

Oh, the shark has such teeth: Did megatooth sharks play a larger role in prehistoric food webs?

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Extinct megatooth sharks were globally distributed and contributed to ocean food chains that were potentially one to two steps longer than any food chain today.

Is it possible to understate anything about an extinct shark that was the length of a city bus? Since the first description of hand-sized fossil shark teeth nearly 180 years ago, paleontologists have fixated on the possible superlatives belonging to *Otodus megalodon*—or better known as megalodon (Fig. 1), the species epithet of its current binomial. Fossils from these sharks have been collected from sites around the world, ranging in age from about 20 to 3.5 million years ago, but their record is almost entirely represented by massive, serrated teeth, which are several times larger than those of the largest living white sharks (1). *O. megalodon* and other megatooth sharks have spurred no shortage of studies on bite forces, body size estimates (body fossils are rare for sharks), and extinction scenarios (2–4). The immense *O. megalodon* likely maintained its extraordinary size by eating calorie-rich marine mammals (2), in an evolutionary escalation from smaller megatooth antecedents that consumed smaller, less nutritious prey since the Cretaceous (3). Recently, some have proposed that such specialization, along with increasing body size, may have been an unsuccessful strategy in the face of relatively smaller and more generalist white sharks, which evolved in the twilight of *O. megalodon* (4). But are we missing anything else? A new chemical technique advanced by Kast *et al.* (5) in this issue of *Science Advances* suggests a provocative rejoinder: Megatooth sharks may have had bigger roles in Cenozoic food webs than any ocean predator before or since.

First, how do we probe the structure of ancient food webs, or even modern food webs in hard-to-study ecosystems such as the open ocean? Forty years ago, biogeochemistry offered an answer. Most chemical elements, such as nitrogen (N), come in isotopes—atoms

of an element with different numbers of neutrons, and therefore different masses. The rare heavy nitrogen isotope, ¹⁵N, concentrates slightly in consumers relative to their food, leading to higher ¹⁵N/¹⁴N ratios at higher trophic levels (¹⁴N is the vastly more common isotope). Nitrogen isotope ratios are now routinely used to investigate trophic level in modern and relatively recent fossil ecosystems (6). But because proteins (the main N-bearing molecules in animals) do not last long in the fossil record, this proxy has not been available to probe deep time ecology—until now. Adapting an approach that team members used on corals and foraminifera, Kast *et al.* (5) extracted and analyzed N isotopes in the trace organic molecules locked inside resistant mineral of the enameloid coating on shark teeth. After testing their method on modern-day sharks, they turned to fossils to illuminate the trophic level of megatooth sharks.

Because the base of marine food webs can vary in N isotope composition across space and time, Kast *et al.* (5) sampled N isotope data from co-occurring, smaller, fish-eating sharks across the entire geologic history of megatooth sharks. In the late Cretaceous, fish-eating sharks and antecedent megatooth sharks had similar ¹⁵N values, but megatooth ¹⁵N values rise above those of fish eaters in the Paleocene, plateauing in the Eocene and continuing with peak values until their demise ~3.5 million years ago. The extraordinarily high ¹⁵N values for megatooth sharks are significantly higher than in the white shark lineage or modern marine mammals that eat seals (i.e., polar bears and orcas). However, post-Eocene megatooth sharks (especially Mio-Pliocene ones) show a wide range of ¹⁵N values—not every large individual was feeding at the top of the food chain.

Wide individual dietary diversity also occurs in today's great white sharks (7). A recently published study on the last half of megatooth shark history that used an entirely new and less well understood proxy based on zinc (Zn) isotopes confirms many of Kast *et al.*'s (5) conclusions, although it finds more overlap between megatooth and white sharks (4). Intriguingly, the Paleocene rise in megatooth shark ¹⁵N values began before the origin of the oldest marine mammals, and the extreme ¹⁵N values appeared long before megatooth sharks reached their maximum, city bus-length size. This decoupling suggests that body size may be a consequence, as much as a driver of the changing ecological roles in megatooth sharks.

