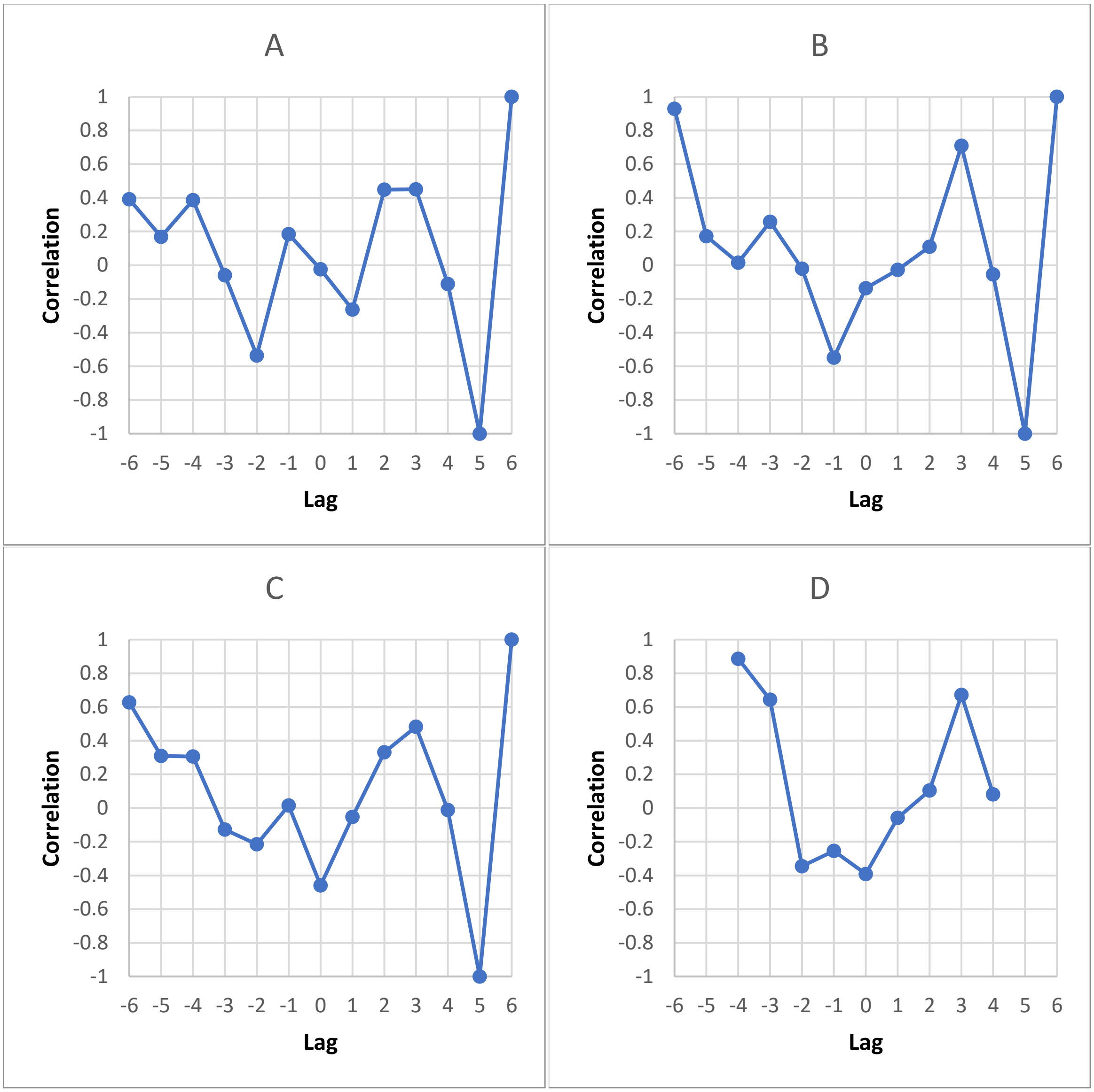

Fig. 28. Ichthyosaur Origination Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note very strong negative correlation at a lag of 5 for tropical (A), temperate (B) and arctic (C) $\delta^{18}O$.

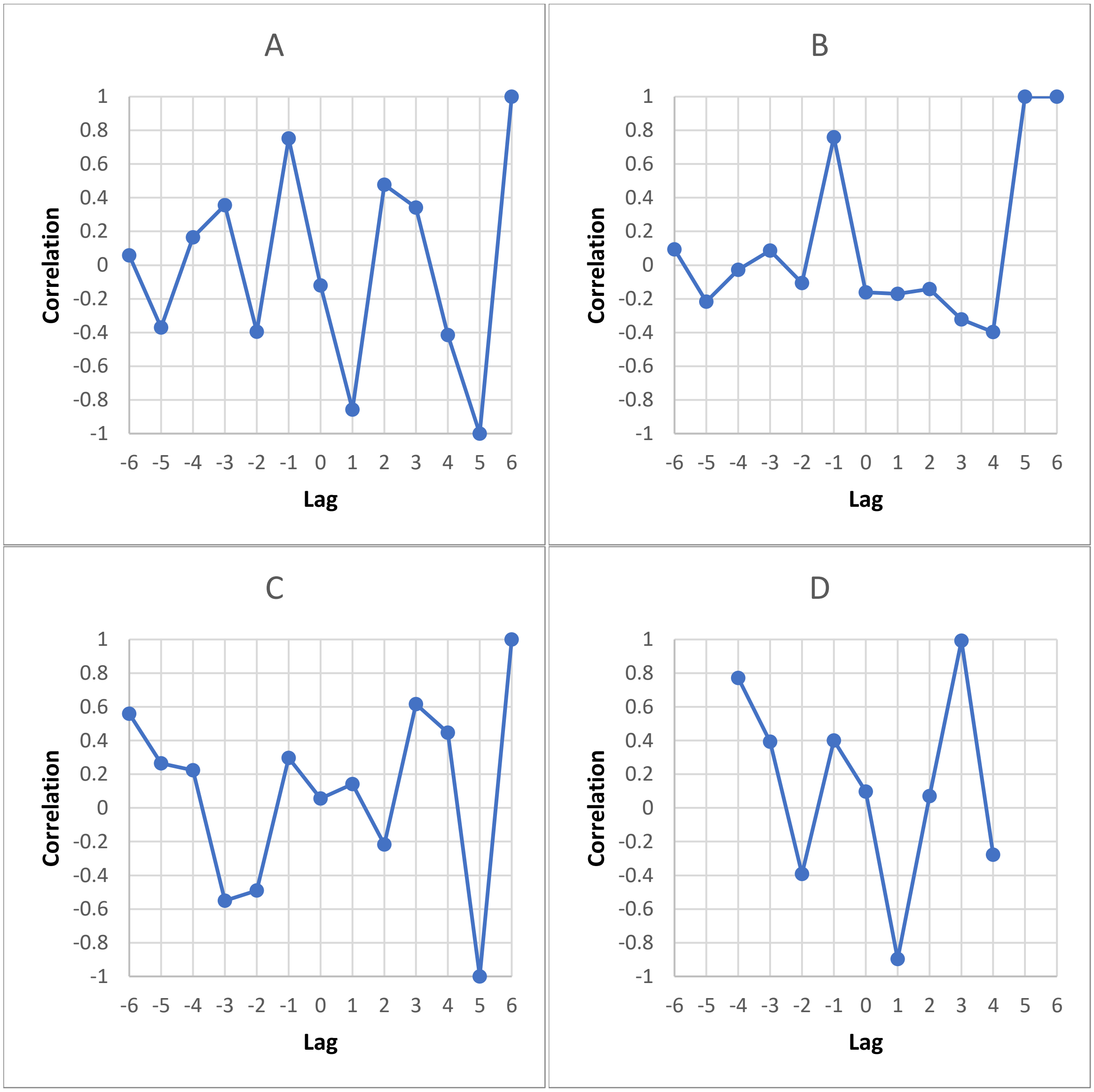

Fig. 29. Ichthyosaur Origination Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note strong negative correlation at a lag of +5 for both tropical (A) and arctic (C) $\delta^{13}C$. Tropical (A) $\delta^{13}C$ also has a large negative correlation at a lag of +1, and deep sea (D) $\delta^{13}C$ has strong negative and positive correlations, respectively, at lags of +1 and +3.

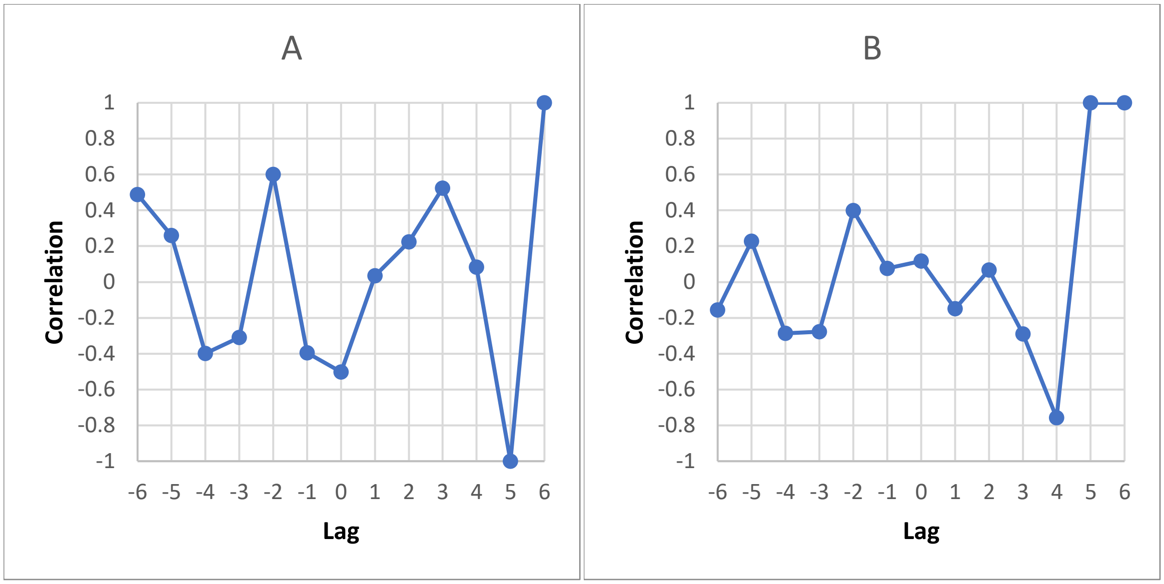

Fig. 30. Ichthyosaur Origination Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. Note strong negative correlation for both $^{87}Sr/^{86}Sr$ (A) and sea level (B) at lags of +5 and +4, respectively, and positive correlation with sea level at a lag of +5.

