

RESEARCH ARTICLE SUMMARY

BIODIVERSITY PATTERNS

Metabolic asymmetry and the global diversity of marine predators

John M. Grady*, Brian S. Maitner, Ara S. Winter, Kristin Kaschner, Derek P. Tittensor, Sydne Record, Felisa A. Smith, Adam M. Wilson, Anthony I. Dell, Phoebe L. Zarnetske, Helen J. Wearing, Brian Alfaro, James H. Brown

INTRODUCTION: One of the most general patterns in ecology is that diversity increases toward the equator. In the ocean, however, mammal and bird richness generally peak in colder, temperate waters. This pattern is especially puzzling given the thermal stress that cold water imposes on warm-bodied endotherms, which must maintain constant, elevated body temperatures through metabolic activity. In contrast, ectothermic fish and reptiles that rely on ambient heat to regulate their body temperature show the highest diversity in tropical and subtropical habitats.

RATIONALE: Large, predatory vertebrates regulate food webs across marine systems. Their distribution varies strongly with thermoregulatory strategy, but the underlying mechanisms are unclear. Using theory and data, we sought to clarify the physiological and ecological processes that lead to opposing patterns of diversity in marine predators.

RESULTS: To identify spatial patterns of diversity, we synthesized range maps from 998 species of marine sharks, teleost fish, mammals, birds, and sea snakes. We found that most

families of endothermic mammals and birds show elevated richness in temperate latitudes, whereas ectothermic sharks and fish peak in tropical or subtropical seas. These findings are reinforced by our analysis of phylogenetic diversity, which weights diversity by species' evolutionary relatedness.

The strong latitudinal signal is suggestive of thermal controls on diversity, but other environmental features may be relevant. In particular, large, productive, or coastal habitats tend to support more species regardless of thermoregulatory strategy. Endotherm phylogenetic diversity and richness generally peak between 45° and 60° latitude, but when we take the ratio of endotherm to ectotherm richness—correcting for shared spatial drivers—endotherm richness increases systematically toward the coldest polar oceans.

We then determined quantitatively and theoretically how these differences are linked to thermal physiology. We found that the metabolic response to ambient temperature is asymmetric between endotherms and ectotherms: Endothermic metabolism is generally constant, but in ectothermic fish, burst speed, routine swimming speed, neural firing rates, saccadic

eye movement, and visual flicker fusion frequencies fall exponentially in colder water. This has trophic and competitive implications for marine species. Ectothermic prey are sluggish in the cold and easier for mammals and birds to capture, whereas slow-moving, predatory sharks are easier to avoid. As a result, marine endotherms are competitively favored over ectothermic predators as water temperatures decline.

We tested our theory against a global dataset of pinniped and cetacean abundance and foraging rates. As predicted, we found that mammal consumption and density increase log-linearly with water temperature after correcting for productivity. From the equator to the poles, marine mammal consumption of available food increases by a factor of ~80.

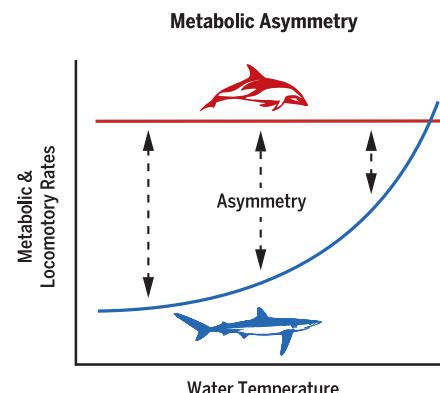
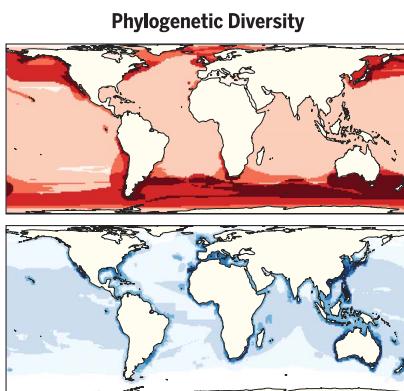
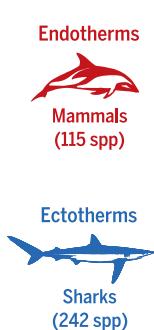
CONCLUSION: Our results and theory highlight the importance of energetics in species interactions and the ecological and evolutionary consequences of endothermy at global scales. Although elevated metabolism is costly, it provides foraging and competitive benefits that underpin the distribution and abundance of marine endotherms. Our findings also have implications for conservation. Rising ocean temperatures are predicted to exert substantial additional constraints on mammal and bird populations independent of food production or habitat conditions, and may alter the balance of marine endotherms and ectotherms across the globe. ■

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Water temperature drives differences in metabolism and diversity between marine endotherms and ectotherms.

Marine endothermic predators show contrasting patterns of phylogenetic diversity with ectotherms, where phylogenetic diversity is the sum of evolutionary distances between co-occurring species and darker colors represent higher diversity. Unlike most other taxa, mammal and bird phylogenetic diversity peaks in cold, temperate latitudes. Theory and data suggest that this reflects differences in thermoregulation. In particular, thermal gradients across latitude generate an asymmetric response in metabolic, sensory, and



locomotory rates between endotherms (which maintain constant rates) and ectotherms (which respond exponentially). As a result, colder water is more favorable to endothermic predators pursuing sluggish ectothermic prey or avoiding slower ectothermic sharks.

