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Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes

Yuuki Y. Watanabe[a,b,1], **Kenneth J. Goldman**[c], **Jennifer E. Caselle**[d], **Demian D. Chapman**[e], **and Yannis P. Papastamatiou**[f]

[a]National Institute of Polar Research, Tachikawa, Tokyo 190-8518, Japan; [b]Department of Polar Science, SOKENDAI (The Graduate University for Advanced Studies), Tachikawa, Tokyo 190-8518, Japan; [c]Alaska Department of Fish and Game, Homer, AK 99603; [d]Marine Science Institute, University of California, Santa Barbara, CA 93106; [e]Institute for Ocean Conservation Science, School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794-5000; and [f]Scottish Oceans Institute, School of Biology, University of St. Andrews, St. Andrews KY16 8LB, Scotland, United Kingdom

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Despite long evolutionary separations, several sharks and tunas share the ability to maintain slow-twitch, aerobic red muscle (RM) warmer than ambient water. Proximate causes of RM endothermy are well understood, but ultimate causes are unclear. Two advantages often proposed are thermal niche expansion and elevated cruising speeds. The thermal niche hypothesis is generally supported, because fishes with RM endothermy often exhibit greater tolerance to broad temperature ranges. In contrast, whether fishes with RM endothermy cruise faster, and achieve any ecological benefits from doing so, remains unclear. Here, we compiled data recorded by modern animal-tracking tools for a variety of free-swimming marine vertebrates. Using phylogenetically informed allometry, we show that both cruising speeds and maximum annual migration ranges of fishes with RM endothermy are 2–3 times greater than fishes without it, and comparable to nonfish endotherms (i.e., penguins and marine mammals). The estimated cost of transport of fishes with RM endothermy is twice that of fishes without it. We suggest that the high energetic cost of RM endothermy in fishes is offset by the benefit of elevated cruising speeds, which not only increase prey encounter rates, but also enable larger-scale annual migrations and potentially greater access to seasonally available resources.

marine predator | swim speed | migration | body temperature

In 1835, the British physician John Davy reported that skipjack tuna have body temperatures 10 °C higher than ambient waters and considered this fish an exception to the general rule that fishes are cold-blooded (1). It is currently known that at least 14 species of tuna (family Scombridae) and five species of shark (four species in the family Lamnidae and one species in the family Alopiidae) have the ability to retain metabolic heat via vascular countercurrent heat exchangers, and to maintain the temperature of slow-twitch, aerobic red muscle (hereafter denoted RM) significantly above that of the ambient water (2–7). This “RM endothermy” (see *SI Materials and Methods* for terminology) in fishes represents a remarkable example of convergent evolution, because bony fishes and cartilaginous fishes diverged as long as 450 million years ago (8). In addition to elevated RM temperature, tunas and endothermic sharks share a number of morphological (e.g., medially located RM), physiological (e.g., high metabolic rates), and ecological (e.g., highly mobile and predatory lifestyle) characteristics (9).

RM endothermy is an energetically expensive thermal strategy (9), and its convergent evolution indicates that the extra energetic costs incurred by RM endothermy can be outweighed by some ecological advantages. This topic has been discussed intensively, and two primary, nonmutually exclusive hypotheses have been proposed: expansion of the thermal niche and elevated cruising speeds (2). The thermal niche hypothesis states that fishes with RM endothermy can tolerate a broader range of water temperatures and, thus, can expand their geographic niche. An increasing suite of evidence supports this hypothesis; tunas and endothermic sharks often range widely and dive well beneath the thermocline and, consequently, experience a broad temperature range (e.g., more than 20 °C in some species; refs. 10 and 11). However, some ectothermic species (e.g., blue shark) experience similar temperature ranges by diving deep (11, 12), suggesting that other factors may also affect the thermal preference and tolerance of pelagic fishes.

The elevated cruising speed hypothesis states that elevated RM temperature enhances the power output of RM and, thereby, increases cruising speed of the fishes (2). This hypothesis is reasonable, because the contraction speed and power output of the isolated RM (13) and the sustained swim speed of ectothermic fishes in captivity (14) all increase with temperature within a species, at least within their normal temperature range. Surprisingly, however, a previous laboratory study found no differences in the sustained swim speeds between two Scombridae species with and without RM endothermy (15). As a result, evidence for the hypothesis is still lacking.