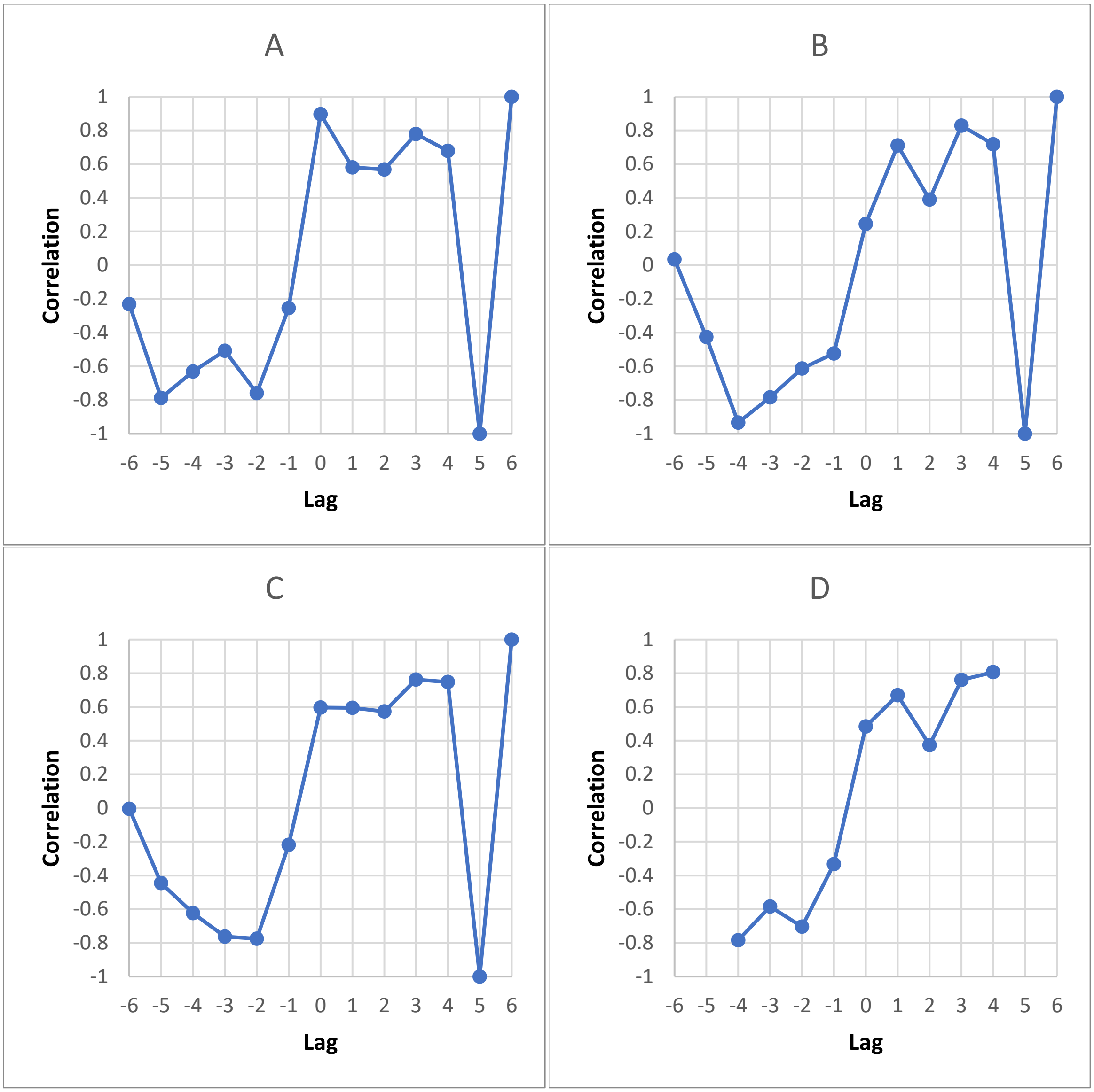

Fig. 31. Ichthyosaur Extinction Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note strong negative correlation in tropical (A), temperate (B) and arctic (C) $\delta^{18}O$ at a lag of +5 as well as a negative correlation for temperate $\delta^{18}O$ at lag -4. Positive correlations are observed for the tropical (lag 0) and temperate (+3) records.

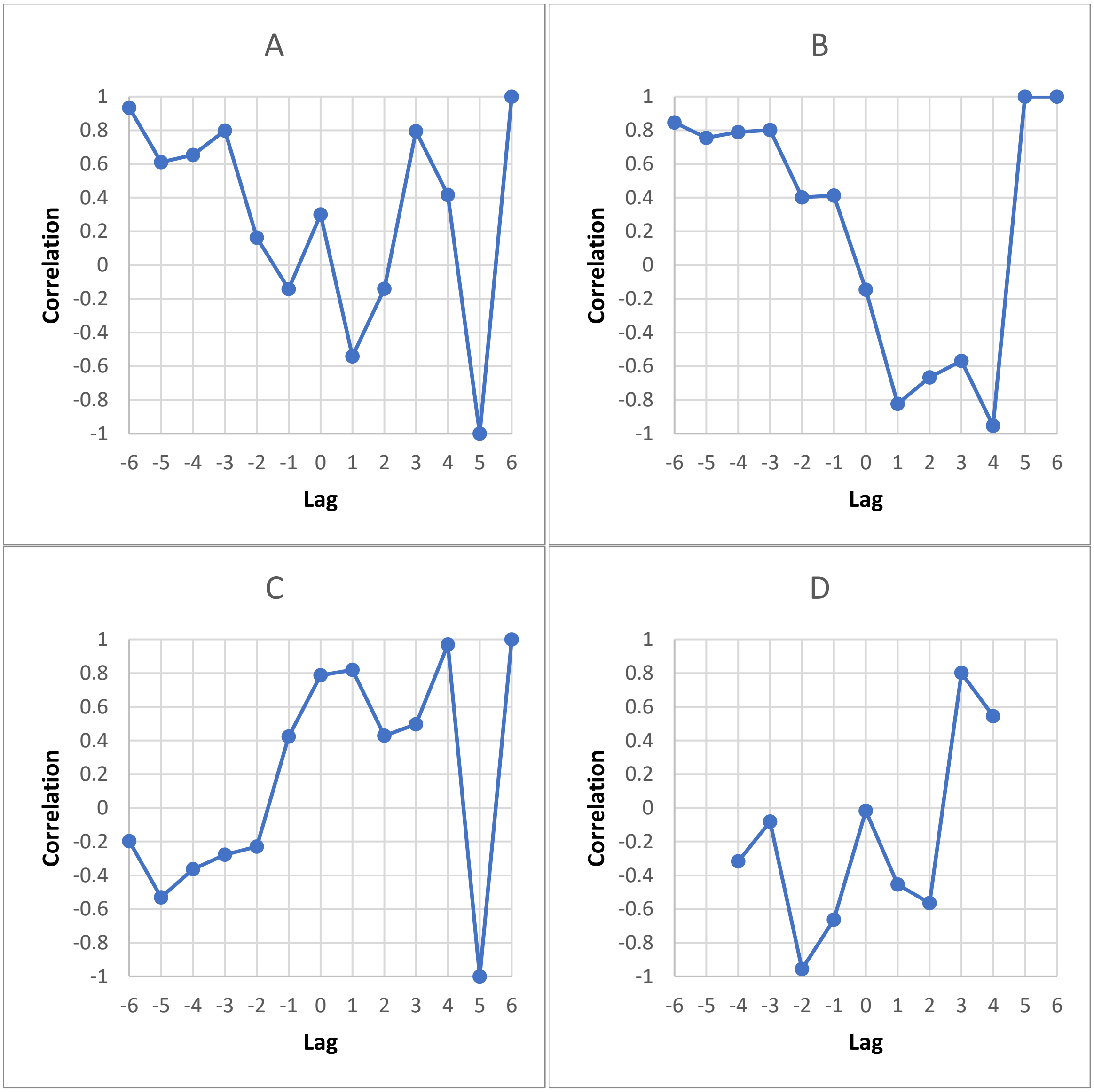

Fig. 32. Ichthyosaur Extinction Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note strong negative correlation for tropical (A) and arctic (C) $\delta^{13}C$ at a lag of +5 and for temperate (B) $\delta^{13}C$ at a lag of +4. Deep sea (D) $\delta^{13}C$ has a strong negative correlation at a lag of -2. Strong positive correlations occur in the tropical record at lag -3, temperate record at lags -3 and +5, and in the arctic record at lags +1 and +4.

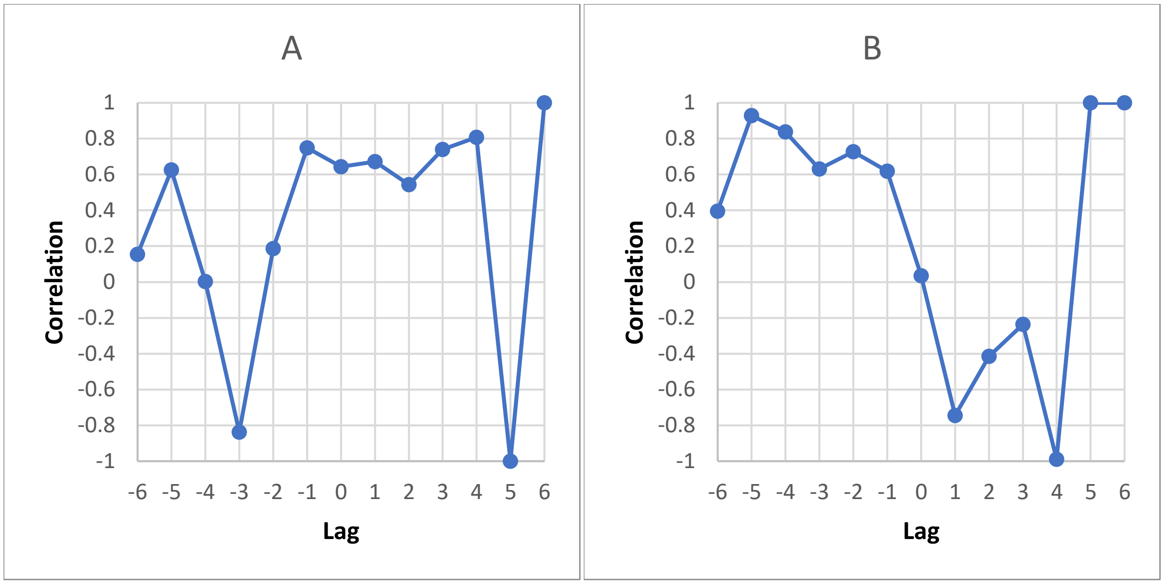

Fig. 33. Ichthyosaur Extinction Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. Note strong negative correlations for $^{87}Sr/^{86}Sr$ (A) at lags of -3 and +5, and similarly, a strong negative correlation for sea level (B) at a lag of +4. Positive correlations occur at lag +4 for $^{87}Sr/^{86}Sr$ and at lags -5, -4, and +5 for sea level.

Origination and extinction for mosasaurs were cross-correlated with the environmental proxy time series (Figs. 34-39). Mosasaurs showed more significant correlations than the other groups. For origination, strong negative correlations are seen for $\delta^{18}O$ at lags of -5, -4 and/or -3 and positive correlations at lags of 0, +1, +4 and +5 for tropical, temperate, and arctic records. Strong positive correlations for tropical, temperate and arctic $\delta^{13}C$ are observed at lags of +4 and/or +5. Strong positive correlations for $^{87}Sr/^{86}Sr$ and sea level are also seen at lags of +4 and/or +5, and there is a negative relationship between origination and sea level at lags of +1, +2, and +4. For extinction, strong positive correlations occur for tropical, temperate and arctic $\delta^{18}O$ at lags 0 to +5. Strong positive correlations of extinction with tropical, temperate and arctic $\delta^{13}C$ are seen at lags of +4 and +5, as well as lag +2 for tropical and lags +2 and +3 for arctic records. Negative correlations with $\delta^{13}C$ are observed at lags 0 through +3 for the temperate record and -5 for the arctic record. Strong positive correlations for $^{87}Sr/^{86}Sr$ are observed at lags of -1 to +5 and for sea level at lags of ±4 and ±5. Negative correlations exist between extinction and sea level at lags of +1 and +3.