RESEARCH ARTICLE

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Metabolic asymmetry and the global diversity of marine predators

John M. Grady^{1,2*}, Brian S. Maitner³, Ara S. Winter⁴, Kristin Kaschner⁵, Derek P. Tittensor^{6,7}, Sydne Record², Felisa A. Smith⁸, Adam M. Wilson⁹, Anthony I. Dell^{10,11}, Phoebe L. Zarnetske¹, Helen J. Wearing^{8,12}, Brian Alfaro⁸, James H. Brown⁸

Species richness of marine mammals and birds is highest in cold, temperate seas—a conspicuous exception to the general latitudinal gradient of decreasing diversity from the tropics to the poles. We compiled a comprehensive dataset for 998 species of sharks, fish, reptiles, mammals, and birds to identify and quantify inverse latitudinal gradients in diversity, and derived a theory to explain these patterns. We found that richness, phylogenetic diversity, and abundance of marine predators diverge systematically with thermoregulatory strategy and water temperature, reflecting metabolic differences between endotherms and ectotherms that drive trophic and competitive interactions. Spatial patterns of foraging support theoretical predictions, with total prey consumption by mammals increasing by a factor of 80 from the equator to the poles after controlling for productivity.

Marine ecosystems are home to a variety of large, active predators representing all major thermoregulatory strategies, including ectothermy (most sharks and bony fish), mesothermy (tuna, billfish, lamnid sharks), and endothermy (mammals, birds). Of particular interest is the rich diversity of marine endotherms, which have repeatedly invaded the ocean despite numerous hurdles to entry, including high rates of heat loss from water (~23 times the rate of heat loss than air), obligate air-breathing, and, for many taxa, energetic and geographic restrictions imposed by terrestrial birth (1, 2). Despite the thermal stress, marine endotherm richness is generally highest in cold, temperate waters—a conspicuous exception to the latitudinal pattern of increasing diversity from poles to tropics observed in nearly all other animal taxa (3). This unusual spatial pattern challenges general theories of diversity

and draws attention to the evolutionary importance of thermoregulation in the abundance, distribution, and richness of species.

To address this physiological, ecological, and biogeographic puzzle, and to better understand the evolutionary implications of endothermy and ectothermy, we synthesized a broad dataset of the distributions of large-bodied marine predators. After demonstrating a systematic covariation of global diversity with thermoregulatory strategy, our analysis builds on existing theory (4, 5) to derive underlying principles and quantitative predictions that link the metabolism and foraging behavior of individual predators to global patterns of energy flow and biodiversity.

Empirical patterns of diversity

Ecologists have long noted that biodiversity tends to peak in the tropics, a pattern linked to the greater stability, productivity, and area in lower latitudes (3). This holds for virtually all major multicellular taxa on land, including mammals, birds, reptiles, amphibians, plants, and insects (3), and in the ocean for fish, mollusks, coral, seagrass, and mangroves (6). Most families of marine endotherms, however, have strikingly different biogeographic patterns. Pinnipeds (walruses, seals, and sea lions) are virtually absent from tropical waters, and all major clades of marine birds that pursue prey via swimming (penguins, auks, grebes, loons, cormorants) are predominantly temperate. Indeed, no species of penguin, auk, or pinniped inhabits the hyperdiverse central Indo-Pacific. Among cetaceans, only dolphins (Delphinidae) have truly diversified in the warm tropics. Nonetheless, the details and causes of these patterns are obscured

by environmental variation across space, such as variation in productivity or proximity to land, that affect both warm- and cold-bodied taxa. To clarify global patterns, we synthesized distributional data for 998 species of marine mammals, birds, sharks, large teleost fish, and sea snakes. We employed a measure of diversity that controls for shared spatial drivers. Although endotherm diversity generally peaks between 45° and 60° latitude (figs. S1 and S2) when we take the ratio of endotherm to ectotherm richness, we observed an inverse latitudinal gradient of diversity in which the endotherms become systematically more speciose than ectotherms in colder waters (Fig. 1).

Another, perhaps more integrative, measure than richness is phylogenetic diversity, which weights diversity by the evolutionary distance between species (7) and may reveal patterns obscured by radiations of specialized taxa. The recent availability of resolved phylogenies and comprehensive species distributions now permits global comparisons. Endothermic mammals and birds show clear phylogenetic diversity peaks in temperate systems, in marked contrast to ectotherms (Fig. 2 and figs. S1 and S2). Mesotherms such as great white sharks and tuna, which use metabolic heat to elevate body temperatures but do not maintain a thermal set point (8, 9), show intermediate and largely cosmopolitan patterns of phylogenetic diversity. For high-powered mesotherms and endotherms, it is also apparent that diversity is less closely tied to coastal habitats relative to ectotherms (Figs. 1 and 2 and fig. S2).

This covariation of spatial diversity with thermoregulatory strategy is striking and largely unexplained by existing theory. Prior analyses have typically focused on narrower taxonomic groups or the origins of elevated tropical diversity, or have suggested that endotherms, with their higher energy demands, are restricted to temperate seas because they are more productive (10, 11). However, areas of high biological productivity occur throughout the world's oceans, including upwelling zones near the equator and along tropical coastlines (12). Indeed, a number of recent models of net primary production (NPP) indicate a modest but significant increase in NPP in warm, tropical waters, where phytoplankton growth and turnover rates are higher (13, 14). These general patterns also extend to larger zooplankton (14). It has been proposed that thermal constraints on predation are responsible for the temperate distributions of marine endotherms (4). However, there have been limited demographic data to test this hypothesis, and the quantitative, theoretical mechanisms are largely unresolved. More broadly, most models of spatial diversity, including temperature-based theories, have generally ignored inverse latitudinal gradients and the role of species interactions [e.g., (15, 16)]. Here, we derive a quantitative theory of species interactions that shows (i) how ambient temperature generates metabolic and foraging asymmetries between endotherms and ectotherms, and (ii) how metabolic asymmetries

