



Selective extinction of Triassic marine reptiles during long-term sea-level changes illuminated by seawater strontium isotopes



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ABSTRACT

The relationship between cycles of sea-level change and marine diversity has long been the subject of debate. Large predators may be particularly sensitive to changes in habitat availability and marine productivity driven by changes in sea-level, especially those dependent on nearshore benthic food resources. To test this relationship, we compared the proportional diversity of differing marine reptile ecotypes through the Triassic with the isotopic composition of seawater strontium ($^{87}\text{Sr}/^{86}\text{Sr}$), a geochemical index linked to tectonically controlled sea-level change. The proportional abundance of marine reptiles adapted toward a diet of shelled prey rose during times of rapid sea-level rise and fell during times of rapid sea-level fall, while open water forms were more resistant to these changes. Our results indicate that the rate of sea-level change, rather than the absolute magnitude of sea-level or flooded shelf area, played a role in shaping patterns of ecological diversification and ecologically selective extinction during the Triassic. The link between the isotopic composition of seawater strontium and the evolution of marine reptiles demonstrates that sea-level change played an important role in the structuring of marine ecosystems over geologic time.

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1. Introduction

The fossil record of marine organisms exhibits cyclic variation in species richness that tracks cycles of long-term sea-level fluctuation (Newell, 1952; Miller et al., 2005; Peters, 2005; Smith and McGowan, 2005; Purdy, 2008). This correlation has been interpreted as evidence of direct influence of sea-level on marine diversity (Hallam and Wignall, 1999) via changes in shallow shelf area or environmental conditions during times of sea-level fluctuation. Alternatively, these correlations have been argued to arise due to major geologic bias in the fossil record linked to temporal variation in rock volume or preservation potential driven by sea-level change (Smith, 2001; Crampton et al., 2003; Uhen and Pyenson, 2007).

Distinguishing geologic bias from the direct influence of sea-level is challenging when only raw taxon counts are considered. Comparison of diversity patterns among organisms adapted to differing habitat preferences or trophic niches (i.e., ecotype) presents one means to test the direct influence of sea-level change on marine ecosystems. The proportion of a given ecotype expressed as a ratio relative to total diversity within a given time interval is less sensitive to fluctuations in fossil richness than simple taxon counting. The underlying presumption is that taxon

counts of different ecotypes share at least some similar geologic bias that cancel out through division. Comparison between groups of differing feeding strategies or habitat preferences can help reveal the influence of sea-level change on marine diversity because nearshore and pelagic taxa may differ in their sensitivity to sea-level change (Kiessling and Aberhan, 2007).

While studies of fossil diversity have tended to focus on invertebrates, there are reasons to examine patterns in marine vertebrates when considering the effects of sea-level change. Large vertebrate predators are thought to play an important role in structuring modern marine ecosystems (Heithaus et al., 2008) and are sensitive indicators of environmental perturbations at regional to global scales (Veit et al., 1997; Reid and Croxall, 2001). While sharks, teleosts, seabirds, and marine mammals are the dominant large predators in modern ocean ecosystems, a diverse assemblage of reptile groups occupied the top trophic tiers in many Mesozoic marine ecosystems (Massare, 1988). These marine tetrapod groups, and their mammalian, avian and reptilian counterparts in the Cenozoic, offer an opportunity to examine the influence of physical changes in the marine environment, including sea-level change, on changes in the structure of marine ecosystems over time.

A recent survey of the Mesozoic marine tetrapod fossil record (Benson et al., 2010) found that observed species diversity over the entire Mesozoic era showed a strong correlation with rock volume, while Lagerstätten effects (intervals with anomalously rich records due to exceptional fossil preservation) and mass extinctions explained short-term departures

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from this underlying trend. The correlation between marine tetrapod diversity and the rock record could reflect geologic bias, parallel effects on rock volume and marine diversity driven by changes in sea-level (the common-cause hypothesis of Peters, 2005) or some combination of these two mechanisms. Understanding the underlying geologic causes and consequences of sea-level change is a prerequisite for any attempt to disentangle the direct and indirect influences of sea-level on marine ecosystems and the fossil record.

Both climate change (e.g., the wax and wane of ice sheets) and tectonics (e.g., the changes in sea-floor spreading rate) can drive large amplitude eustatic sea-level change. These two mechanisms differ markedly in their rates, with climate driving much more rapid ($\leq 10^6$ -year) sea-level change than tectonics ($\geq 10^6$ -year) (Miller et al., 2005). The greenhouse conditions of the Mesozoic are thought to have inhibited the growth of large ice sheets (Hallam, 1985), although some relatively rapid, high-amplitude sea-level fluctuations suggest the presence of transient ice in the Cretaceous (Miller et al., 2005). Additional mechanisms of climate driven sea-level change such as thermal expansion of the oceans or changes in lake and groundwater storage cannot account for more than ~10 m of rise or fall (Miller et al., 2005). Thus, tectonics likely played the dominant role in driving longer duration high-amplitude sea-level change observed during the Mesozoic (Hallam, 1984; Miller et al., 2005), especially during the Triassic.