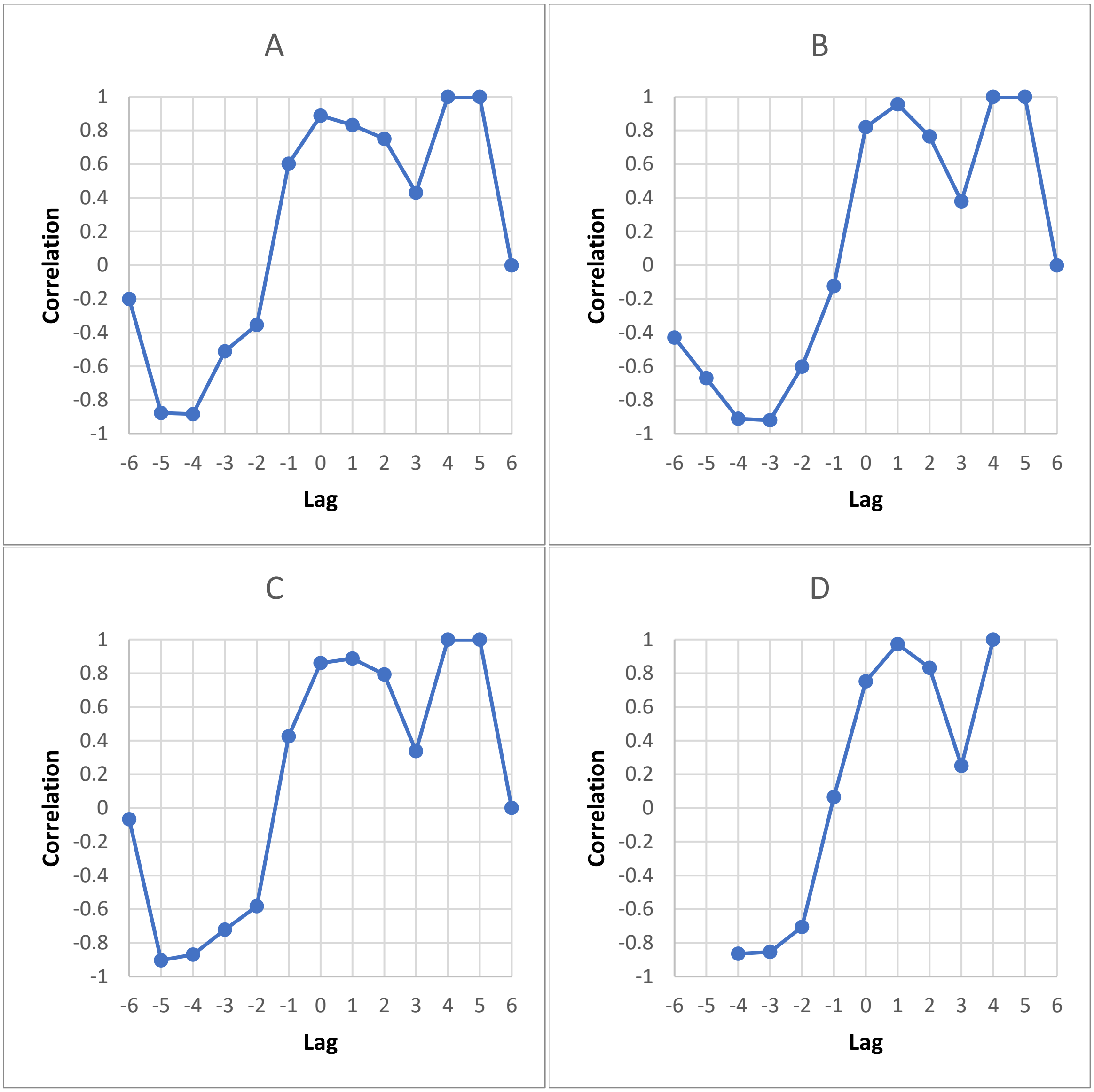

Fig. 34. Mosasaur Origination Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note strong positive correlation for tropical (A), temperate (B) and arctic (C) $\delta^{18}O$ at lags of 0, +1, +4 and +5, and for deep sea (D) $\delta^{18}O$ at lags of +1 and +2. Strong negative correlations are observed for tropical (A) and arctic (C) $\delta^{18}O$ at a lag of -5 and -4 while a similar strong correlation is seen in temperate (B) and deep sea (D) $\delta^{18}O$ at lags of -4 and -3.

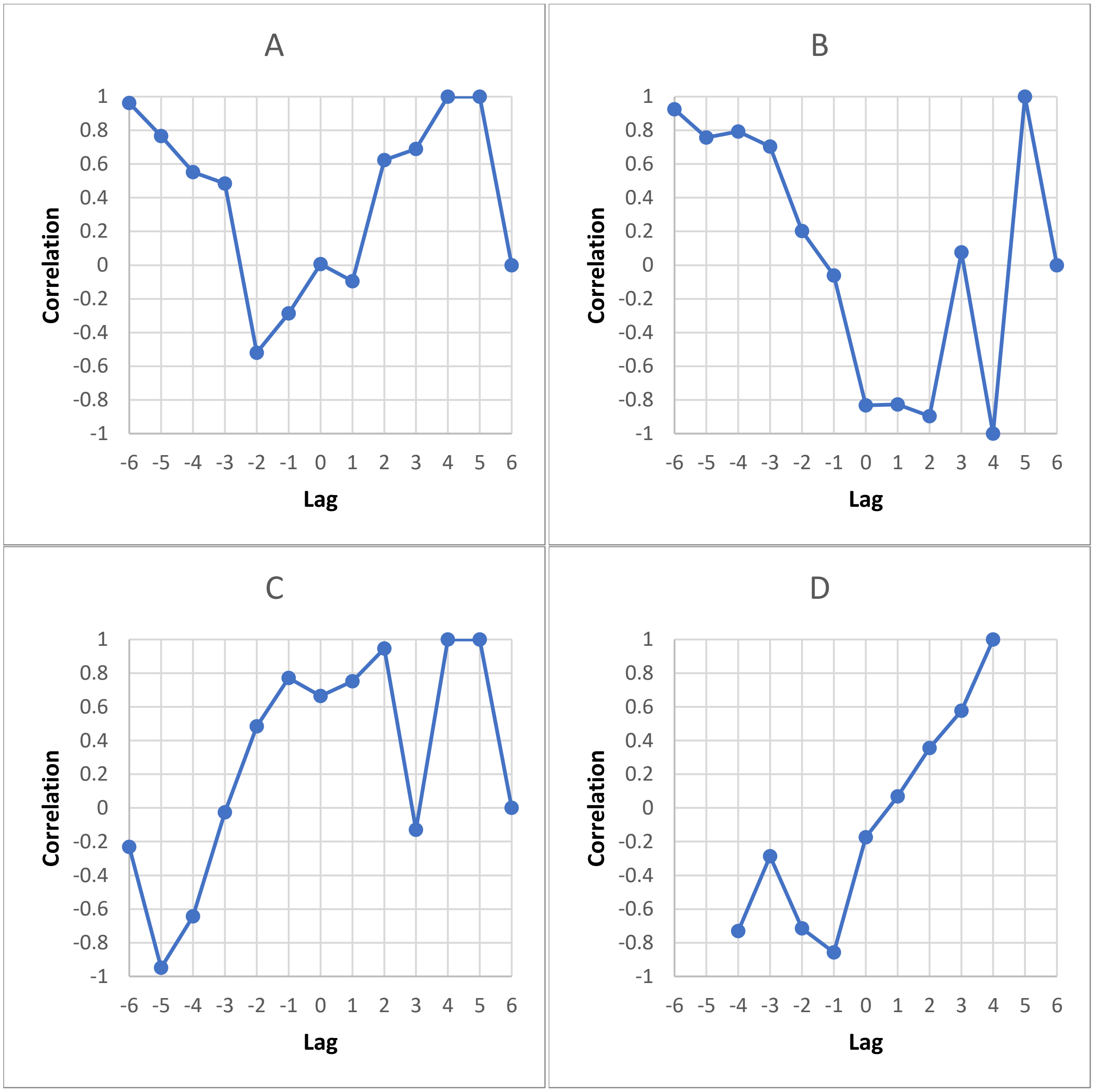

Fig. 35. Mosasaur Origination Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note the strong positive correlations for tropical (A) and arctic (C) $\delta^{13}C$ at lags of +4 and +5 (arctic also at lag +2) and a strong positive correlation for temperate (B) $\delta^{13}C$ at a lag of 5. Strong negative correlations occur for temperate (B) $\delta^{13}C$ at lags of 0, +1, +2, and +4, for arctic (C) $\delta^{13}C$ at a lag of -5, and for deep sea (D) $\delta^{13}C$ at a lag of -1.

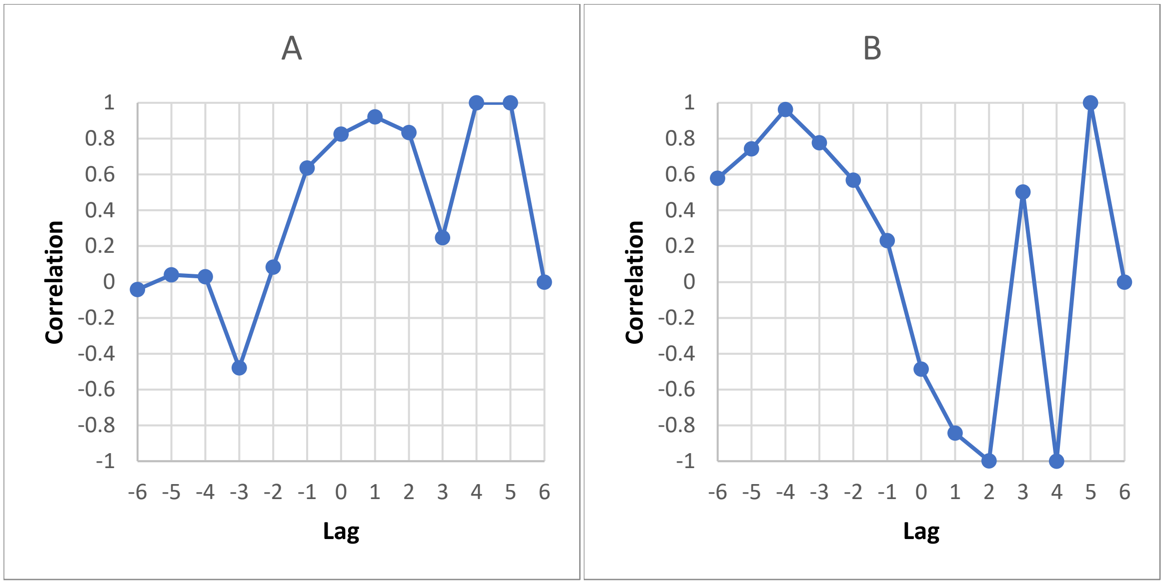

Fig. 36. Mosasaur Origination Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. Note strong positive correlation for $^{87}Sr/^{86}Sr$ (A) at lags of 0, +1, +2, +4 and +5, strong negative correlation for sea level (B) at lags of +1, +2, and +4, and strong positive correlation for sea level (B) at lags of -4 and +5.