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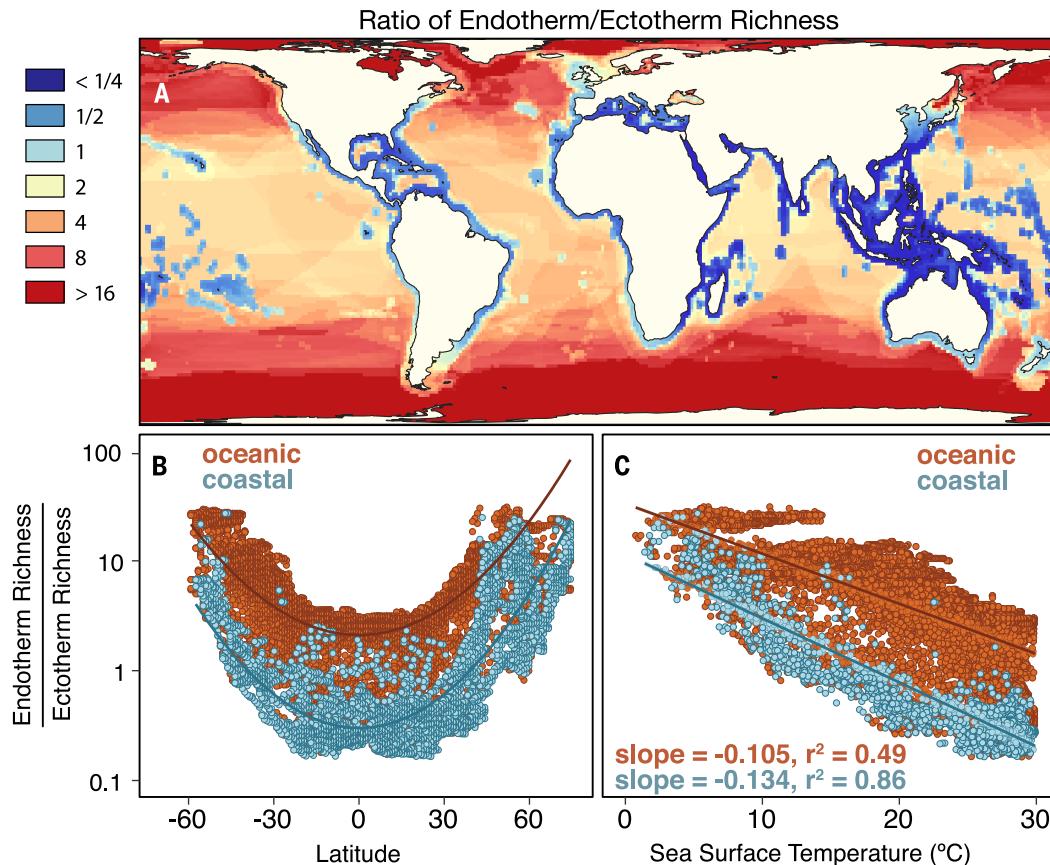


Fig. 1. Relative richness of marine predators across space. (A) Large ectothermic predators (sharks, teleosts, sea snakes) dominate predator richness in tropical and subtropical coastal waters (blue), while endothermic swimming birds and mammals dominate cold waters and open oceans (red) (19). Where ectothermic species are absent, the highest value is

shown. (B and C) Coastal and oceanic spatial cell values are distinguished by color, where coastal areas are cells < 200 m depth or include land. Quadratic fits are shown in (B) ($r^2_{\text{coastal}} = 0.80$, $r^2_{\text{oceanic}} = 0.47$); cells are $1^\circ \times 1^\circ$. For (A) and (C), cells are $110 \text{ km} \times 110 \text{ km}$. All taxa are primarily shallow-water predators (< 200 m depth); $P < 0.0001$ for all analyses. See also table S1.

lead to competitive differences between endotherm and ectotherm predators that drive opposing latitudinal gradients in diversity. We validate theoretical predictions using data on endotherm and ectotherm metabolism and global patterns of abundance and consumption rates by marine mammals. Warm-bodied mammals and birds are more successful hunters and therefore better competitors than their ectothermic counterparts when their metabolism is comparatively higher, leading to a systematic increase in the relative abundance and richness of endotherms toward the poles.

Metabolic model of predation and competition

Individual predation rates

Foraging and locomotion, like all activity, is fueled by metabolism. The rate of metabolism is strongly temperature-dependent (17), as are rates of locomotion and foraging (18). Endothermic mammals and birds maintain a constant body temperature in the ocean, but the body temperature of ectothermic predators and prey varies closely and passively with ambient temperature. Overall, the kinetics of metabolic

rates (R) for endotherms (R_{Endo}) and ectotherms (R_{Ecto}) can be written as

$$\begin{aligned} R_{\text{Endo}} &\propto T^0 \\ R_{\text{Ecto}} &\propto \exp\left(-\frac{E_0}{kT}\right) \\ \frac{R_{\text{Endo}}}{R_{\text{Ecto}}} &\propto \exp\left(\frac{E_0}{kT}\right) \end{aligned} \quad (1)$$

where E_0 is a metabolic “activation energy” (~0.65 eV), k is Boltzmann’s constant, T is absolute ambient temperature (17), and $R_{\text{Endo}}/R_{\text{Ecto}}$ is the ratio of metabolic rates that quantifies their metabolic asymmetry with respect to T . Body size is also an important driver of metabolic rates, but here we contrast thermoregulatory guilds that overlap in size; in effect, this is a correction for size differences, although body size can be incorporated for individual species (19).

