INSIGHTS

PERSPECTIVES

MARINE MAMMALS

Where to find fantastic beasts at sea

Why do cold-blooded and warm-blooded marine predators live in different parts of the world?

By **Nicholas D. Pyenson**

The biggest predators in the oceans captivate us for good reasons: Sharks, billfishes, whales, and penguins have big appetites, range over large distances, and have achieved similar body forms from vastly different starting points on the tree of life. Evolutionary convergences among large marine predators are also more than skin deep; those with ancestries on land, such as marine mammals and seabirds, have independently evolved an array of molecular and tissue specializations for maximizing oxygen and warmth (*1*). Beyond these fantastic traits, marine predators also possess large body sizes and trophic linkages that make them ecologically important consumers in marine food webs. On page 366 of this issue, Grady *et al.* (*2*) reveal why these top marine predator species—all the high trophic level consumers—are not found together in different regions of the world, despite their shared traits.

Macroecologists who study marine predators have long known that convergences in form do not yield similar ecological distributions over geographic space. Most marine mammal species occur at higher latitudes, whereas sharks and fishes are found closer to the equator (*3*, *4*). Endothermic marine mammals are also most plentiful in polar and temperate seas. This latitudinal distribution contrasts with that of nearly every other marine animal group, which shows peaks in equatorial to temperate seas. Why the difference? Grady *et al.* tackled this question by connecting taxonomically broad database analytics with functional ecological theory to illuminate a possible answer: A fundamental asymmetry in metabolism gives endotherms an advantage when hunting in colder, more prey-rich waters.

Grady *et al.* compiled a distributional database of the geography of 995 top marine predators, including not just whales and sharks but also bony fishes, swimming seabirds, and marine reptiles such as sea turtles. The basic distribution maps show startling gaps in top predator occupancy across the globe. For example, there is a lack of marine mammals in the Indo-Australian Archipelago, despite this region being an epicenter for marine biodiversity (*5*). When Grady *et al.* looked at the ratio of endotherm predator species to ectotherm predator species, the higher values in colder waters held for both coastal and pelagic taxa. Even when controlling for history by

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A leopard seal lunges at a penguin off Antarctica, an example of hypercarnivory at high latitudes.

calculating phylogenetic diversity across predators, there is a clear trend for endotherm occupancy in colder waters.

Explaining this geographic pattern requires revisiting the models that describe the cost-benefit trade-offs of top predators feeding on their prey. On first principles alone, individual endothermic predators maintain consistent metabolism across latitudes, whereas the metabolism of ectotherms plummets in colder waters, which would affect relative foraging performance. Scaling up to the ecosystem level, where prey production is relatively uniform, each endothermic and ectothermic predator species should have strongly differential consumption rates across latitudes—all driven by water temperature as a primary structuring factor.

Grady *et al.* tested this model using data from the marine predator literature on tissue metabolism for locomotion and other core sensory functions. The authors also employed specific tests using the global datasets of pinniped and small toothed whale abundances and consumption rates compared with proxies of water temperature and ocean productivity. Although both pinnipeds and toothed whales hunt at sea in different ways, their annual consumption in the polar regions is many orders of magnitude greater than their consumption in temperate regions. This asymmetry in geography may also be an evolutionary driver for marine mammal speciation at high latitudes, where high prey abundance permits specialization into hypercarnivorous modes, as seen in leopard seals (see the photo) and killer whales, for example (*1*, *6*).

Like the phenomenon of evolutionary convergence, asymmetries in physiology can structure biological diversity across allometric scales (*7*) and, as Grady *et al.* argue, geographic ones. Is metabolic asymmetry alone a sufficient explanation for the origins of this disparity at sea? The phylogenetic divergences among top predators are hundreds of millions of years old. Many shark and bony fish lineages have been ectotherms for the entirety of their history, yet marine tetrapod predators descend from ancestors that invaded ocean ecosystems many times, in mostly asymmetric ecological transitions [i.e., more land-to-sea than sea-to-land transitions (*8*)]. Moreover, these invasions seem to have happened almost exclusively in equatorial to temperate seas (*1*). Are they accidents of history and plate tectonics, or do they reflect something more fundamental for vertebrates—such as the asymmetry of heat transfer between air and water? More data, especially from the fossil record, might better test these questions.

Biologging technology may also provide another dataset for testing these ideas, especially for filter-feeding whales, which were not in the dataset examined by Grady *et al.* Filter-feeding whales appear to follow the same trends as pinnipeds and toothed whales, but their abundances, especially in the Southern Hemisphere, were vastly depleted during the 20th century because of whaling, which removed millions of tons of their biomass from high-latitude ecosystems (*9*). Nonetheless, continuing advances in biologging tags on filter-feeding whales promise to yield more insight into energetic trade-offs of foraging, especially for datasets that include nearby prey density mapping (*10*). Such actualistic field data are valuable for reasons of context. The same environmental factors that concentrated seasonally available prey and promoted the geologically recent evolution of their extremely large body size (*11*) will also apply to a rapidly warming cryosphere, potentially altering prey availability (*12*). If water temperature is a strong structuring factor on baleen whale abundance, too, then the findings of Grady *et al.* foretell a challenging world for the largest marine predators ever. ■

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