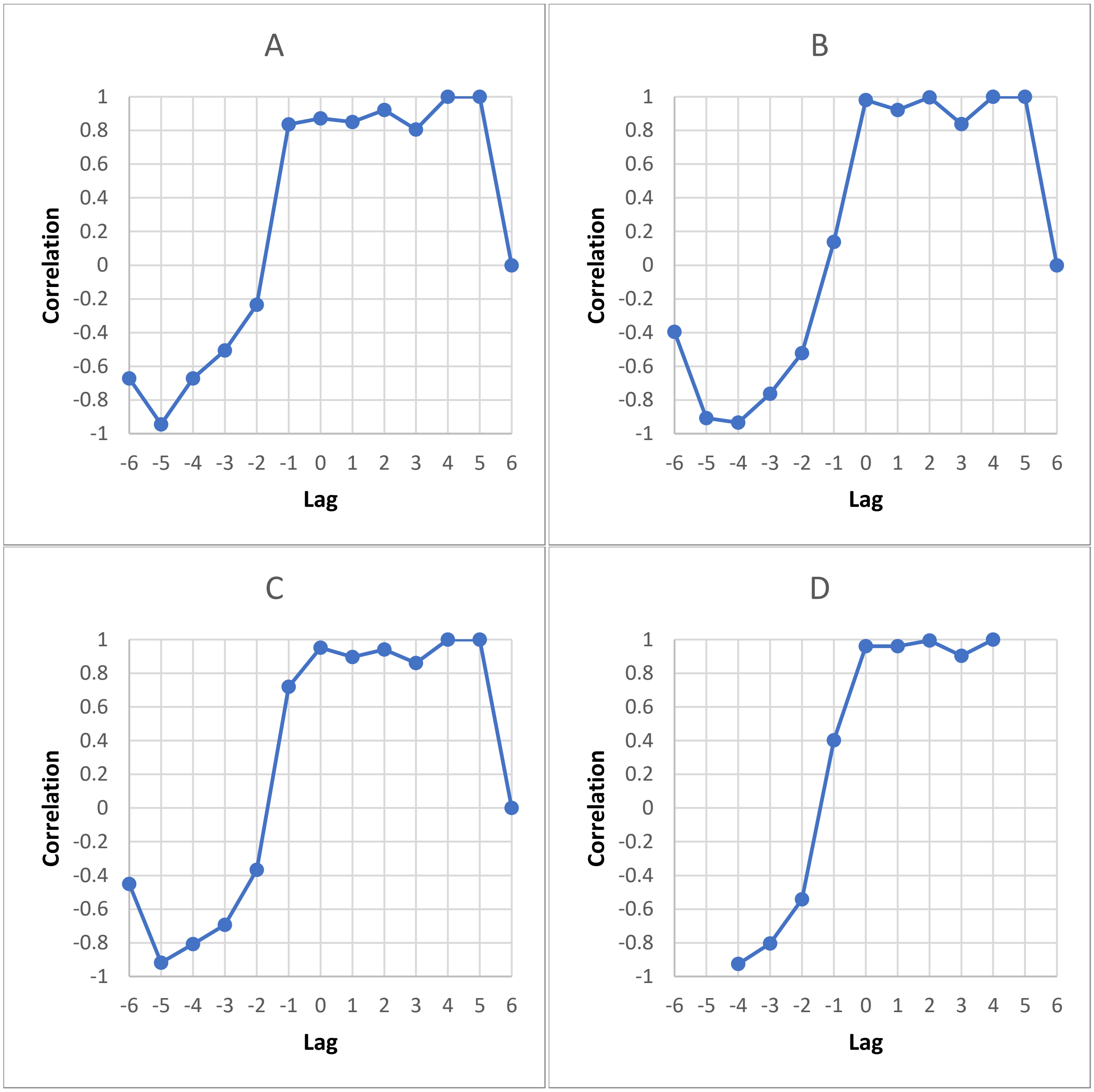

Fig. 37. Mosasaur Extinction Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note consistent strong positive correlations for tropical (A), temperate (B) and arctic (C) $\delta^{18}O$ spanning lags 0 to 5. Negative correlations are observed in the tropical, temperate, arctic, and deep sea records at lags of -5, -5 and -4, -5, and -3, respectively.

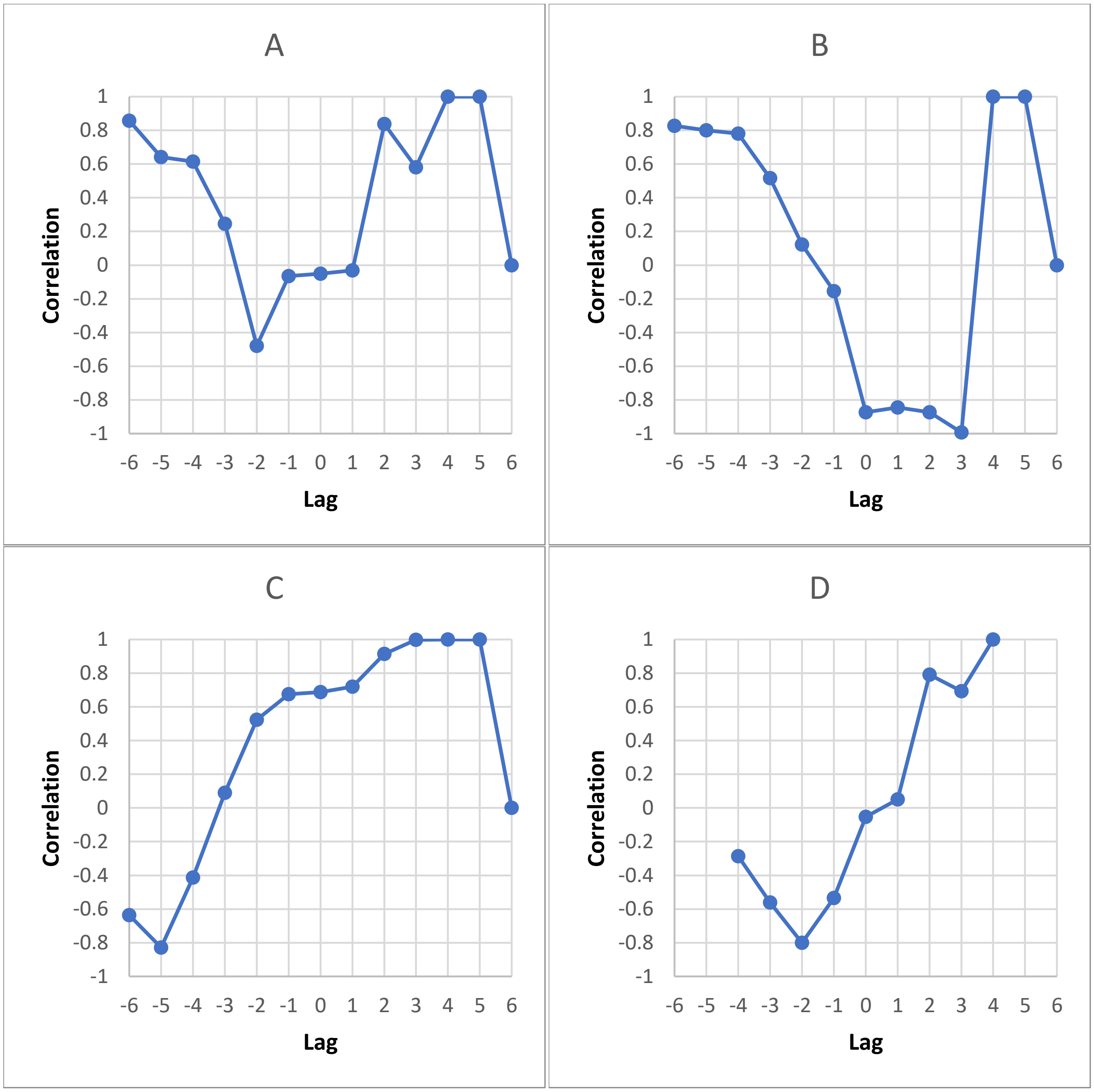

Fig. 38. Mosasaur Extinction Cross-Correlated with δ^{13}C. δ^{13}C values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note strong positive correlation for tropical (A), temperate (B) and arctic (C) δ^{13}C at lags of +4 and +5 (also at +2 for tropical and +2 and +3 for arctic), and strong negative correlation for temperate (B) δ^{13}C at lag 0 through +3 and arctic (C) at lag -5.

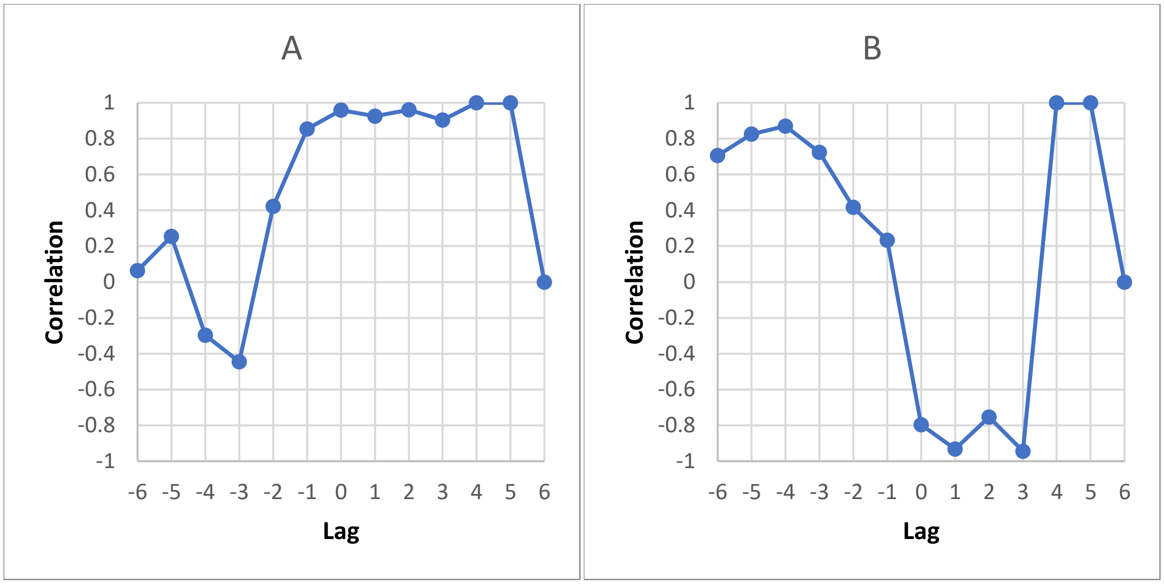

Fig. 39. Mosasaur Extinction Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. Note strong positive correlation for $^{87}Sr/^{86}Sr$ (A) at lags of 0-5, and for sea level at lags -5, -4, +4 and +5, while a strong negative correlation exists for sea level (B) at lags of +1 and +3.

Origination and extinction time series for plesiosaurs was cross correlated with $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$ and sea level (Figs. 40-45). Plesiosaurs had many fewer significant correlations than the other marine reptile groups. For origination, plesiosaurs show a strong positive correlation with tropical $\delta^{18}O$ at a lag of +5. There is also a strong positive correlation with arctic $\delta^{13}C$ at a lag of +4. For extinction, plesiosaurs show no correlations with $\delta^{18}O$. There are strong positive correlations for tropical, arctic and deep sea $\delta^{13}C$ at a lag of +5. Finally, there is a strong positive correlation with $^{87}Sr/^{86}Sr$ at a lag of +5.

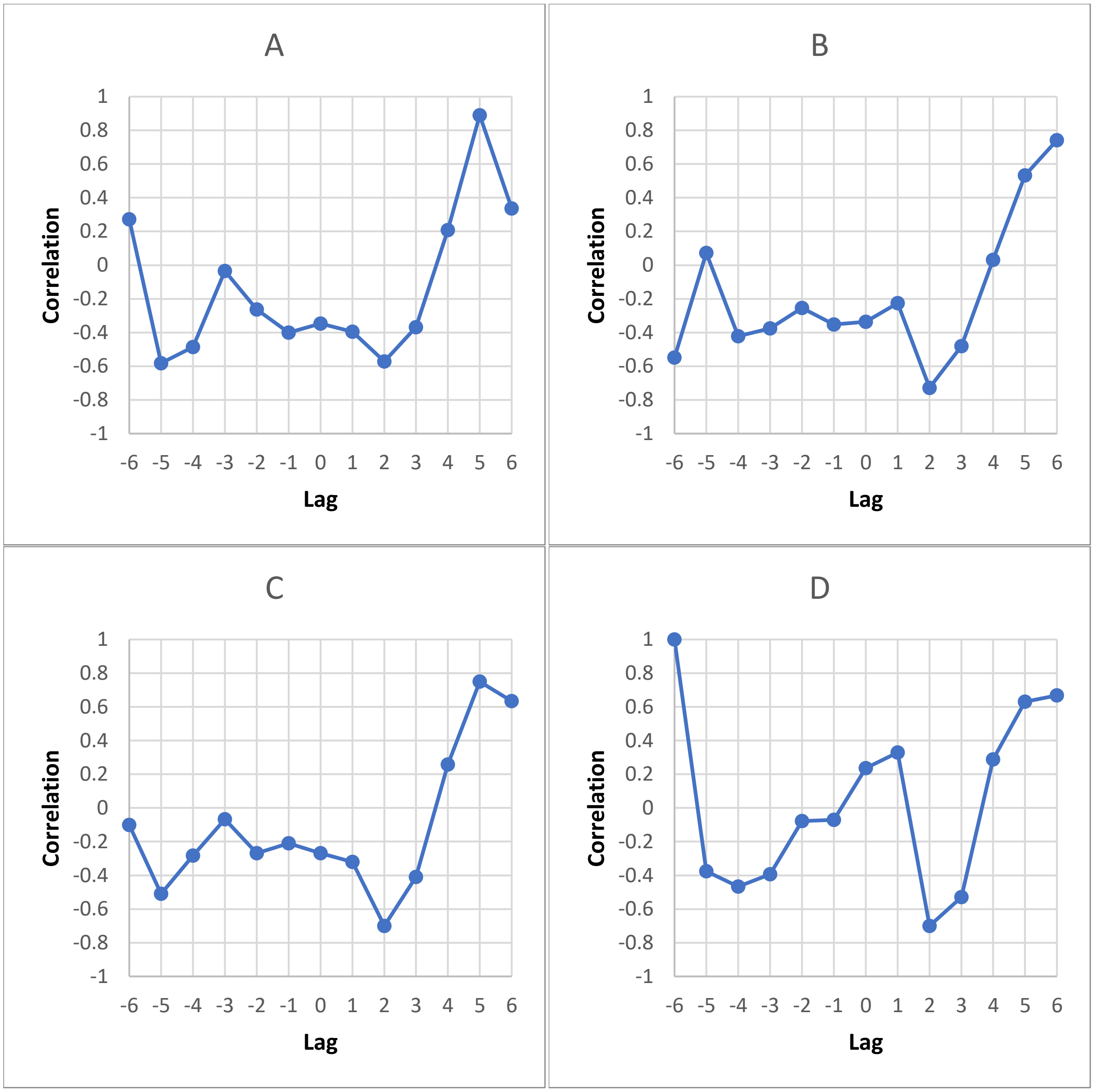

Fig. 40. Plesiosaur Origination Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). No correlations greater than ±0.8 are observed, except for the tropical record at a lag of +5.