Although rarely studied, metabolic asymmetries between endotherms and ectotherms have important implications for foraging and competition (Eq. 1 and Fig. 3). To illustrate, we decompose the rate of prey capture (C_a) into two

basic components (fig. S3): the encounter rate of predators with their prey (E_n) and the probability of capture per encounter (C_e). Encounter rates reflect detection distance, prey density, environment dimensionality, and the combined speed of predator and prey (20). In marine ecosystems, food webs are structured with larger predators consuming smaller prey, so combined speed is closely approximated as the larger and faster predator’s speed S_{Pred} , where $E_n \propto S_{\text{Pred}}$ (19). Thus, the speed of ectothermic predators and their encounter rates with prey will increase in warm water, consistent with the temperature dependence in Eq. 1, where $E_n \propto \exp(-E_0/kT)$. In contrast, the speed and prey encounter rates of marine mammals and birds are largely independent of water temperature, and so $E_n \propto T^0$. Taking the ratio $E_n \text{Endo}/E_n \text{Ecto}$, the temperature-independent components cancel and the thermal dependence of relative encounter rates is

$$\frac{E_n \text{Endo}}{E_n \text{Ecto}} \propto \exp\left(\frac{E_0}{kT}\right) \quad (2)$$

Following an encounter, the probability or efficiency of capturing prey is C_e where $C_e \equiv C_a/E_n$.

Capture efficiency should increase as $S_{\text{Pred}}/S_{\text{Prey}}$ increases, where the most ecologically relevant speeds are typically maximum rates, such as burst speed during attack and escape (21). For ectothermic hunters of ectothermic prey, C_{eEcto} are predicted to be approximately invariant along thermal gradients because the metabolic rates

of predator and prey have similar temperature dependence: $C_{\text{eEcto}} \propto S_{\text{PredEcto}}/S_{\text{PreyEcto}} \propto T^0$. In contrast, for endothermic hunters of ectothermic prey, asymmetry in their metabolic response to water temperature (Fig. 3A) should lead to a higher capture efficiency in colder waters, where prey are comparatively sluggish:

$C_{\text{eEndo}} \propto S_{\text{PredEndo}}/S_{\text{PreyEcto}} \propto \exp(E_1/kT)$. Overall, the relative capture efficiencies of endothermic and ectothermic predators are predicted to vary with water temperature as

$$\frac{C_{\text{eEndo}}}{C_{\text{eEcto}}} \propto \exp\left(\frac{E_1}{kT}\right) \quad (3)$$

Although temperature constrains locomotory and other metabolic-dependent rates given by E_0 (Eqs. 1 and 2), behavioral strategies by both predator and prey can modulate capture efficiency and the value of E_1 in Eq. 3, where $E_1 = \alpha E_0$ and α is a multiplier. For example, when ambient temperatures drop on land, ectothermic lizards have been observed to increase the distance they flee endothermic predators (22).