Direct comparison of the history of sea-level change with the marine tetrapod fossil record requires a quantitative metric for sea-level change. While estimates of sea-level are available (e.g., Vail et al., 1977; Haq et al., 1987), these records exhibit marked discrepancies especially for the early Mesozoic (Miller et al., 2005). In contrast, seawater $^{87}\text{Sr}/^{86}\text{Sr}$ provides an independent index of long-term (10^6 – 10^8 -year) sea-level change (Montañez et al., 1996), by reflecting changes in the relative input of strontium from continental weathering (enriched in ^{87}Sr) versus hydrothermal activity at sea-floor spreading centers (depleted in ^{87}Sr). Increased sea-floor spreading results in shallower ocean basins, rising sea level (Miller et al., 1987), and a relative increase in ^{86}Sr supply to the oceans (Jones and Jenkyns, 2001; McArthur et al., 2001). Falling sea levels result in increased terrestrial runoff to the oceans and a relative increase in ^{87}Sr supply to the oceans (Montañez et al., 1996). Thus, much as oxygen isotopes provide a geochemical proxy for glacially driven sea-level change, strontium isotopes can provide an indicator of tectonically driven sea-level fluctuation.

Seawater strontium is derived primarily from two sources: terrestrial weathering of silicates and runoff and isotopic exchange at mid-ocean ridges (MOR) (McArthur et al., 2001). These sources differ in their isotopic signature, with riverine strontium enriched in ^{87}Sr relative to MOR input. In the modern oceans, the isotopic value of seawater strontium is globally homogenous, reflecting its long residence time (approximately 2.5 Ma; Jones and Jenkyns, 2001). Strontium isotopic data derived from marine rocks from different regions exhibit a generally uniform temporal trend suggesting that this global homogenization has been the norm throughout geologic history (McArthur et al., 2001). Increased seafloor spreading drives long term sea-level rise and leads to declining seawater $^{87}\text{Sr}/^{86}\text{Sr}$ values, while falling sea level exposes greater land area to continental weathering and leads to increasing seawater $^{87}\text{Sr}/^{86}\text{Sr}$ values. Thus the slope of $^{87}\text{Sr}/^{86}\text{Sr}$ within a time interval reflects the direction and rate of change in the relative balance of continental weathering and MOR activity and by extension, changes in sea level (Montañez et al., 1996). The ability of strontium isotopes to provide a global summary of long-term, tectonically driven sea level change makes it an attractive source of quantitative data for comparison with global scale diversity compilations when bin size is relatively long. The long residence time of strontium in the ocean buffers it from shorter-term local or regional variations in tectonics or sedimentation that may partially account for observed discrepancies in sea level curves.

Recent studies of Phanerozoic fossil diversity have identified correlations between the isotopic composition of seawater strontium and

patterns of extinction and origination (Purdy, 2008; Cárdenas and Harries, 2010). These results are consistent with the hypothesis that the geologic processes that affect the isotopic balance of strontium input to the oceans also have consequences on long-term marine diversity patterns. However, the broad taxonomic and temporal scope of this previous work did not permit investigation of how these changes affected specific taxa or ecological niches.

In this study, we examined the response of distinct ecomorphological groups (ecotypes) of marine predator predicted to contrast in their response to Triassic sea-level fluctuations. Multiple lineages of reptiles invaded marine environments during the Triassic, and radiated to fill a variety of ecological roles although only two of these lineages survived into the Jurassic (Rieppel, 2002; Motani, 2009). Triassic marine reptiles occupied a great variety of environmental and dietary niches from small, toothless lagoon-dwelling forms to large-bodied ambush predators with ziphodont dentition. We focused on two specialized ecotypes: “durophages,” or taxa that exhibit specialized crushing tooth morphology suggesting a specialized diet of shelled prey (durophagy); and “pelagics,” taxa exhibiting specialized locomotory systems associated with efficient open-water cruising (Fig. 1). While these two ecotypes are defined by different sets of cranial and postcranial morphological criteria respectively, they comprise two distinct, mutually exclusive groups. We hypothesized that marine reptiles specialized in a diet of benthic invertebrates should be especially sensitive to changes in shallow marine habitat driven by fluctuations in sea-level while those adapted to open water habitats should be buffered against such changes. Thus, changes in the proportion of these ecotypes relative to total diversity over time should reveal the influence of sea-level on marine reptile diversity independent of transient fluctuations in fossil richness. Because marine strontium isotopes are sensitive both to tectonic drivers and erosive consequences of sea-level rise and fall, the slope of strontium isotopic change within a given time period (rise or fall) should correlate with the proportional abundance of durophagous species relative to total diversity. In contrast, pelagic species are not predicted to be strongly affected by sea-level change although their proportional diversity may rise or fall as a consequence of fluctuations in nearshore marine reptile diversity that is directly linked to sea-level changes.

2. Methodology

2.1. Diversity compilation

We compiled global stratigraphic occurrence data (presence/absence) for 137 early Mesozoic marine reptile species across twelve geologic substages. Occurrence data were drawn from the primary literature and recent taxonomic reviews (Rieppel, 2000; McGowan and Motani, 2003). This dataset expands upon a database used for a previous analysis of marine reptile diversity (Benson et al., 2010) by adding to the taxonomic scope of that study (e.g., incorporating additional marine groups such as tanystropheids and hupehsuchians) and refining stratigraphic resolution to allow better scrutiny of temporal patterns within the Triassic. Furthermore, we have included representative specimen numbers, locality and horizon data to facilitate future analysis and scrutiny of this dataset (see Supplementary data). The finer stratigraphic resolution permitted both an increased sample size of Triassic bins for statistical analysis and the potential to capture changes on the order of ~4 Ma (the mean duration of a substage in this analysis) vs. the > 10 Ma that characterizes some Triassic stages.

While stratigraphic uncertainty necessitated that some species be included in multiple substages, most species are confined to a single substage (114 out of 137). Only 15 species are represented with certainty by occurrences from two or more Triassic substages. Four species with gaps in their stratigraphic occurrences were ranged through substages between their first and last appearances. Twelve ghost lineages were added to fill prominent phylogenetic gaps (see Supplementary information). Substage designation follows Gradstein et al. (2004).

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