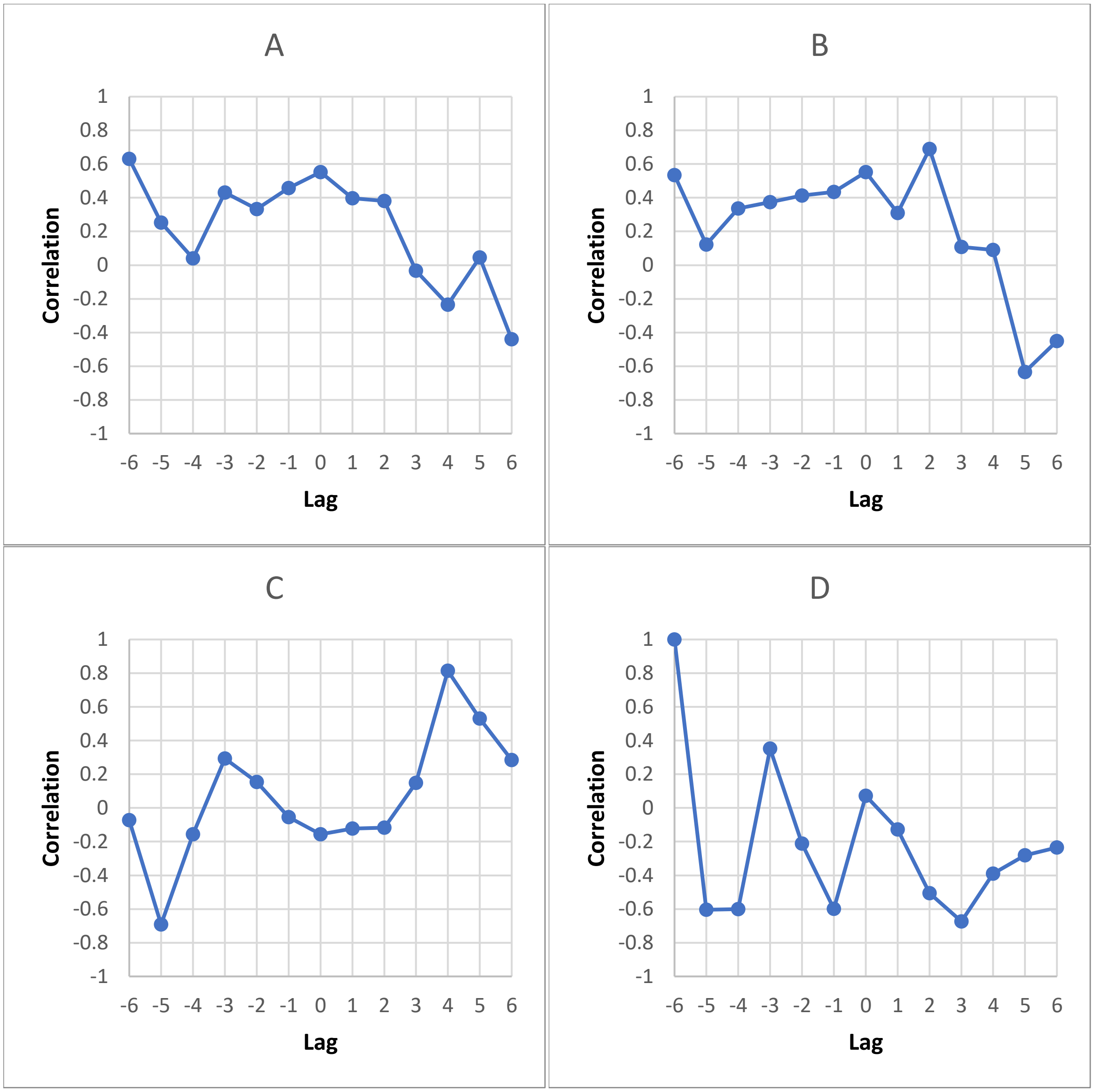

Fig. 41. Plesiosaur Origination Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Note the strong positive correlation with the arctic $\delta^{13}C$ record at a lag of +4.

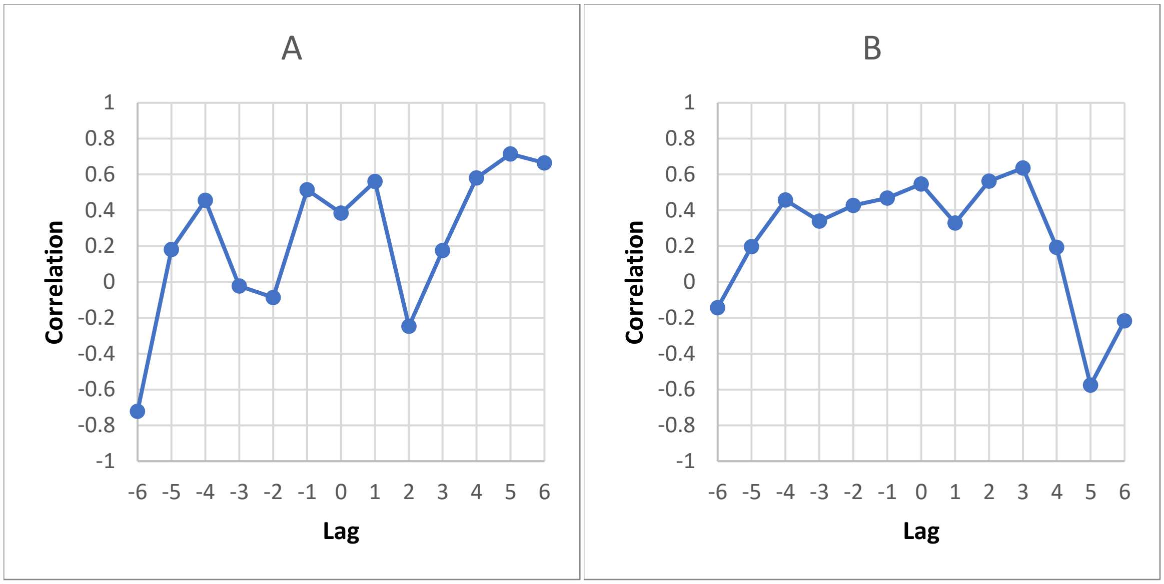

Fig. 42. Plesiosaur Origination Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. $^{87}Sr/^{86}Sr$ (A) and seal level (B) show no strong correlations.

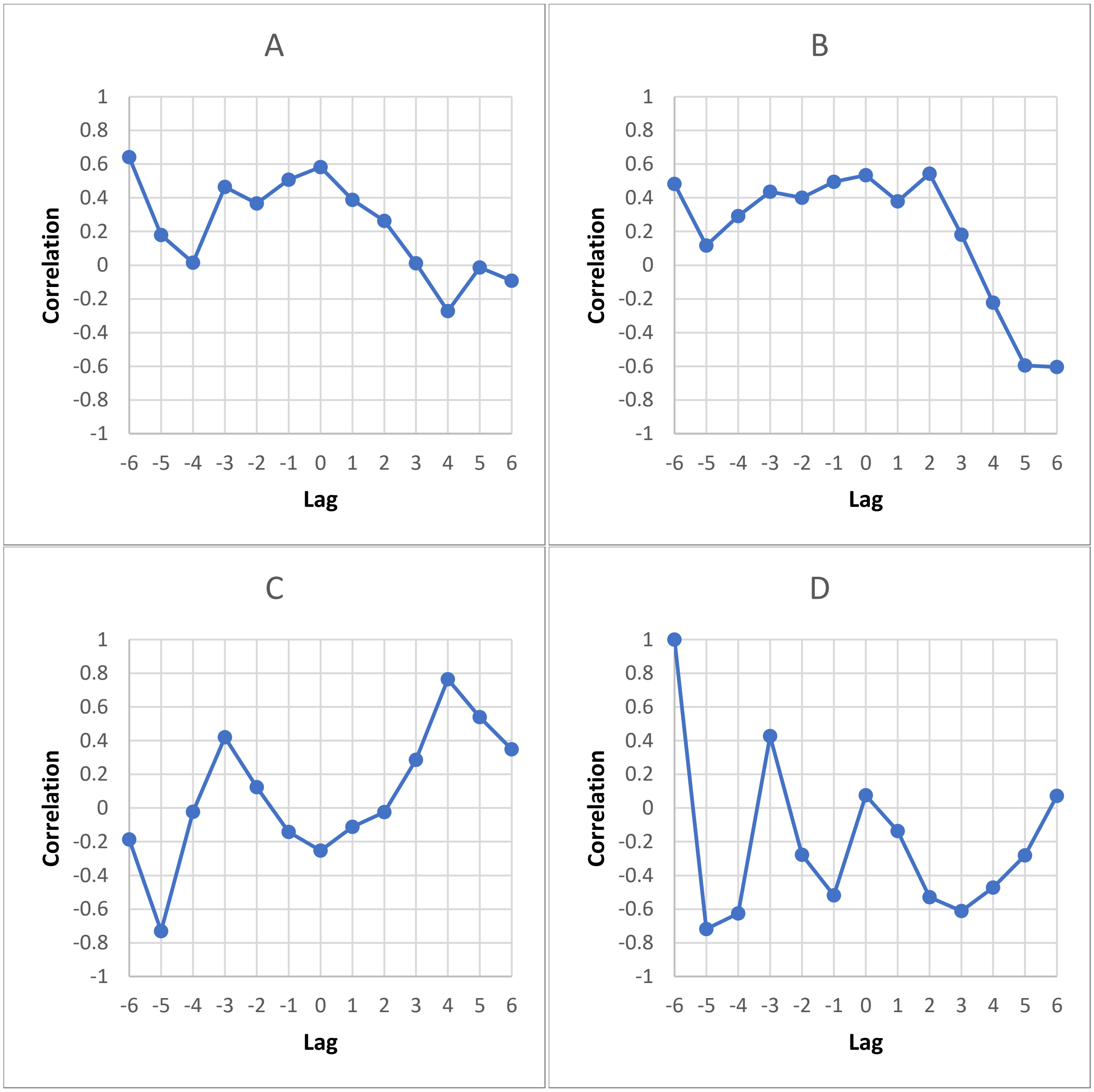

Fig. 43. Plesiosaur Extinction Cross-Correlated with $\delta^{18}O$. $\delta^{18}O$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). No correlations exceeding ±0.8 are observed.