If fishes with RM endothermy are shown to cruise faster in nature, what ecological benefits could they achieve from doing so? Fishes can increase prey encounter rates and, thus, potential energy gains by cruising faster (16); however, this benefit may be counteracted if energetic costs incurred by cruising faster and being endothermic are high. It is therefore important to examine whether the cost of transport (i.e., the energy needed to move a unit body mass over a unit distance) at their cruising speeds is higher for fishes with RM endothermy.

In addition to the benefit of increased prey encounter rates, fishes with RM endothermy may be able to move greater distances in a given time period, such as a year, because of their fast cruising speed. Annual migrations are common in fishes, often

Significance

Most fishes are cold-blooded, but tunas and some sharks (e.g., white sharks) maintain their exercising muscles warmer than ambient waters. This ability is a remarkable example of convergent evolution because bony and cartilaginous fishes diverged as long as 450 million years ago. What are the ecological benefits driving the evolution of warm muscles in fishes? Despite extensive discussion, no previous studies have tested a simple possibility that fishes with warm muscles may swim faster in nature. We demonstrate that fishes with warm muscles swim faster and perform larger-scale annual migrations than similar-sized cold-blooded fishes. Our results suggest that warm muscles enhance power output and, thus, cruising speeds, which may enable longer-distance migrations and potentially greater access to seasonally available resources.

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[1]To whom correspondence should be addressed. Email: watanabe.yuuki@nipr.ac.jp.

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Table 1. Fitting of phylogenetic regression models

Model	R^2	AIC	ΔAIC	wAIC
Swim speed ~ Body mass + Body temp + Endothermy	0.66	−4.5	0	0.73
Swim speed ~ Body mass + Endothermy	0.60	−2.4	2.1	0.26
Swim speed ~ Body mass + Body temp	0.51	3.4	7.9	0.01
Swim speed ~ Body mass	0.44	6.5	11.1	<0.01
Swim speed ~1	0	29.8	34.4	<0.01
COT ~ Body mass + Body temp + Endothermy	0.90	−53.3	0	0.88
COT ~ Body mass + Body temp	0.88	−49.2	4.1	0.12
COT ~ Body mass + Endothermy	0.84	−34.4	18.9	<0.01
COT ~ Body mass	0.8	−25.5	27.8	<0.01
COT ~1	0	45.9	99.2	<0.01
Migration range ~ Body mass + Endothermy	0.67	0.3	0	0.99
Migration range ~ Body mass	0.35	9.7	9.4	<0.01
Migration range ~1	0	16.2	15.9	<0.01

The best models are shown in bold. wAIC, Akaike weight.

between foraging grounds and reproductive habitats (10, 11, 17); therefore, it is hypothesized that fishes with RM endothermy exhibit annual migrations over larger spatial scales than fishes without it. If such difference is observed, large-scale migration could be an ecological advantage, because it allows the fishes with RM endothermy to better exploit seasonal peaks of resource abundance and avoid seasonal resource depression (18).

Because of the rapid development and improvement of various data-recording or transmitting tags, information on fish movements in the wild is increasingly available, both from fine-scale (e.g., recording swim speed; ref. 19) and long-term (e.g., recording migration path; ref. 11) animal-tracking studies. Such information has provided much insight into the ecology of many species; however, no previous studies have examined the possible differences in the movement patterns or swimming energetics in nature between fishes with and without RM endothermy. In this study, therefore, we compiled data on cruising swim speed and migration range of fishes, recorded by various animal-tracking tools, both from the literature and our own fieldwork. We also estimated the cost of transport for each species swimming at each cruising speed. Using phylogenetically informed allometry, we examined whether fishes with RM endothermy (*i*) swim faster, (*ii*) have higher cost of transport, and (*iii*) exhibit larger-scale annual migrations.