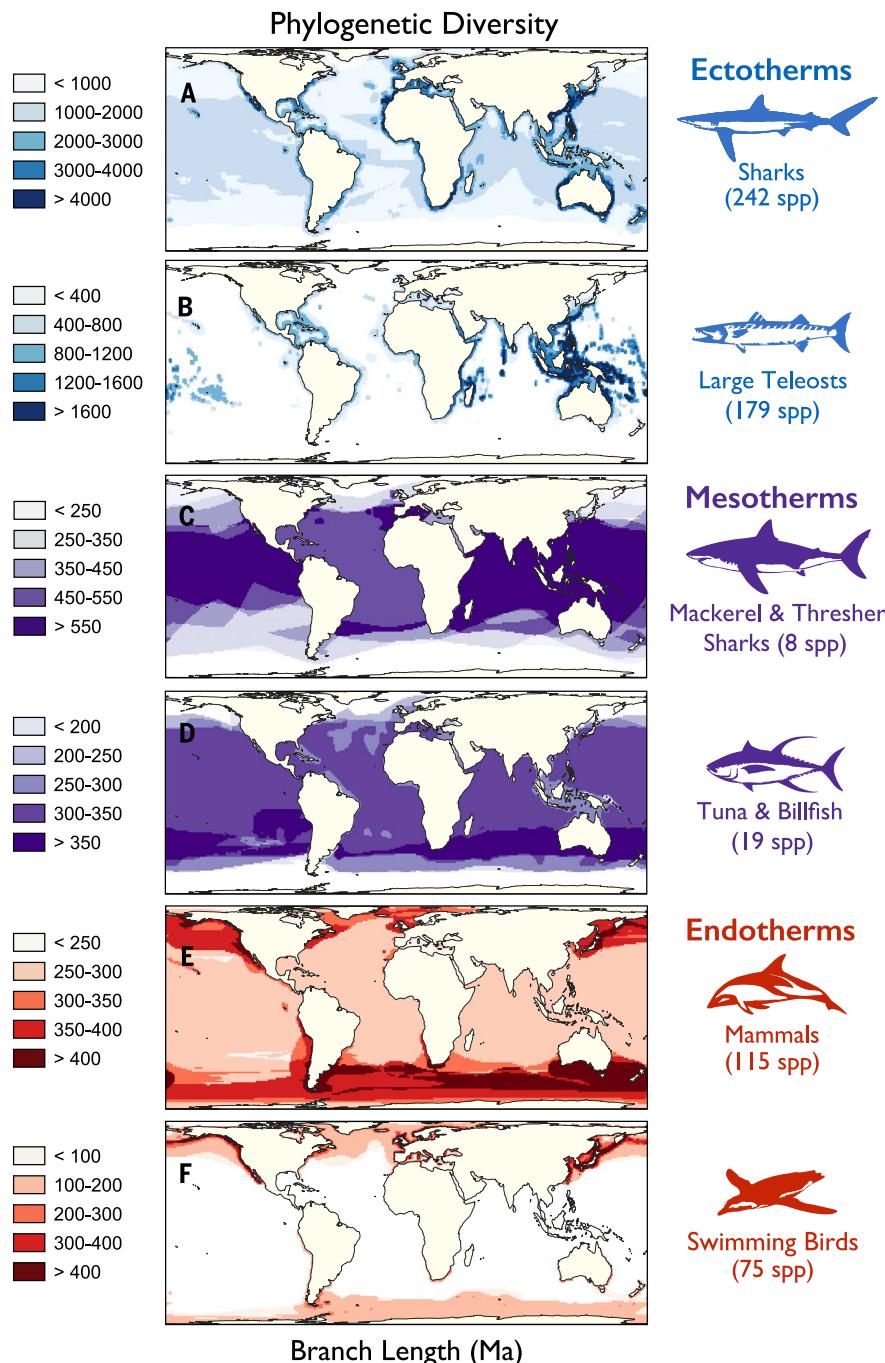


Fig. 2. Phylogenetic diversity of large marine predators. Phylogenetic diversity, expressed as the sum of evolutionary times of divergence [in millions of years (Ma)] between co-occurring species (7), is largely tropical or subtropical for ectothermic sharks (A) and teleost fish (B), cosmopolitan for mesotherms (excluding poles) (C and D), and peaks in cold, temperate waters for endothermic mammals (E) and birds (F). Spatial cells are 110 km × 110 km; cells lacking species are unshaded.

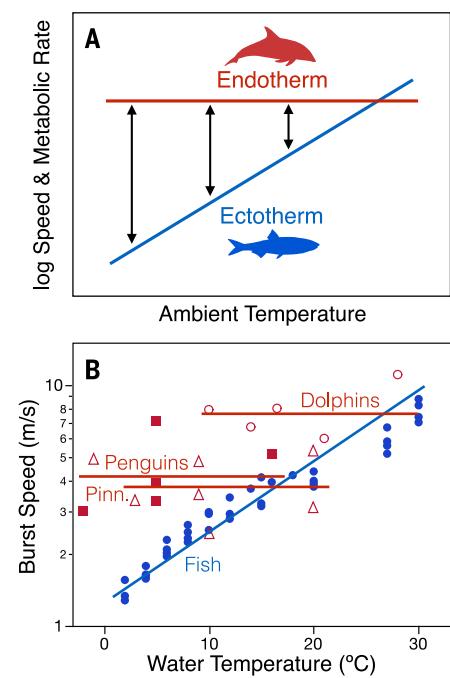


Fig. 3. Metabolic and performance asymmetry between endotherms and ectotherms. (A) Endotherm metabolic and performance rates are predicted to be insensitive to water temperature, whereas ectotherm rates respond in an approximately exponential fashion, promoting endotherm foraging and escape from sharks in colder water. (B) Data from the literature on fish and endotherm speed support predictions. Red lines and symbols represent endotherms; blue, ectotherms. Solid circles, fish; open circles, dolphins; solid squares, penguins; open diamonds, pinnipeds. Endotherm lines are mean values (9.1 for dolphins, 4.3 for penguins, 3.9 for pinnipeds). For fish, five species were analyzed, with temperature and species as predictor variables, yielding $\ln(y) = 0.068t$, $n = 43$, $r^2 = 0.98$ (shown) or $\ln(y) = -0.48(1/kT)$, where t and T are temperature in °C and K, respectively; $P < 0.001$. See (19).

or switch from flight to crypsis (23). Conversely, some marine endothermic predators, such as dolphins, use cooperative hunting techniques to herd fish and increase capture efficiency in warmer waters (24) (see below). In these instances, we expect behavioral strategies to generally dampen the thermal sensitivity of capture efficiency relative to metabolism (i.e., $E_1 \leq E_0$). The ratio of endothermic to ectothermic capture rate provides a general measure of relative foraging performance:

$$\frac{C_{a\text{Endo}}}{C_{a\text{Ecto}}} \propto \exp\left(\frac{E_f}{kT}\right) \quad (4)$$

where the thermal foraging constant $E_f = E_0 + E_1$, and $0.65 \leq E_f \leq 1.30$. Equations 2 to 4 define the major individual foraging asymmetries between predatory endotherms and ectotherms in the ocean.

Scaling individual to ecosystem consumption

The total rate of prey consumption by predators in an ecosystem or geographic region is simply the sum of the rates of all the individuals. Treating capture rate as a type I functional response (i.e., ignoring handling and satiation) is useful for linking individuals to ecosystem scales: Values of C_a that exceed metabolic requirements represent excess foraging capacity that promotes population growth (Fig. 4). Recognizing that total endotherm consumption (C_{TotEndo}) is limited by total prey production (P_{Prey}) and treating $C_{a\text{Endo}}/C_{a\text{Ecto}}$ as a rate variable, individual capture rate can be linked to total ecosystem consumption using a Hill function:

$$C_{\text{TotEndo}} = \frac{P_{\text{Prey}}}{1 + b/\left(\frac{C_{a\text{Endo}}}{C_{a\text{Ecto}}}\right)} \quad (5)$$

where b is a normalization constant. The ratio $C_{a\text{Endo}}/C_{a\text{Ecto}}$ in Eq. 5 connects differences in individual foraging rates to competition for re-

sources at ecosystem scales: The proportion of available prey consumed by endotherms is predicted to increase as $C_{a\text{Endo}}/C_{a\text{Ecto}}$ increases, and to decline as it falls. Thus, although productive waters will benefit all consumers, water temperature shifts the share of resources toward endotherms in cold systems and toward ectotherms in warm waters (Fig. 4). To isolate the effects of water temperature, we transform and substitute from Eq. 4 to generate the slope-intercept form of Eq. 5:

$$\text{logit}\left(\frac{C_{\text{TotEndo}}}{P_{\text{Prey}}}\right) = E_f \left(\frac{1}{kT}\right) - \ln(b_1) \quad (6)$$

where b_1 is a normalization constant, $1/kT$ is the predictor variable, and E_f is the fitted slope (19), predicted to be 0.65 to 1.30 (see Eq. 4).