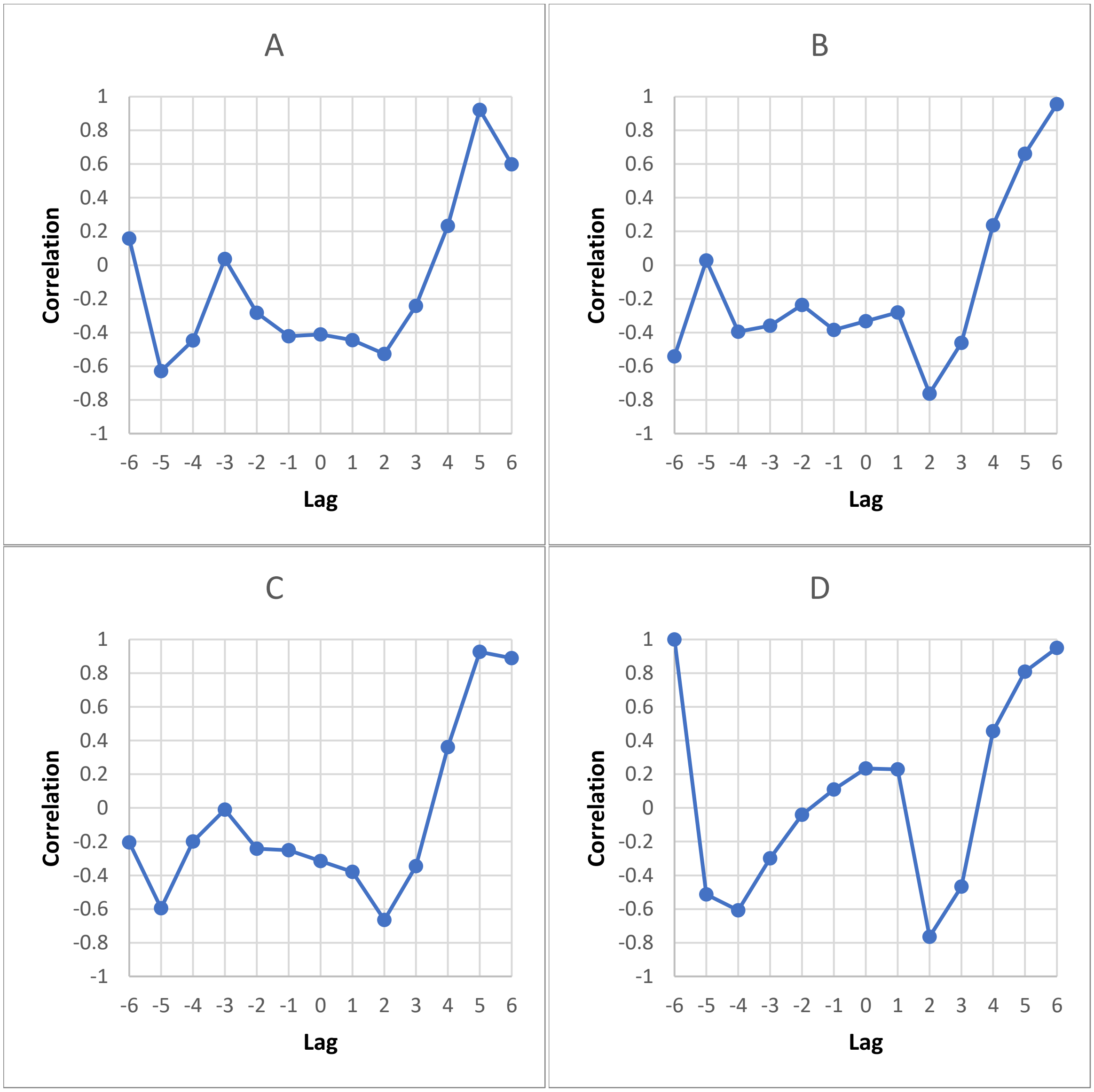

Fig. 44. Plesiosaur Extinction Cross-Correlated with $\delta^{13}C$. $\delta^{13}C$ values for tropical (A), temperate (B), arctic (C) and deep sea (D). Strong positive correlation with tropical, arctic and deep sea records are observed at a lag of +5.

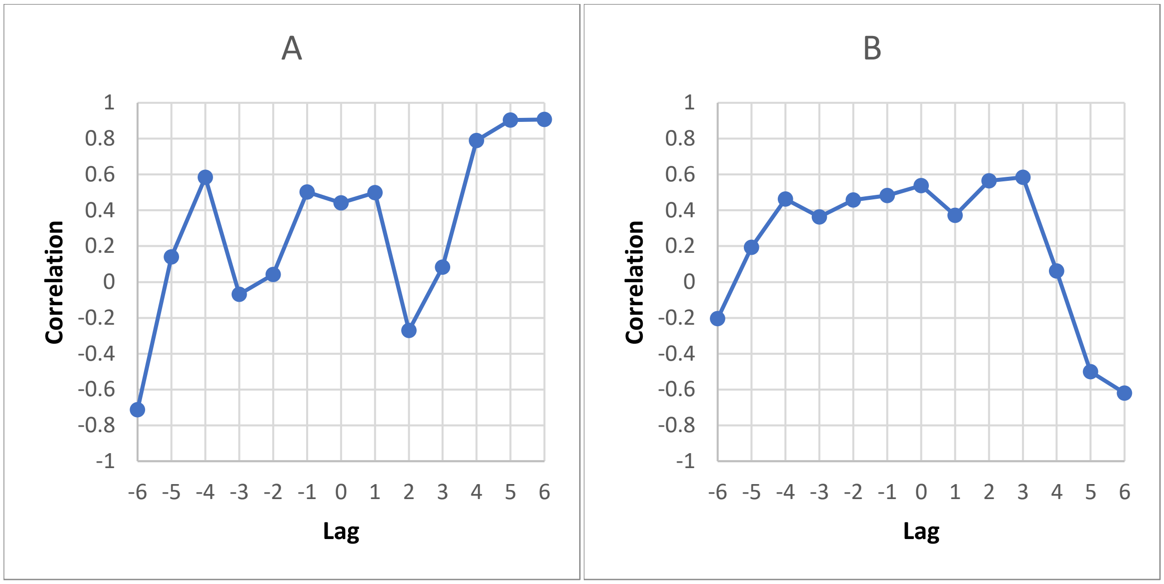

Fig. 45. Plesiosaur Extinction Cross-Correlated with $^{87}Sr/^{86}Sr$ and Sea Level. $^{87}Sr/^{86}Sr$ (A) and sea level (B) showing no strong correlations.

Table 16. Summary of Cross-Correlations between Diversity and Turnover Metrics and Environmental Proxies.

Group	Metric	Proxy	Positive Correlation at Lag Size =	Negative Correlation at Lag Size =
All marine reptiles	Rarified species diversity	$\delta^{18}O$ - tropical	none	none
		$\delta^{18}O$ - temperate	none	none
		$\delta^{18}O$ - arctic	none	none
		$\delta^{18}O$ - deep sea	+5	none
		$\delta^{13}C$ - tropical	none	none
		$\delta^{13}C$ - temperate	none	none
		$\delta^{13}C$ -arctic	none	none
		$\delta^{13}C$ - deep sea	+5	**+1**, +4
		$^{87}Sr/^{86}Sr$	none	none
		Sea level	none	none
Ichthyosaurs	Rarified species diversity	$\delta^{18}O$ - tropical	-5, -4, +4	**0**
		$\delta^{18}O$ - temperate	-5	-1
		$\delta^{18}O$ - arctic	-5, +4, +5	-1, **0**
		$\delta^{18}O$ - deep sea	+3	-1
		$\delta^{13}C$ - tropical	-6, -5, -4	-2
		$\delta^{13}C$ - temperate	none	-5, -3
		$\delta^{13}C$ -arctic	-5, +5	**+1**
		$\delta^{13}C$ - deep sea	none	-2
		$^{87}Sr/^{86}Sr$	-5	-1
		Sea level	none	+5
	Origination	$\delta^{18}O$ - tropical	none	+5
		$\delta^{18}O$ - temperate	none	+5
		$\delta^{18}O$ - arctic	none	+5
		$\delta^{18}O$ - deep sea	none	none
		$\delta^{13}C$ - tropical	none	**+1**, +5
		$\delta^{13}C$ - temperate	+5	none
		$\delta^{13}C$ -arctic	none	+5
		$\delta^{13}C$ - deep sea	+3	**+1**
		$^{87}Sr/^{86}Sr$	none	**+5**
		Sea level	+5	**+4**
	Extinction	$\delta^{18}O$ - tropical	**0**	+5
		$\delta^{18}O$ - temperate	+3	-4, +5
		$\delta^{18}O$ - arctic	none	+5
		$\delta^{18}O$ - deep sea	none	none
		$\delta^{13}C$ - tropical	-3	+5
		$\delta^{13}C$ - temperate	-3, +5	**+1**, +4
		$\delta^{13}C$ -arctic	**+1**, +4	+5
		$\delta^{13}C$ - deep sea	none	-2
		$^{87}Sr/^{86}Sr$	+4	-3, -5
		Sea level	-5, -4, +5	+4

Table 16, continued

Group	**Metric**	**Proxy**	**Positive Correlation at Lag Size =**	**Negative Correlation at Lag Size =**
Mosasaurs	Rarified species diversity	$\delta^{18}O$ - tropical $\delta^{18}O$ - temperate $\delta^{18}O$ - arctic $\delta^{18}O$ - deep sea	-5, -4 -5, -4 -5, -4 none	none none none none
		$\delta^{13}C$ - tropical $\delta^{13}C$ - temperate $\delta^{13}C$ -arctic $\delta^{13}C$ - deep sea	-5, -4 -5, 1 -5, -4 none	-1 -4 none none
		$^{87}Sr/^{86}Sr$	-5, -4	none
		Sea level	+5	+4
	Origination	$\delta^{18}O$ - tropical $\delta^{18}O$ - temperate $\delta^{18}O$ - arctic $\delta^{18}O$ - deep sea	**0**, **+1**, +4, +5 **0**, **+1**, +4, +5 **0**, **+1,** +4, +5 **+1**, +2	-5, -4 -4, -3 -5, -4 -4, -3
		$\delta^{13}C$ - tropical $\delta^{13}C$ - temperate $\delta^{13}C$ -arctic $\delta^{13}C$ - deep sea	+4, +5 +5 +2, +4,+5 none	none **0**, **+1**, +2, +4 -5 -1
		$^{87}Sr/^{86}Sr$	**0**, **+1**, +2, +4, +5	none
		Sea level	-4, +5	**+1**, +2, +4
	Extinction	$\delta^{18}O$ - tropical $\delta^{18}O$ - temperate $\delta^{18}O$ - arctic $\delta^{18}O$ - deep sea	-1, **0**, **+1**, +2, +4, +5 **0**, **+1**, +2, +3, +4, +5 **0**, **+1**, +2, +3, +4, +5 **0**, **+1**, +2, +3	-5 -5, -4 -5 -3
		$\delta^{13}C$ - tropical $\delta^{13}C$ - temperate $\delta^{13}C$ -arctic $\delta^{13}C$ - deep sea	+2, +4, +5 +4, +5 +2, +3, +4, +5 none	none **0, +1,** +2, +3 -5 none
		$^{87}Sr/^{86}Sr$	-1, **0**, **+1**, +2, +3, +4, +5	none
		Sea level	-5, -4, +4, +5	**+1**, +3

Table 16, continued

Group	**Metric**	**Proxy**	**Positive Correlation at Lag Size =**	**Negative Correlation at Lag Size =**
Plesiosaurs	Rarified species diversity	$\delta^{18}O$ - tropical	none	none
		$\delta^{18}O$ - temperate	none	none
		$\delta^{18}O$ - arctic	none	none
		$\delta^{18}O$ - deep sea	none	none
		$\delta^{13}C$ - tropical	none	none
		$\delta^{13}C$ - temperate	none	none
		$\delta^{13}C$ -arctic	-4	none
		$\delta^{13}C$ - deep sea	none	none
		$^{87}Sr/^{86}Sr$	none	none
		Sea level	none	none
	Origination	$\delta^{18}O$ - tropical	+5	none
		$\delta^{18}O$ - temperate	none	none
		$\delta^{18}O$ - arctic	none	none
		$\delta^{18}O$ - deep sea	none	none
		$\delta^{13}C$ - tropical	none	none
		$\delta^{13}C$ - temperate	none	none
		$\delta^{13}C$ -arctic	+4	none
		$\delta^{13}C$ - deep sea	none	none
		$^{87}Sr/^{86}Sr$	none	none
		Sea level	none	none
	Extinction	$\delta^{18}O$ - tropical	none	none
		$\delta^{18}O$ - temperate	none	none
		$\delta^{18}O$ - arctic	none	none
		$\delta^{18}O$ - deep sea	none	none
		$\delta^{13}C$ - tropical	+5	none
		$\delta^{13}C$ - temperate	none	none
		$\delta^{13}C$ -arctic	+5	none
		$\delta^{13}C$ - deep sea	+5	none
		$^{87}Sr/^{86}Sr$	+5	none
		Sea level	none	none

Lag sizes of +1 or zero (in boldface) indicate the change in the proxy occurred just prior to or within the same stage as the change in the diversity or turnover metric and therefore may be a driver of the metric's change.