Results

Cruising Speed. We compiled cruising speed data for 46 fish species with body masses ranging from 0.025 to 2,200 kg, including six species with RM endothermy (three sharks and three tunas) (Table S1). Phylogenetically informed regressions (20) (see Fig. S1 for the phylogenetic tree), coupled with model selection analysis based on Akaike information criterion (AIC), showed that cruising speed is best explained by body mass, body temperature, and whether the fish has RM endothermy (R^2 = 0.66, Akaike weight = 0.73) (Table 1). Body temperature was set at specific values based on previous measurements for fishes with RM endothermy, and at ambient temperature of the swimming depths for fishes without RM endothermy. For a given body mass, cruising speed was 2.7 times faster for fishes with RM endothermy ($\text{speed} = 0.70 \times \text{mass}^{0.20}$) than fishes without it ($\text{speed} = 0.26 \times \text{mass}^{0.20}$) (Fig. 1*A*). For a given body mass and body temperature, cruising speed was 2.4 times faster for fishes with RM endothermy ($\text{speed} = 0.29 \times \text{mass}^{0.20} \times \text{temp}^{0.28}$) than fishes without it ($\text{speed} = 0.12 \times \text{mass}^{0.20} \times \text{temp}^{0.28}$).

The cruising speeds of fishes were compared with those of other vertebrate swimmers (seabirds, marine mammals, and sea turtles) compiled previously (21) (Fig. 1*A*). There was considerable variation in swim speed for a given body mass in each group, and the slopes of the phylogenetic regression lines were steeper for fishes (exponent, 0.20) than seabirds (0.04) and marine mammals (0.10). Nevertheless, cruising speeds of fishes with RM endothermy were closer to those of nonfish endotherms (seabirds and marine mammals) than to fishes without RM endothermy. The speeds of sea turtles (ectotherms, except for the leatherback turtle; ref. 22) were close to those of fishes without RM endothermy.

Cost of Transport. Cost of transport (COT) estimated for each species with each cruising speed (Table S1) was also best explained by body mass, body temperature, and whether the fish has RM endothermy (R^2 = 0.90, Akaike weight = 0.88) (Table 1). For a given body mass, COT was 1.9 times higher for fishes with RM endothermy ($\text{COT} = 2.92 \times \text{mass}^{-0.35}$) than fishes without it ($\text{COT} = 1.54 \times \text{mass}^{-0.35}$) (Fig. 1*B*). For a given body mass and body temperature, COT was 1.5 times higher for fishes with RM endothermy ($\text{COT} = 0.78 \times \text{mass}^{-0.36} \times \text{temp}^{0.40}$) than fishes without it ($\text{COT} = 0.53 \times \text{mass}^{-0.36} \times \text{body}^{0.40}$).

Migration Range. Annual migration patterns vary greatly among individuals, ages, and populations in some species (11, 23), and the "average" migration pattern might not be informative. Therefore, the maximum, rather than average, annual migration range was compiled for 20 fish species with body masses ranging from 0.6 to 315 kg, including nine species with RM endothermy (four sharks and five tunas), and 17 species of nonfish vertebrate swimmers (Fig. 2 and Table S2). The migration range of fishes was best explained by body mass and whether the fish has RM endothermy (R^2 = 0.67, Akaike weight = 0.99) (Table 1; see also Fig. S2 for the phylogenetic tree). For a given body mass, maximum migration range was 2.5 times larger for fishes with RM endothermy ($\text{range} = 1{,}754 \times \text{mass}^{0.23}$) than fishes without it ($\text{range} = 707 \times \text{mass}^{0.23}$) (Fig. S3). In 13 species for which both maximum migration ranges and cruising speeds were available, the two parameters were linearly related (R^2 = 0.77) (Fig. 3).

Maximum migration ranges of fishes with RM endothermy were closer to those of marine mammals, penguins, and leatherback turtles than to fishes without RM endothermy (Fig. 2).

Finally, we repeated the regression analyses of cruising speed, COT, and migration range by using ordinary least-squares (i.e., nonphylogenetic) method and found a similar amount of support (R^2 value and Akaike weight) for each candidate model (Table S3). Thus, our results are not specific to our choice of evolutionary process models (*Materials and Methods*).

Discussion

Fast Cruising Speed. We show that fishes with RM endothermy cruise at faster speeds than fishes without it. Our result is inconsistent with a previous laboratory experiment (15) that swam two Scombridae species with and without RM endothermy and found no support for the elevated cruising speed hypothesis. However, because of the size limitation of the water tunnel, the fishes swum in that study were small juveniles (<300 g). RM endothermy develops gradually with body size (24), and potential differences in the swimming performance might not have been detected in that study. In contrast, we took a phylogenetic comparative approach by using data for a range of wild fishes, including adult tunas (up to 240 kg) and endothermic sharks (up to 428 kg), and provided a statistically robust result.