Testing the model

Individual performance

To test predictions of metabolic asymmetries (Eq. 1 and Fig. 3A), we compiled and analyzed data on metabolism and thermal performance from the literature (19). We found that muscle contraction rates, acceleration, and burst and routine swimming speeds of ectothermic fish decline in an approximately exponential fashion with falling water temperature (Fig. 3B and fig. S4, A to C), supporting theoretical predictions and consistent with prior findings (18). In contrast, burst speeds of endotherms are generally insensitive to temperature, generating an asymmetry in performance in which endothermic predators become increasingly faster than their ectothermic prey and predators as water temperature decreases (Fig. 3B). Metabolic asymmetries not only underlie asymmetries in locomotion, but also drive asymmetries in sensory and information-processing rates, such as flicker fusion rates, saccadic eye movement, and cerebral neural firing, all of which generally support the theoretical expectations from Eq. 1 (fig. S4, D to F). The ecological im-

portance of elevated sensory rates is underscored by the unique physiology of mesothermic billfish (swordfish and sailfish), which channel metabolic heat production to elevate temperatures in the eyes and brain, thereby increasing neurosensory rates (25). Overall, warm-bodied predators are favored where prey are slow, stupid, and cold.

Ecosystem consumption

To test predictions of total consumption in Eq. 6, we considered two major taxa of predatory endotherms whose abundance and global consumption have been spatially mapped: pinnipeds and toothed whales (fig. S5). These taxa were generally not among the marine mammals most targeted by hunting in past centuries, and the taxonomic breadth of our data, robustness of predictions to global abundance fluctuations, and substantial recovery of most species (26) permits inferences into underlying ecological processes (19). We used data from Kaschner *et al.* (27, 28) on the consumption rates for pinnipeds and small odontocetes (toothed whales, excluding beaked and sperm whales) to estimate C_{TotEndo} in Eq. 6. Pinnipeds and small odontocetes generally feed at a similar trophic level and forage in shallow waters that can be linked to available sea surface data (29). We used NPP from the Carbon-based Production Model (17) as a proxy for prey production, in line with several fishery analyses (30, 31), but also considered other NPP models and more complex trophic approaches (19). We also assessed the effects of additional environmental variables, such as ocean depth and distance from land, and models that partition spatial autocorrelation (19). We focus on differences between endothermic and ectothermic predators, but the more complex temperature dependence of mesotherms can be modeled and included in our framework.

Endotherm consumption reflected both production and temperature, but only sea surface

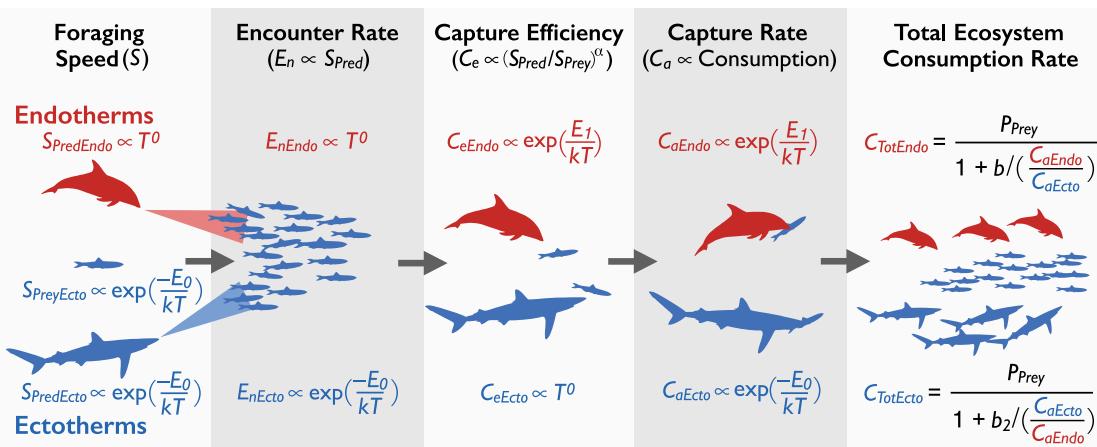


Fig. 4. A metabolic model of predation and competition. Water temperature T drives ectothermic prey and predator metabolism and speed S , generating shifts in trophic interactions between endotherms and ectotherms. In particular, per capita encounter rates (E_n), capture efficiency (C_e), and maximum capture rate (C_a) diverge over thermal

gradients for predators of different thermoregulatory guilds. As water temperatures fall and $C_{a\text{Endo}}$ increases relative to $C_{a\text{Ecto}}$, endotherms are expected to collectively consume a proportionally larger share of the available prey production (P_{Prey}) and ectothermic predators a lesser share. See also fig. S3.