Multiple Regression and Random Forest Analysis

All outputs of multiple regressions in PAST are tabulated in supplementary Excel file 3 while all outputs of the multiple regressions are tabulated in supplementary Excel file 4; only the results that showed significance will be discussed below.

For PAST multiple regression, ichthyosaur origination percentages (Table 17) also show a moderate ($p = 0.063$) positive relationship with sea level. Ichthyosaur extinction percentages (Table 18) have a very strong negative correlation with tropical $\delta^{18}O$, tropical $\delta^{13}C$, and arctic $\delta^{13}C$, and a positive correlation with arctic $\delta^{18}O$ and temperate $\delta^{13}C$; a moderate association with sea level ($p = 0.073$) is also observed. Ichthyosaur per capita extinction rates (Table 19) show a strong positive correlation with tropical $\delta^{13}C$ and moderate ($0.05 < p < 0.10$) negative correlations with temperate $\delta^{13}C$ and sea level. Finally, the per-capita extinction rate for plesiosaurs (Table 20) showed a positive correlation with arctic $\delta^{18}O$, and a moderate negative correlation with tropical $\delta^{18}O$ ($p = 0.067$) and temperate $\delta^{18}O$ ($p = 0.062$).

Mosasaurs showed no significant correlations in any of the multiple regressions. A summary of the multiple regression results is provided in Table 21.

Table 17. Ichthyosaur Origination Percentage Multiple Regression.

	p	R	R^2
Origination %	0.287		
Tropical $\delta^{18}O$	0.083	R>0	0.008
Temperate$\delta^{18}O$	0.676	R<0	0.002
Arctic $\delta^{18}O$	0.370	R<0	0.002
Tropical $\delta^{13}C$	0.208	R<0	0.159
Temperate $\delta^{13}C$	0.973	R>0	0.058
Arctic $\delta^{13}C$	0.138	R<0	0.0104
$^{87}Sr/^{86}Sr$	0.287	R>0	0.001
Sea Level	**0.063**	R>0	0.006

Sea level is somewhat positively correlated with origination percentage ($p = 0.063$).

Table 18. Ichthyosaur Extinction Percentage Multiple Regression.

	p	R	R^2
Extinction %	0.167		
Tropical $\delta^{18}O$	**0.012**	R<0	0.491
Temperate $\delta^{18}O$	0.167	R<0	0.170
Arctic $\delta^{18}O$	**0.002**	R>0	0.167
Tropical $\delta^{13}C$	**0.002**	R<0	0.239
Temperate $\delta^{13}C$	**0.001**	R>0	0.407
Arctic $\delta^{13}C$	**0.001**	R<0	0.254
$^{87}Sr/^{86}Sr$	0.167	R>0	0.057
Sea Level	0.073	R<0	0.459

Independent variables showing a significant ($p < 0.05$) relationship with extinction percentage are indicated in boldface. Tropical $\delta^{18}O$ and tropical and arctic $\delta^{13}C$ are negatively correlated with extinction percentage, while arctic $\delta^{18}O$ and temperate $\delta^{13}C$ are positively correlated. Sea level shows a moderate negative association.

Table 19. Ichthyosaur Per-Capita Extinction Multiple Regression.

	p	R	R^2
Per-Capita Extinction	0.136		
Tropical $\delta^{18}O$	0.571	R<0	0.158
Temperate $\delta^{18}O$	0.083	R>0	0.0002
Arctic $\delta^{18}O$	0.592	R<0	0.096
Tropical $\delta^{13}C$	**0.038**	R>0	0.141
Temperate $\delta^{13}C$	0.057	R<0	0.047
Arctic $\delta^{13}C$	0.812	R<0	0.375
$^{87}Sr/^{86}Sr$	0.136	R<0	0.001
Sea Level	0.084	R>0	0.055

Independent variables showing a significant ($p < 0.05$) relationship with per-capita extinction rate are indicated in boldface. Tropical $\delta^{13}C$ is positively correlated with extinction. Temperate $\delta^{13}C$ (negative, $p = 0.057$) and temperate $\delta^{18}O$ and sea level (positive, $p = 0.083$, 0.084) are moderately associated with per-capita extinction rate.

Table 20. Plesiosaur Per-Capita Extinction Multiple Regression.

	p	R	R^2
Per-Capita Extinction	0.406		
Tropical $\delta^{18}O$	0.067	R<0	0.040
Temperate $\delta^{18}O$	0.062	R<0	0.0002
Arctic $\delta^{18}O$	**0.014**	R>0	0.008
Tropical $\delta^{13}C$	0.478	R<0	0.004
Temperate $\delta^{13}C$	0.997	R>0	0.002
Arctic $\delta^{13}C$	0.112	R<0	0.071
$^{87}Sr/^{86}Sr$	0.406	R<0	0.005
Sea Level	0.701	R<0	0.037

Independent variable showing a significant ($p < 0.05$) relationship with per-capita extinction rate is indicated in boldface. Arctic $\delta^{18}O$ is positively correlated with per-capita extinction rate. Tropical and temperate $\delta^{18}O$ show moderate negative correlations with per-capita extinction rate ($p = 0.067$, 0.062).

Table 21. Summary of Multiple Regression Results.

Proxy	Positive Correlation With:	Negative Correlation With:
Tropical $\delta^{18}O$	---	Ichthyosaur extinction percentage
Temperate $\delta^{18}O$	---	---
Arctic $\delta^{18}O$	Ichthyosaur extinction percentage Plesiosaur per-capita extinction rate	---
Tropical $\delta^{13}C$	Ichthyosaur per-capita extinction rate	Ichthyosaur extinction percentage ---
Temperate $\delta^{13}C$	Ichthyosaur extinction percentage ---	---
Arctic $\delta^{13}C$	---	Ichthyosaur extinction percentage
$^{87}Sr/^{86}Sr$	---	---
Sea Level	---	---

Proxies with significant ($p < 0.05$) correlations to diversity and turnover metrics are tabulated. Mosasaurs showed no significant correlations.

Multiple Regression was also performed in R, the only significant values are for plesiosaur diversity, percent origination and extinction. Plesiosaur diversity (Table 22) is predicted strongly for both tropical $\delta^{18}O$ (p=0.0255) and arctic $\delta^{13}C$ (p=0.0256) while percent origination (Table 23) is predicted strongly by all $\delta^{18}O$ values (p=0.001, 0.002, 0.001) along with tropical and temperate $\delta^{13}C$ (p=0.001) and $^{87}Sr/^{86}Sr$ (p=0.005). Finally, percent extinction (Table 24) of plesiosaurs is predicted most strongly by arctic $\delta^{18}O$ (p=0.488) and $^{87}Sr/^{86}Sr$ (p=0.261).

AIC values for each of the independent variables were also calculated to assess the strength of the model in relation to the variables (Table 25). For plesiosaur diversity tropical $\delta^{18}O$ is the strongest model factor while arctic $\delta^{13}C$ is the strongest model for percent originate and finally temperate $\delta^{18}O$ is the strongest model for percent extinct.

Table 22. Plesiosaur Diversity Multiple Regression in R.

Plesiosaur Diversity				
	Estimate	Std. Error	t value	p value
Tropical $\delta^{18}O$	4.3010	1.0380	4.1450	**0.0255**
Temperate $\delta^{18}O$	1.1690	0.5998	1.9490	0.1464
Arctic $\delta^{18}O$	-3.5400	1.0350	-3.4220	0.0418
Tropical $\delta^{13}C$	-0.9242	0.5681	-1.6270	0.2022
Temperate $\delta^{13}C$	1.8490	1.2400	1.4910	0.2328
Arctic $\delta^{13}C$	-1.7770	0.4291	-4.1420	**0.0256**
$^{87}Sr/^{86}Sr$	4984.0000	2950.0000	1.6900	0.1896
Sea Level	0.0468	0.0143	3.2840	0.0463

Independent variables showing a significant ($p < 0.05$) relationship with diversity is indicated in boldface. Both Tropical $\delta^{18}O$ and Arctic $\delta^{13}C$ are considered significant towards predicting plesiosaur diversity.

Table 23. Plesiosaur Origination Percentage Multiple Regression in R.

Plesiosaur Origination Percentage				
	Estimate	Std. Error	t value	p value
Tropical $\delta^{18}O$	43.970	3.456	12.723	**0.001**
Temperate $\delta^{18}O$	20.100	1.998	10.059	**0.002**
Arctic $\delta^{18}O$	-55.600	3.446	-16.135	**0.001**
Tropical $\delta^{13}C$	-30.260	1.892	-15.993	**0.001**
Temperate $\delta^{13}C$	58.440	4.130	14.152	**0.001**
Arctic $\delta^{13}C$	-1.421	1.429	-0.994	0.393
$^{87}Sr/^{86}Sr$	71070.000	9824.000	7.234	**0.005**
Sea Level	0.110	0.048	2.317	0.103

Independent variables showing a significant ($p < 0.05$) relationship with origination percentage is indicated in boldface. Plesiosaur Origination Percentage most likely predicted by tropical, temperate and arctic $\delta^{18}O$ along with tropical and temperate $\delta^{13}C$ and $^{87}Sr/^{86}Sr$.

Table 24. Plesiosaur Extinction Percentage Multiple Regression in R.

Plesiosaur Extinction Percentage				
	Estimate	Std. Error	t value	p value
Tropical $\delta^{18}O$	14.070	33.950	0.414	0.706
Temperate $\delta^{18}O$	-4.284	19.630	-0.218	0.841
Arctic $\delta^{18}O$	-26.720	33.850	-0.789	**0.488**
Tropical $\delta^{13}C$	4.349	18.590	0.234	0.830
Temperate $\delta^{13}C$	-2.982	40.570	-0.074	0.946
Arctic $\delta^{13}C$	-5.098	14.040	-0.363	0.741
$^{87}Sr/^{86}Sr$	133500	96510.000	1.383	**0.261**
Sea Level	-0.321	0.467	-0.689	0.541

The two independent variables that predict plesiosaur extinction percentage are in boldface, these variables are arctic $\delta^{18}O$ and $^{87}Sr/^{86}Sr$.

Table 25. AIC values for Plesiosaur Multiple Regression.

Plesiosaur AIC Values			
	Diversity	% Originate	% Extinct
Tropical $\delta^{18}O$	**-5.5331**	64.769	72.193
Temperate $\delta^{18}O$	-4.5971	59.259	**71.714**
Arctic $\delta^{18}O$	-4.161	70.387	73.789
Tropical $\delta^{13}C$	-2.3662	70.178	71.742
Temperate $\delta^{13}C$	6.1142	67.28	71.547
Arctic $\delta^{13}C$	6.8908	**18.689**	72.041
$^{87}Sr/^{86}Sr$	10.6715	51.666	77.445
Sea Level	10.6879	28.997	73.286

AIC values of each independent variable calculated in R. Tropical $\delta^{18}O$ is the best strongest value for diversity while arctic $\delta^{13}C$ is for percent originate and finally temperate $\delta^{13}C$ for percent extinct.