Our result indicates that convergent evolution of RM endothermy in fishes has not only allowed the expansion of thermal niche, as shown in previous studies (10, 11), but also enhanced cruising speeds, as shown here for the first time to our knowledge. Fishes with RM endothermy are faster even after the effect of body temperature is controlled for, suggesting that their elevated cruising speeds are not simply a result of thermal effects on RM, but are enhanced by other characteristics shared by these fishes. Such characteristics include high metabolic rates (higher than what would be predicted for their body temperature based on the Q_{10} effect from the metabolic rates of ectothermic fishes; ref. 2) and thunniform swimming mode (where lateral movements are largely confined to the caudal region) associated with a unique force-transmission system from RM to the caudal region (25).

Interestingly, the cruising speeds of fishes with RM endothermy are close to those of nonfish endotherms (seabirds and marine mammals), whereas speeds of fishes without RM endothermy are comparable to sea turtles. We suggest that thermal strategy (endothermy or ectothermy) is a major determinant of cruising speed not only in fishes, but also in marine vertebrates in general, presumably through its strong effect on metabolic rates and muscle contractile properties.

High Energetic Cost. Elevated cruising speed of fishes with RM endothermy should enable increased prey encounter rates and, thus, increased potential energy gains, as shown by a predator–prey interaction model in 3D space (16). However, we also show that COT of fishes with RM endothermy is approximately twice that of fishes without it. The high COT can be attributed to their high standard metabolic rates (9) and the exponential increase in energy requirements with swim speed (26). A previous comparison of swimming energetics of fishes studied in water tunnels provided a similar result, but with a smaller dataset including only bony fishes (27). Although our estimates for COT are inevitably based on many assumptions (e.g., a universal Q_{10} value among fishes, and the extrapolation of scaling relationship of basal metabolic rate in large species; *Materials and Methods*), our analyses indicate that any energetic benefit of increased prey encounter rates is, at least partly, counteracted by the higher energetic costs incurred by swimming faster and being endothermic. High energetic costs may also be linked to fast somatic and gonadal growth and elevated digestion rates in tunas (28), although the link is less clear in endothermic sharks (29).

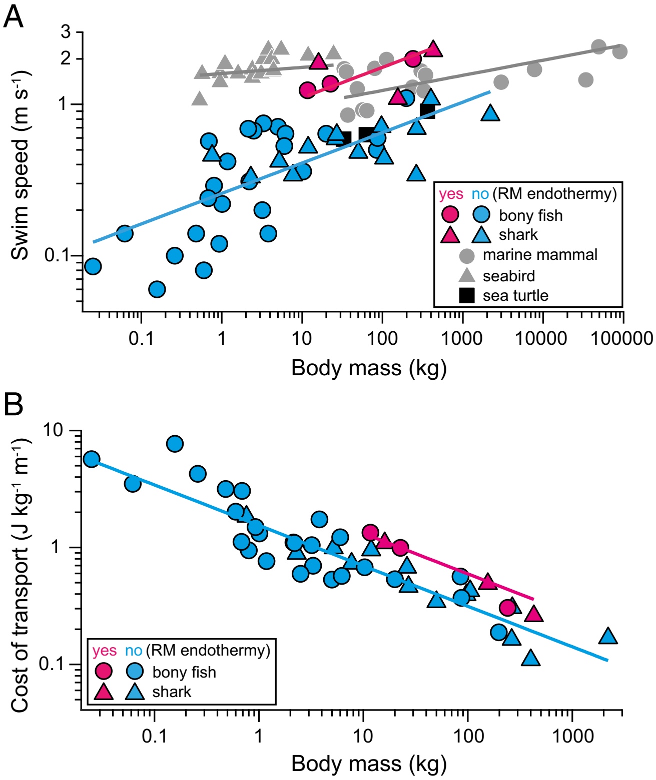

Fig. 1. Cruising speed and the cost of transport as a function of body mass. (*A*) Cruising speed of fishes with RM endothermy (pink) and fishes without it (light blue) recorded in the wild, with other vertebrates swimmers [seabirds, marine mammals (gray), and sea turtles (black)] for comparison. (*B*) Cost of transport (i.e., the energy needed to move a unit body mass over a unit distance) estimated for each fish species with each cruising speed. See main text for the equations of phylogenetically informed regression lines shown in the figure, except for seabirds (speed = 1.60 × mass$^{0.04}$) and marine mammals (speed = 0.78 × mass$^{0.10}$) (21) in *A*.

