

# Comment on “Climate, Critters, and Cetaceans: Cenozoic Drivers of the Evolution of Modern Whales”

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Marx and Uhen (Reports, 19 February 2010, p. 993) suggested that correlated diversity changes in the fossil record of whales and diatoms reflects secular evolutionary signals of underlying ecological drivers. We question the meaning of this association and outline avenues for more complete testing of correlations between productivity and marine consumers through geologic time.

Given the densely sampled micropaleontological record and the comparatively sparse fossil record of cetaceans, we were surprised to see the strong correlation between diatom and cetacean richness patterns through time presented by Marx and Uhen (1). We applaud their test of broad-scale evolutionary patterns with paleobiological occurrence data but note several concerns.

First, the authors mischaracterize the structure of marine food webs in equating total global species richness of primary producers with consumer taxonomic richness, abundance, and body size. Ecologists continue to debate the relationships among species richness (the number of species), composition (identity of those species), and productivity (2, 3). Although the large spatial scale of marine systems prevents controlled field experiments, decades of observational research have demonstrated the co-occurrence of large-sized diatom productivity with the presence of large consumers (including cetaceans) in nutrient-

rich, upwelling waters (4). Close trophic linkages between diatoms and cetaceans only occur for filter-feeding cetaceans in specific regions (e.g., the Southern Ocean), which have lower cetacean richness than temperate and tropical ecosystems (5), despite higher abundances. In upwelling systems that occur across temperate and tropical latitudinal gradients, both cetacean abundance and richness are high (5), whereas diatom richness is low despite having high abundances, because of the dominance of large-sized diatoms (3). This heterogeneous diatom distribution across the oceans confounds any interpretation of increased productivity as reflected by correlated rises in producer and secondary consumer richness in the fossil record, from the standpoint of global diversity metrics. Moreover, these associations are complicated by secondary consumer feeding specializations (e.g., lunge-feeding or hypercarnivory), which have demonstrably changed in extant cetacean lineages since the Oligocene [e.g., 6, 7]. High secondary productivity likely affects the evolution of body size for some cetacean species (8), but a positive relationship between body size and species richness is not supported by global extant cetacean data (5, 9). Because questions about marine macroecology and its fossil record are similarly limited by an inability to directly investigate large-scale ecological phenomena, drawing the necessary comparisons between productivity and consumers requires an understanding of the relationship between productivity and species richness. Recent analytical advancements have improved our understanding of secular trends in the diatom fossil record (10), but the evolutionary consequences of these trends for the global

richness of primary and secondary consumers are unclear because such global analyses include nanoplankton and smaller diatoms, which are too small and insufficiently abundant to substantially impact cetacean trophic ecology.

Second, the record of fossil cetacean richness yields peaks driven by unusually abundant collections from a small number of mostly Northern Hemisphere assemblages. This overwhelming bias in the crown cetacean fossil record, and a deficiency in reported sampling for rock units older than ~23 million years (11), hamper our ability to test hypotheses about the origin of neocetes or their possible linkage with the formation of the Antarctic Circumpolar Current in the Southern Hemisphere. The cetacean fossil record lacks widespread, fine-scale geochronological calibration, and even the richest and best-known assemblages are time-averaged, which overinflates certain measures of diversity (12).

To surmount these issues, we advocate more robust comparisons of marine producer and consumer diversity (measured by both abundance and richness), using well-sampled local-regional assemblages, as terrestrial paleoecologists have done [e.g., 13]. Such studies, considered in tandem with global data sets, would better resolve whether correlated diversity patterns from disparate trophic levels truly indicate ecological drivers at geologic time scales.

## References and Notes

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