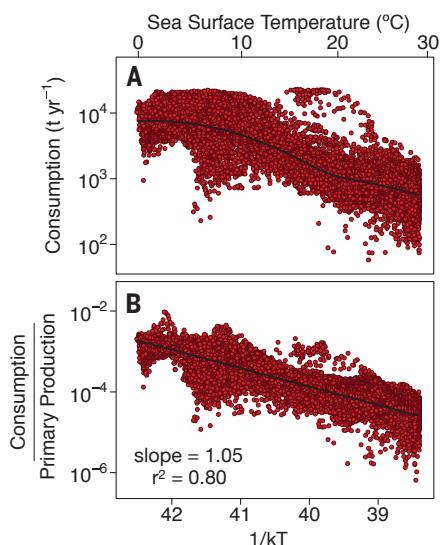


Fig. 5. Consumption across thermal gradients in marine mammals. (A) As sea surface temperatures decline, pinniped and small odontocete predators generally increase their total consumption in a nonlinear fashion, as indicated by the loess regression fit. (B) Normalizing for primary production reduces nonlinearity and generates a dimensionless ratio of relative consumption. The fitted slope provides a measure of E_f ($P < 0.0001$); the y axis is logit transformed. In (A) and (C), all values are per $110 \text{ km} \times 110 \text{ km}$ spatial cell; temperature ($^{\circ}\text{C}$) is shown for visualization.

temperature showed a strong latitudinal gradient (fig. S7). Equation 6 predicts increasing total energy consumption, higher overall abundance and biomass, and, by extension, higher species richness of endotherms in colder waters after controlling for production. We observed absolute prey consumption by mammals to increase markedly in cooler waters, reflecting a concurrent shift in their abundance (Fig. 5, fig. S5, and table S1). Consistent with predictions, annual total consumption by pinnipeds and small odontocetes increased by a factor of ~80 from the tropics to the poles after controlling for production (29° to -1°C ; Fig. 5B and figs. S5 and S6), where $E_f = 1.05$ [95% confidence interval (CI), 1.04 to 1.05; $r^2 = 0.80$]. Although temperature was a strong predictor of total prey consumption by mammals ($r^2 = 0.71$; table S1), the relationship with NPP was poor. Only one NPP model showed a positive association with mammal consumption but had almost no explanatory power ($r^2 = 0.038$; table S1). Inclusion of additional predictor variables (chlorophyll density, distance to land, ocean depth), partitioning of spatial autocorrelation, use of alternate NPP models, and incorporation of more complex trophic assumptions had little qualitative effect on our results (table S1 and figs. S7 and S8).

Differences in speed and foraging strategy within endotherms will modulate thermal sen-

sivities of consumption. Pinnipeds are slower than dolphins (Fig. 3B) and do not cooperate while foraging (see below); thus, we expect a comparatively higher thermal sensitivity of consumption rates in pinnipeds. Indeed, E_f for pinnipeds is 1.7, near the upper bound of predictions, and significantly higher than observed for toothed whales (fig. S9 and table S1).

The increase in relative prey consumption by mammals observed in Fig. 5B implies a concurrent decrease in relative consumption by ectothermic competitors in colder waters. Recent analyses of fish stocks lend support to this prediction. Pelagic fish dominate fishery landings of predatory fish in the tropics, but large demersal fish—which should experience less competition and predation from air-breathing endotherms—constitute approximately an order of magnitude higher proportion of landings in colder, temperate regions (32). Analysis of seabird consumption rates, which peak in cold latitudes, also reinforces the spatial-thermoregulatory linkages observed here (11). Further support for declines in ectothermic predation in cold temperatures comes from land, where insect predation from ectotherms declines away from the equator and at high elevations, unlike predation from endotherms (33).

We suggest that thermal shifts in endotherm abundance and prey consumption underlie their latitudinal patterns of phylogenetic diversity. Higher abundances and foraging success reduce extinction rates and permit specialization, which promotes speciation (34). With higher relative performance in cold waters, endotherms can consume a higher fraction of their preferred prey, expand their dietary breadth, or specialize on a subset of their potential prey base. For instance, incipient speciation of killer whales (*Orcinus orca*) is in progress in the North Pacific, where “transient” mammal-eating populations overlap but do not interbreed with fish-eating “residents” or “offshore” populations specializing on sharks and pelagic teleosts (35). In addition, species with high abundances tend to have large ranges (36) and subsequent fragmentation may promote allopatric speciation, particularly across ocean basins or hemispheres (37). The shift in intercept observed in Fig. 1, B and C, and the strong coastal signal of ectotherm richness (fig. S2) indicate that endotherm diversity is comparatively less responsive to the presence of coastal habitat. This may reflect the advantages of speed and stamina in the exposed, open ocean. In addition, high metabolism may increase range size and reduce allopatric speciation, and respiratory constraints may limit utilization of benthic resources near coastlines.

Exceptions that support the rule

Temperature modulates metabolic asymmetries between endotherms and ectotherms that are relevant to active-capture interactions. Because sea surface temperature shows a latitudinal gradient, our theory predicts a general latitudinal gradient in competitive success and relative