Large-Scale Migration. In addition to the benefit of increased prey encounter rates, we find that the maximum annual migration range of a species is larger for fishes with RM endothermy than fishes without it, even after controlling for the effect of body size. Notably, all sharks with RM endothermy in our dataset (salmon, porbeagle, white, and shortfin mako sharks) are capable of larger scale migrations than any ectothermic sharks (broadnose sevengill, tiger, oceanic whitetip, and blue sharks), despite their similar ecological niches as upper trophic-level predators and relatively large numbers of tracking records available.

Our result can partly be explained by greater tolerance to broad temperature ranges in species with RM endothermy, because long, latitudinal migrations involve significant changes in water temperature. However, the migration range of fishes with RM endothermy is 2.5 times larger than similar-sized fishes without RM endothermy, a similar value to what we find for cruising speeds (2.7 times). Moreover, the relationship between maximum migration ranges and cruising speeds across fishes is linear. Together, these results indicate that the spatial scale of annual migration of fishes is strongly affected by their cruising speed.

Intriguingly, the maximum migration ranges of fishes with RM endothermy are closer to those of nonfish, endothermic swimmers than to fishes without RM endothermy. For example, the Atlantic bluefin tuna (30), salmon shark (11), blue whale (31), northern fur seal (32), and leatherback turtle (a turtle with warmed body core) (33) migrate between temperate and tropical (or subpolar and subtropical) habitats, and no fishes without RM endothermy perform migrations over similar spatial scales. Another notable example is the swordfish, which migrates between temperate and tropical habitats (34), a spatial scale that is the largest among fishes without RM endothermy (Fig. 2). RM of this species is not significantly warmer than surrounding waters (35), but located medially in the body (similarly to fishes with RM endothermy) with a simple form of heat exchangers present, a morphology that suggests the ability to reduce heat loss from

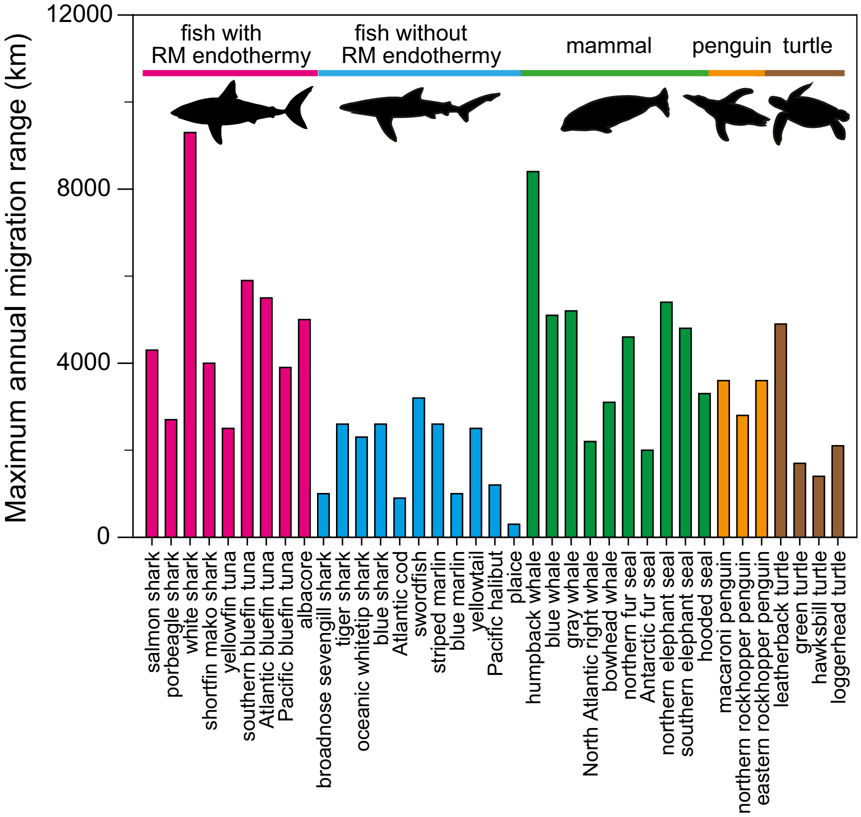

Fig. 2. The maximum annual migration ranges for various vertebrate swimmers. The range for a species is measured from long-term animal-tracking studies as the maximum value (among individuals) of linear distances along the Earth's surface between the two furthest points on an individual's annual migration loop.