Kast *et al.*'s (5) results strongly suggest that, for much of the Cenozoic, marine food chains were about one to two steps longer than they are today. But how is this possible? Trophic processing is inefficient—energy and mass are lost at every step—yet the controls on the food chain length remain poorly understood because primary productivity, species richness, and ecosystem size and structure have all been considered as determinant factors (8). Perhaps the existence of super-high trophic level megatooth sharks points to higher productivity early in the Cenozoic when global climate was warmer and atmospheric CO₂ levels were higher. But even so, what exactly were these high trophic level megatooth sharks eating?

The N isotope data suggest that many individual megatooth sharks had a diet composed entirely of top carnivores that themselves ate other large carnivores, the way polar bears and orcas do today. Orca-sized toothed whales and walrus-sized pinnipeds did not evolve until the late Cenozoic (9), but the other obvious potential candidate prey are slightly smaller megatooth sharks. In other words, Cenozoic marine food webs might have been dominated by giant cannibals. Cannibalism does occur among extant

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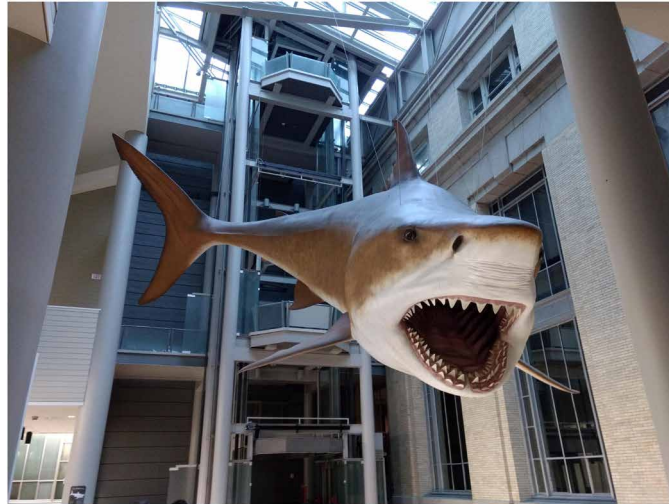


Fig. 1. A 52-foot-long model of a female megalodon shark, commonly known as megalodon, as seen at the National Museum of Natural History, Washington, D.C. Weighing perhaps 12 to 30 tons in life, megalodon had a highly varied diet. Photo credit: Nicholas Pyenson.

sharks and other marine predators (3), but if it was the main cause of extremely high ^{15}N values in megalodon sharks, these ecosystems would be strange indeed. That said, the spread to lower ^{15}N values in the Miocene and Pliocene [supported by Zn isotope data in (4)] suggests that, for the last half of their history, megalodon sharks acquired a wider variety of tastes; some individuals consumed now-extinct diminutive baleen whales (2), which fed lower on the food chain.

It often seems that extinct life is an aberration in comparison with the lineages that live alongside us today. But paleontologists know that this retrospective view is a bias of the present: Our world today has a far different configuration of species (and climates and oceans) than those that persisted in past worlds for millions of years. For example, megalodon sharks were globally distributed ocean predators that were giants for most of the Cenozoic, whereas whales only recently achieved extremely large body sizes (10).

Kast *et al.*'s results seem to weigh against the Plio-Pleistocene disappearance of diminutive baleen whales as a trigger for the extinction of *O. megalodon*, while pointing to other possible explanations that can now be

tested. The advances in N and Zn isotope analyses augur well as avenues to test those ideas, especially given their ability to get reliable data from the relatively thin enameloid of shark teeth. Last, in the late Cenozoic, ocean productivity appears to be linked to trends in maximal body size for nearshore and pelagic marine mammals (9), yet it remains unclear why megalodon sharks defied this trend by achieving and maintaining trophic dominance for most of their history.

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