abundance for active, shallow-water foragers. However, not all tropical habitats are warm and shallow, and not all endothermic predators pursue fast prey. In these instances, we expect departure from general patterns. In particular, we expect tropical species to show a higher frequency of foraging in cool habitats (strategy 1), pursuit of comparatively slow prey (strategy 2), possession of exceptional foraging speeds (strategy 3), or behavioral strategies that limit prey escape (strategy 4). These strategies are evident in the limited diversity of tropical endotherms (Fig. 1 and figs. S1 and S10). For example, sperm and beaked whales forage in cold depths across the globe, while the penguins and pinnipeds of tropical South America are restricted to cool upwelling currents (strategy 1), but at lower abundances than southern, cold-water relatives (figs. S5 and S7); rare monk seals specialize on slower benthic fish and invertebrates in warm seas (38), and tropical petrels and other “dippers” frequently alight on the water surface to feed on plankton (strategy 2); some baleen whales species pursue entire fish schools in the tropics by lunge feeding (39), mitigating caloric and maneuverability challenges of hunting small prey while exploiting speed differences associated with larger body size and rapid gape expansion (21) (strategies 2 and 4); plunge-diving birds, such as gannets, can reach exceptionally high speeds upon water entry [$\sim 24 \text{ m/s}$ (40) versus $\sim 4 \text{ m/s}$ for swimming birds in Fig. 3B] to feed on pelagic fish in tropical surface waters (strategy 3); cosmopolitan dolphins (Delphinidae), in addition to being fast (Fig. 3B), are large-brained foragers that cooperate to herd fish into balls for easier capture, among other techniques (24) (strategies 3 and 4). Among swimming endotherms, only dolphins have truly diversified in the warm, shallow tropics (fig. S2), perhaps reflecting the importance of intelligence for mastering complex strategies to tackle fast-moving prey. The elevated tropical diversity in dolphins is also consistent with their spatial patterns of consumption, which show a weaker response to water temperature relative to slower, solitary-foraging pinnipeds (fig. S9).

Biogeography of ectotherms and mesotherms

The importance of metabolic asymmetry is not restricted to endothermic predation of ectotherms. Many species of ectothermic sharks and even fish (41) are capable of preying on marine mammals and birds. Our theory suggests that predation pressure by ectothermic predators on endothermic prey should decline as water temperatures fall (Fig. 3A). To deal with these constraints, we expect the following behavioral or thermoregulatory shifts in sharks foraging on endotherms: from pursuit in the warm tropics to ambush or scavenging in cold temperate seas, and/or an increase in mesothermic shark predators in cooler waters. Indeed, high predation pressure from tropical Galapagos and tiger sharks is recognized as an important

factor in the slow recovery of endangered tropical monk seals, which have failed to rebound from human persecution, unlike many over-hunted temperate species (42). At mid-latitudes, mesothermic great white sharks are common hunters of pinnipeds, relying on ambush and elevated metabolism to seize their endothermic prey (43). In the coldest polar oceans, large Greenland and sleeper sharks are generally too slow to capture alert pinnipeds, but opportunistically scavenge or hunt seals when they are sleeping (44). Instead, warm-bodied orcas and leopard seals dominate the apex predator niche.

The high diversity of mesotherms in tropical and warm temperate waters is also consistent with foraging theory. Elevated body temperatures in mesothermic tuna, billfish, and sharks (9) offer locomotory and sensory advantages for foraging and a degree of metabolic parity with endothermic competitors. In the warm tropics, species of tuna, swordfish, and other mesotherms will dive to cooler depths to feed (45), exploiting the favorable asymmetries shown in Fig. 3. Indeed, even large ectotherms can exploit metabolic advantages offered by thermal inertia when descending to forage (46). The appearance of many active mesothermic tuna and billfish species in the clear waters of the open ocean, in the company of fast-swimming dolphins (Fig. 1 and fig. S2), suggests that elevated metabolism is especially favored where prey is conspicuous and cannot hide. In cold temperate and polar seas, however, mesotherm body temperatures decline along with their performance relative to endotherms. It is probably no accident that the tuna species occupying the coldest waters is also the largest, with thermal inertia buffering the bluefin tuna from falling water temperatures (47).

Conservation implications

Our results have implications for vulnerable marine mammal and avian populations. Both theory and data indicate that the ongoing increase in global ocean temperatures will impair endotherm populations independent of thermal tolerance, habitat preference, or prey availability. In the North Atlantic Barents Sea, researchers have documented an increase in capelin and other small fish stocks over the past several decades, with a corresponding shift in the fortunes of two capelin predators: harp seal and cod (48). Harp seal populations have fallen while cod populations have surged, coinciding with a period of unprecedented regional warming. Rising sea temperatures near Antarctica are also associated with widespread declines in seabird populations that cannot be consistently linked to changes in productivity or habitat (49). Indeed, after controlling for production, we find that each 1°C increase in sea surface temperature corresponds to a 12% decline in marine mammal abundance, and a 24% decline for pinnipeds (Fig. 5B, table S1, and fig. S9). Recent IPCC projections indicate that a 2° to 3°C increase by 2100 is likely (50), underscoring this issue. For solitary foragers in particular, such

as seals and penguins, warming waters are predicted to exert substantial foraging and demographic repercussions.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/363/6425/eaat4220/suppl/DC1
Materials and Methods
Table S1
Figs. S1 to S10
Data S1
References (51–110)

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Metabolic asymmetry and the global diversity of marine predators

John M. Grady, Brian S. Maitner, Ara S. Winter, Kristin Kaschner, Derek P. Tittensor, Sydne Record, Felisa A. Smith, Adam M. Wilson, Anthony I. Dell, Phoebe L. Zarnetske, Helen J. Wearing, Brian Alfaro and James H. Brown

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Cold is better for polar predators

Generally, biodiversity is higher in the tropics than at the poles. This pattern is present across taxa as diverse as plants and insects. Marine mammals and birds buck this trend, however, with more species and more individuals occurring at the poles than at the equator. Grady *et al.* asked why this is (see the Perspective by Pyenson). They analyzed a comprehensive dataset of nearly 1000 species of shark, fish, reptiles, mammals, and birds. They found that predation on ectothermic ("cold-blooded") prey is easier where waters are colder, which generates a larger resource base for large endothermic ("warm-blooded") predators in polar regions.

Science, this issue p. eaat4220; see also p. 338

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