RM during steady swimming (36). Overall, our finding suggests that, in marine vertebrates in general, thermal strategy (endothermy or ectothermy) is a major determinant of the spatial scales of annual migrations through its effect on cruising speeds and tolerance to broad temperature ranges.

In conclusion, our comparative analyses indicate that a potential ecological advantage of RM endothermy in fishes is the ability to cruise faster, which not only increases prey encounter rates, but also enables larger-scale annual migrations and greater access to seasonally available resources. We suggest that this advantage, coupled with the previously recognized benefit of thermal niche expansion, could outweigh high energetic costs incurred by RM endothermy and, thus, has facilitated the radiation and diversification of tunas and endothermic sharks. Our analyses also indicate that fishes with RM endothermy are similar to birds and mammals in many respects, including not only high metabolic rates (2) and temperature dependence of muscle function (37), but also fast cruising speeds and the capabilities of large-scale migrations.

Materials and Methods

Cruising Speed. Mean speeds of fishes swimming freely in the wild were compiled from the literature and our own field experiments (Table S1). For the published sources, the main methods of recording swim speed were (*i*) attaching a speed sensor (a propeller in most cases) directly to the fish ("Speed sensor" in the method column of Table S1); and (*ii*) tracking the fish with an acoustic transmitter attached and recording its movement path over a time period ("Acoustic tracking 2D" or "Acoustic tracking 3D"; see *SI Materials and Methods* for details). In addition, we accepted swim speed data from (*iii*) flow-speed measurements taken on the boat that was driven alongside the surface-swimming fish ("Boat"), (*iv*) vertical speed detected by depth sensors and divided by the sine of the pitch angle estimated from acceleration records ("Pitch"), and (*v*) the tail-beat frequency of the fish in the wild detected by attached magnetic sensors, coupled with the linear relationship between swim speed and tail-beat frequency examined in captivity ("Tailbeat").

Our field experiments recorded swim speeds for the salmon shark *Lamna ditropis* (July 2012, in Prince Williams Sound in Alaska), oceanic whitetip shark *Carcharhinus longimanus* (May 2013 and April–May 2014, off Cat Island, The Bahamas), blacktip reef shark *Carcharhinus melanopterus* and gray reef shark *Carcharhinus amblyrhynchos* (July 2013, at Palmyra Atoll). Sharks were hooked and restrained alongside a boat, except for the salmon shark that was hooked and then lifted in a stretcher up on the deck of a boat. A PD3GT logger (21-mm diameter, 115-mm length, and 60 g; Little Leonardo) was incorporated into a package for the instrument recovery (38), which was composed of a time-scheduled release mechanism (Little Leonardo), float, very high frequency (VHF) radio transmitter (Advanced Telemetry Systems),

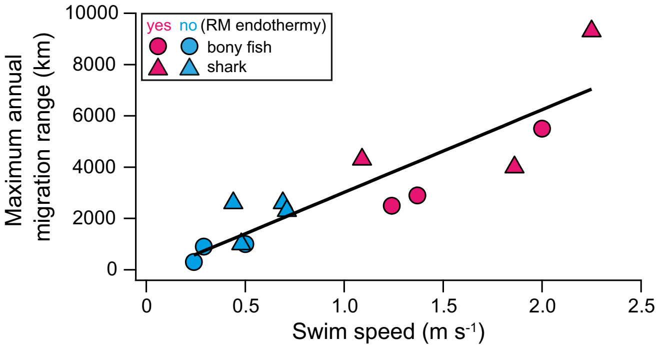

Fig. 3. The relationship between cruising speed and maximum annual migration range in fishes. Among the species shown in Figs. 1*A* (cruising speed) and 2 (maximum annual migration range), only 13 species for which both parameters are available are used in this figure. The least-squares regression line is as follows: range = 3,095 × speed − 117.

and Argos transmitter (Wildlife Computers). The package was attached to the dorsal fin of the sharks, before the sharks were released. Once the package detached from the animals after a 1–4 d free-swimming period, it was located by using VHF and Argos signals and recovered by a boat. The logger recorded relative swim speed as the number of rotations of a propeller at 1-s interval, as well as depth, temperature (at 1-s interval), and three-axis accelerations (at 1/16-s interval). The propeller rotation values were converted to the actual swim speeds ($m \cdot s^{-1}$) by using the equation from a previous calibration experiment (39).