The results of the random forests regression analyses indicate that for overall marine reptile diversity, the most important independent variable is arctic $\delta^{13}C$, while for ichthyosaur, mosasaur and plesiosaur species diversity, the most important variable is temperate $\delta^{18}O$ (Table 26). Ichthyosaurs and plesiosaurs are also strongly influenced by arctic $\delta^{13}C$ while mosasaurs are also influenced by tropical $\delta^{18}O$ and tropical $\delta^{13}C$. However, the analyses do not indicate whether the relationship is positive or negative therefore these results only show how predictive the environmental factors, independent variables, are towards marine reptile diversity, the dependent variable. Turning to origination and extinction percentages and per-capita rates (Table 27), ichthyosaur and mosasaur per-capita rates did not have enough values to produce any results and were therefore excluded. Tropical $\delta^{13}C$ is the most important predictor of ichthyosaur origination percentage, while temperate $\delta^{13}C$ and temperate $\delta^{18}O$, respectively, are the most important predictors of mosasaur and plesiosaur origination percentage. Sea level, temperate $\delta^{18}O$, and arctic $\delta^{18}O$ were the most important predictors of, respectively, ichthyosaur, mosasaur, and plesiosaur extinction percentages. Arctic $\delta^{13}C$ has the highest importance value for plesiosaur per-capita origination rate.

Table 26. Marine Reptile Diversity Importance Values.

	Diversity	Ichthyosaurs	Mosasaurs	Plesiosaurs
Tropical $\delta^{18}O$	3.40	0.67	2.00	2.56
Temperate $\delta^{18}O$	**4.49**	**1.30**	**2.12**	**3.47**
Arctic $\delta^{18}O$	1.64	0.83	0.62	2.60
Tropical $\delta^{13}C$	1.15	0.42	**2.10**	1.11
Temperate $\delta^{13}C$	1.34	0.44	1.52	2.16
Arctic $\delta^{13}C$	**8.66**	**0.89**	1.58	**2.99**
$^{87}Sr/^{86}Sr$	1.34	0.23	0.62	0.60
Sea Level	1.62	0.36	0.84	2.21

Largest importance value is for arctic $\delta^{13}C$ as a predictor of overall marine species diversity, and for temperate $\delta^{18}O$ as a predictor of ichthyosaur, mosasaur and plesiosaur diversity.

Table 27. Marine Reptile Origination and Extinction Importance Values.

	Ichthyosaurs		Mosasaurs		Plesiosaurs		
	% originate	% extinct	% originate	% extinct	% originate	% extinct	Per-capita originate
Tropical $\delta^{18}O$	533.26	703.56	79.72	136.47	167.87	294.46	0.006
Temperate $\delta^{18}O$	282.62	410.31	36.59	**202.58**	**289.47**	201.61	0.004
Arctic $\delta^{18}O$	280.00	715.66	48.93	120.63	139.12	**546.26**	0.012
Tropical $\delta^{13}C$	**1472.74**	240.64	40.86	74.45	240.47	348.65	0.005
Temperate $\delta^{13}C$	839.46	619.69	123.33	138.86	187.69	204.45	0.006
Arctic $\delta^{13}C$	290.55	733.78	**125.68**	136.55	157.93	431.70	**0.013**
$^{87}Sr/^{86}Sr$	700.04	205.71	54.71	118.28	220.13	303.82	0.011
Sea Level	595.11	**924.56**	43.48	171.39	237.85	237.89	0.002

Highest importance values for each turnover metric are indicated in boldface. These represent the proxy most predictive of the turnover metric.

DISCUSSION

Hypothesis 1 predicted that during times of lower sea level, ocean anoxia and/or lower temperatures, marine reptile diversity would have decreased. Overall diversity for all the cross-correlation analyses only shows a negative correlation with deep ocean anoxia. However, since the deep-sea record is not as extensive for carbon, this correlation can be discounted. Therefore, overall marine reptile diversity, origination and extinction are not influenced by the environmental factors used in cross-correlation. Hence, for overall marine reptile diversity, the first hypothesis is not supported. Ichthyosaur diversity seems to drop under the influence of both tropical and arctic cooling along with arctic anoxia. These correlations show that for ichthyosaurs, the first hypothesis is supported. Ichthyosaur origination also seems to decrease during times of anoxia in tropical regions while ichthyosaur extinction has a mixed signal for anoxia. Ichthyosaur extinction decreased during times of anoxia in temperate areas while it seems to have increased during times of cooling in tropical areas along with anoxia in arctic areas. However, it should be noted that the majority of ichthyosaur specimens were recovered in a temperate climate zone, followed by the arctic zone (Table 13). Mosasaur diversity only shows an increase during a time of anoxia in temperate climates but origination and extinction seem to be influenced greatly by environmental factors. For mosasaur diversity, the first hypothesis is therefore not supported. Mosasaur origination and extinction both increased during times of cooling for all climate zones while decreasing during times of anoxia in temperate zones along with decreasing during times of sea level fall. Finally, plesiosaur diversity, origination and extinction do not seem to be influenced in any way by the environment, showing no strong cross-correlations at all. The first hypothesis is therefore not supported for plesiosaur diversity when looking at the cross-correlations, further tests show some support. However, it is very interesting that plesiosaurs show no correlations between diversity metrics and environmental proxies. The reason for this is likely because other factors caused plesiosaur diversity to change. One possibility may be the extinction of ichthyosaurs causing a diversification in plesiosaurs in the early Late Cretaceous, while later the rise of mosasaurs caused a decrease in plesiosaurs.

Multiple regression in PAST showed some results for both ichthyosaurs and plesiosaurs. Ichthyosaur multiple regression shows that the extinction percentage decreased due to cooling and anoxia, cooling in tropical zones and anoxia in tropical and arctic zones. Ichthyosaur extinction percentages also increased due to cooling and anoxia, the cooling being in arctic zones and the anoxia being in temperate zones. For ichthyosaurs the majority of the specimens were found to be in areas that were once temperate zones, with arctic zones making up the next sizable amount, and tropical zones comprising a small percentage of ichthyosaur localities. This means that of the two contradicting instances in cooling, the arctic cooling was probably the greater influence on these specimens, therefore, ichthyosaur extinction percentages likely increased due to cooling. The anoxia correlations are more mixed and seem to indicate that ichthyosaur extinction percentages were increased or decreased depending on the location. Finally, plesiosaur per-capita extinction rate shows increases due to cooling and anoxia. Mosasaurs did not show any correlation to environmental factors from multiple regression. Multiple regression done in R showed that plesiosaur diversity was most likely influenced negatively by anoxia and temperature. Because of this Hypothesis 1 is supported for plesiosaurs.

Random forest analyses indicate the importance of one environmental factor over another. Overall marine reptile diversity was predicted largely by arctic anoxia and temperate cooling. Ichthyosaur diversity was influenced largely by temperate cooling and arctic anoxia while mosasaur diversity was predicted by temperate cooling but also tropical cooling and tropical anoxia. Finally, plesiosaur diversity was influenced largely by temperate cooling and arctic anoxia. These values did not indicate positivity or negativity and therefore only show how likely it is that one environmental factor would influence the diversity of each marine reptile group. Importance values for origination and extinction show which environmental factors are most predictive for each marine reptile group. Ichthyosaur origination is predicted strongly by tropical anoxia while extinction is predicted strongly by sea level. Mosasaur origination is predicted strongly by temperate anoxia while extinction is predicted strongly by temperate cooling. Finally, plesiosaur extinction is predicted strongly by temperate cooling, extinction by arctic cooling and per-capita origination by arctic anoxia. The random forest analysis indicates that for all marine reptile groups, ocean cooling in temperate zones is the strongest influencer on their diversity. This conclusion is supported by the fact that the majority of the specimens for each group were found to have lived in temperate zones. Origination and extinction importance values for ichthyosaurs and mosasaurs do not correlate with the multiple regression values for either group. Plesiosaur importance values for origination and extinction do correlate with the multiple regression values and therefore these results from the random forest tests are the supported ones.

Hypothesis 2 predicted that intervals with faster rates of environmental change would be associated with reductions in marine reptile diversity. The stages with the overall faster rates of environmental change were the Barremian, Aptian and Albian (4,5, and 6). Mosasaurs were not present during these three stages and therefore would not have had any diversity increases or decreases. Ichthyosaur diversity during these stages was notable high and low, high during stage 4 and low during stage 6. Plesiosaurs also had diversity that was both high and low during these stages, notably low during stage 4 and notably high during stage 6, the opposite of ichthyosaurs.

The results for ichthyosaurs could be interpreted as low diversity being a result at the end of these three stages of environmental volatility, since the diversity started high and ended low. This pattern supports Hypothesis 2 for ichthyosaurs. Plesiosaurs, however, do not seem to have diversity highs and lows that link to environmental volatility and therefore Hypothesis 2 is not borne out for plesiosaurs.

Hypothesis 3 sought to test whether diversity decreases would be associated with elevated extinction and/or decreased origination rates. Ichthyosaurs show mirrored results, for one stage when diversity decreased, both origination and extinction also decreased, while for another stage of decreased diversity, both origination and extinction increased. These results do not unambiguously support Hypothesis 3. Mosasaurs show overall extinction increase during times of diversity decrease with mixed results of increasing and decreased origination. These results seem to support Hypothesis 3 for mosasaurs, with diversity drops driven by elevated extinction and not a failure to originate. For all stages of decreasing diversity, except one, plesiosaurs show both decreasing origination and extinction. The overwhelming decrease in origination during times of diversity decrease supports Hypothesis 3, but unlike for mosasaurs, diversity decreases appear to have been driven by a failure to originate new species rather than heightened extinction of existing species.

Relating these observations to known facts about marine reptiles include how ichthyosaurs and plesiosaurs reproduce. Ichthyosaurs were typical of reptiles meaning that they were r selected for reproducing. R selected for reproducing means that ichthyosaurs had multiple offspring with the intention to get as many offspring alive and to adulthood as possible with a lot of those offspring also dying early. Plesiosaurs were believed to be K selected for breeding meaning that they have only one offspring at a time and take time caring for their offspring until adulthood. K selected species tend to dominate for the group during times of stability while r selection grow during times of volatility and extinction. Ichthyosaurs, the r selected group, were reacting negatively to the volatility of the environment during the Cretaceous while also experiencing an extinction event in the late Cretaceous. Plesiosaurs, that did not have any correlations in the cross-correlation analyses were K selected breeders indicating that they were reacting just fine to the environmental factors during the Cretaceous.

CONCLUSION

In this thesis, three hypotheses addressing Cretaceous marine reptile diversity dynamics in light of environmental changes were tested: 1) that during times of lower sea level, ocean anoxia, and/or lower temperatures, marine reptile diversity decreased; 2) that times with faster rates of environmental change were associated with reductions in marine reptile diversity; and 3) that these diversity decreases were associated with either elevated extinction and/or decreased origination rates.

Ichthyosaurs and plesiosaurs show some indication of Hypothesis 1 being supported. During times of cooling and anoxia, ichthyosaur diversity decreased. For plesiosaurs, diversity also decreased during times of anoxia. On the other hand, mosasaur diversity actually increased during times of anoxia, opposite to what Hypothesis 1 predicted. These results indicate that all three marine reptile groups were influenced by ocean anoxia, but negatively in the case of ichthyosaurs and plesiosaurs and positively in the case of mosasaurs.

The second hypothesis is only supported by ichthyosaurs, with diversity declining through the three-stage interval of highest environmental volatility (stages 4-6, Barremian through Albian). The third hypothesis is supported by mosasaurs and plesiosaurs, but in a different way: mosasaur diversity drops are associated with elevated extinction while plesiosaur diversity declines are associated with lower origination rates.

Overall, these results indicate that each marine reptile group was influenced by environmental factors, most notably episodes of anoxia and carbon cycle perturbations, however the volatility of these environmental factors did not have a large influence over marine reptile diversity, or how drastically it changed. Similarly, diversity decreases also were associated slightly with elevated extinction and/or decreased origination for each marine reptile group, except for ichthyosaurs. Clearly the different Cretaceous marine reptile clades responded differently to environmental change.

Further work to be done on this topic would include the application of the tests done during this study to the other periods of the Mesozoic, that is, the Triassic and Jurassic. Overall trends for the Mesozoic may reveal dominant environmental factors that influenced marine reptile diversity. Also, studying the other periods of the Mesozoic would allow for more specimens for each group, excluding mosasaurs, and therefore a larger sample size to draw from. In addition, it seems evident that the different marine reptile clades had unique responses to environmental changes during the Cretaceous. Reasons for these clade-specific patterns need to be explored.

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