For comparative analyses of swim speeds, body mass and body temperature were estimated for each species in the dataset. See *SI Materials and Methods* for details.

COT. COT (i.e., the energy required to move a unit body mass over a unit distance) ($J \cdot kg^{-1} \cdot m^{-1}$) was computed for each species in our dataset by estimating its routine metabolic rate (W) and dividing it by its cruising speed ($m \cdot s^{-1}$) and body mass (kilograms) (Table S1). Routine metabolic rate was assumed to be composed of basal (or standard) metabolic rate (BMR) and the net locomotion cost at the cruising speed.

BMR of ectothermic fishes was estimated from body mass and body temperature, using the scaling relationship ($BMR = 0.224 \times mass^{0.879}$ at 38 °C, where BMR is in mL of $O_2 \cdot h^{-1}$ and mass is in grams) and Q_{10} value (1.65) reported in fishes (40). Because the maximum body mass is only 2 kg in the published source (40), we had to extrapolate the scaling relationship of BMR for the species with larger body mass. Fishes with RM endothermy have higher BMR (2) and were considered separately. BMR reported for yellowfin tuna (91 mg of $O_2 \cdot kg^{-1} \cdot h^{-1}$ for 5.4 kg of body mass in 20 °C water) (41) was adjusted for body mass and water temperature [using the slope of the scaling relationship (0.879) and Q_{10} value (1.65); ref. 40] to estimate BMR of this species in our dataset. Similarly, BMR reported for Pacific bluefin tuna (120 mg of $O_2 \cdot kg^{-1} \cdot h^{-1}$ for 8.3 kg of body mass in 20 °C water) (41) and shortfin mako shark (124 mg of $O_2 \cdot kg^{-1} \cdot h^{-1}$ for 6.1 kg of body mass in 18 °C water) (42) were used to estimate BMR of two bluefin tuna species (Pacific and Atlantic) and three lamnid shark species (salmon, white, and shortfin mako) in our dataset, respectively. BMR expressed in the volume of oxygen consumed per unit time was converted to the physical unit (W), by assuming that 1 mol oxygen occupies 22.4 L and equates to the utilization of 434 kJ.

The net locomotion cost (i.e., the elevation of metabolic cost above BMR during steady swimming) has been measured in water tunnels for many fish species. When oxygen consumption rate (in log scale) is plotted against swim speed (in linear scale, in body $length \cdot s^{-1}$), the relationships are linear, and the slopes are similar among different species with different body sizes (26). That is, for a unit increase in swim speed (in body $length \cdot s^{-1}$), there is approximately a corresponding 2.3-fold elevation in metabolic rates for many species. Therefore, we used this value and the relative cruising speed of each species in our dataset [cruising speed ($m \cdot s^{-1}$) divided by body length (meters); Table S1] to estimate its net locomotion cost.

Migration Range. The maximum annual migration range for a species was examined from the literature that tracked marine vertebrates (fishes, penguins, seals, whales, and sea turtles) for a long period (Table S2). Among seabirds, only penguins (which migrate by swimming) were considered, because we focused on swimming behavior rather than flight. The main methods of recording migration paths in the collected literature were (*i*) satellite tracking by using Argos transmitting tags ("Argos tag" in the method column of Table S2), (*ii*) light-level–based geolocation by using archival tags ("Archival tag"), and (*iii*) the combination of Argos satellite tracking and light-level–based geolocation, using pop-up archival transmitting tags ("Pop-up tag"). In addition, the data from (*iv*) the tidal location method (based on the time of high water and tidal range measured by depth sensors attached to benthic fish) ("Tidal location"), (*v*) the photo identification ("Photo ID"), and (*vi*) the conventional radio tracking ("Radio tag") used for some whales were also included.

Any migration paths making a complete loop in a year were accepted as a candidate. For species known to return to the same area every year, paths representing an incomplete loop (i.e., in the case that tracking ended long before a year) were also accepted. For each species, the maximum value (among individuals) of the linear distances along the Earth's surface between two furthest points on an individual's migration loop was measured by using Google Earth. Incomplete loops only available for some species, and the photo identification and radio tracking methods used for some whales (in which individual animals are located only limited times), precluded us from estimating the distance traveled along the migration loops.

For comparative analyses of migration ranges, body mass was estimated for each species in the dataset. See *SI Materials and Methods* for details.

Data Analyses. Phylogenetic trees for the species in our dataset were created by using the software Mesquite (43), with the published sources for the phylogenetic relationships among species (44–47) and an arbitrary branch length (48) (Figs. S1 and S2). The trees were transferred to the software Matlab (MathWorks), where further regression analyses were conducted by using the Regressionv2.m program (20).

All continuous variables (i.e., swim speed, cost of transport, migration range, body mass, and body temperature) were log_{10} transformed to improve linearity of relationships among the variables, and whether the fish have RM endothermy was input as a categorical value (Table 1). The regression equation, the coefficient of determination (R^2 value), and AIC for each model was computed under the Ornstein–Uhlenbeck evolutionary process model, and the model with best support was determined based on Akaike weights. To examine the robustness to our choice of evolutionary process model, the procedure was repeated by using ordinary least-squares (i.e., nonphylogenetic) regression method.

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Supporting Information

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SI Materials and Methods

Terminology. The ability to maintain slow-twitch, aerobic RM warmer than ambient water in tunas and some sharks is called RM endothermy in this paper, following the frequent use of the term endothermy for these fishes in previous studies (1–3). However, we are aware that the term endothermy may refer exclusively to birds and mammals (where relatively high and more or less constant internal body temperatures are maintained, with high resting metabolic rates as the main source of heat; ref. 4), and that the thermal strategy of tunas and some sharks may be called heterothermy (4) or mesothermy (5). Some teleosts, including billfishes (Xiphiidae and Istiophoridae), the opah *Lampris guttatus*, and possibly the butterfly mackerel *Gasterochisma melampus*, do not have warmed RM but have warmed eyes and brain, a thermal strategy called cranial endothermy (2, 6).

Swim Speed from Acoustic Tracking Studies. A difficulty associated with extracting swim speed data from acoustic tracking studies was that the authors often reported only the horizontal speed of the fish (as "rate of movements") calculated from the horizontal track. Horizontal speed can be an underestimate of the true speed in the water column because fishes generally move vertically as well. To attain the best balance between the quantity and quality of the data collection, we grouped the acoustic tracking studies into those made in coastal or inland waters, and those made in pelagic waters. For the studies made in coastal or inland waters, horizontal speed of the fish was accepted as its true speed ("Acoustic tracking 2D" in the method column of Table S1), assuming that vertical movement is sufficiently small compared with horizontal movement in those shallow environments. In the pelagic waters, in contrast, many fishes show large, frequent vertical movement (7), and, thus, horizontal speed was not accepted as the true speed of the fish. Instead, we only accepted studies that estimated the speed of the pelagic fish in the 3D coordinates by combining the horizontal track and depth record of the fish ("Acoustic tracking 3D" in Table S1).

Body Mass and Body Temperature. In our comparative analyses of swim speed, body mass was used as a measure of body size of the animals (Table S1), although body length was normally easier to measure in fishes and, thus, more frequently reported. This choice is because fishes in our dataset vary greatly in body shape (e.g., ocean sunfish, flounder, and eel), presumably making body length a poor predictor of swim speed. Body mass is likely a better predictor of the amount of locomotory muscle and, hence, swimming performance. Moreover, the collection of body mass data for the fishes in our datasets allowed the direct comparison of allometric relationships of swim speed between fishes (this study) and nonfish vertebrate swimmers reported (8). When body mass was not reported in the data source for swim speed (9–22), it was estimated from body length by using published length–mass relationships for the species or a closely related species. Length–mass relationships have not been published for the whale shark, the largest fish species in the world. The mass for this species was set on the basis of catch records for an individual of a similar length (2.2 tons for a 5.7-m individual; ref. 23).

Body temperature was also estimated for each species in the swim speed dataset (Table S1). For fishes with RM endothermy, it was set at the value reported for the species (24–29). For fishes without RM endothermy, body temperature was set as the mean water temperature experienced by the fish at their swimming depth. When such data were unavailable (9, 10, 15, 19, 20, 22, 30–32), it was estimated by using global water temperature maps available for each month at various depths, provided by the National Oceanic and Atmospheric Administration (33).

In our comparative analyses of migration range, body mass was used as a measure of body size (Table S2). When only body length was reported in the data source (34–46), body mass was estimated by using the length-mass relationships for the species or a closely related species. When neither body mass nor length was reported (47–54), an average body mass for the species was used.

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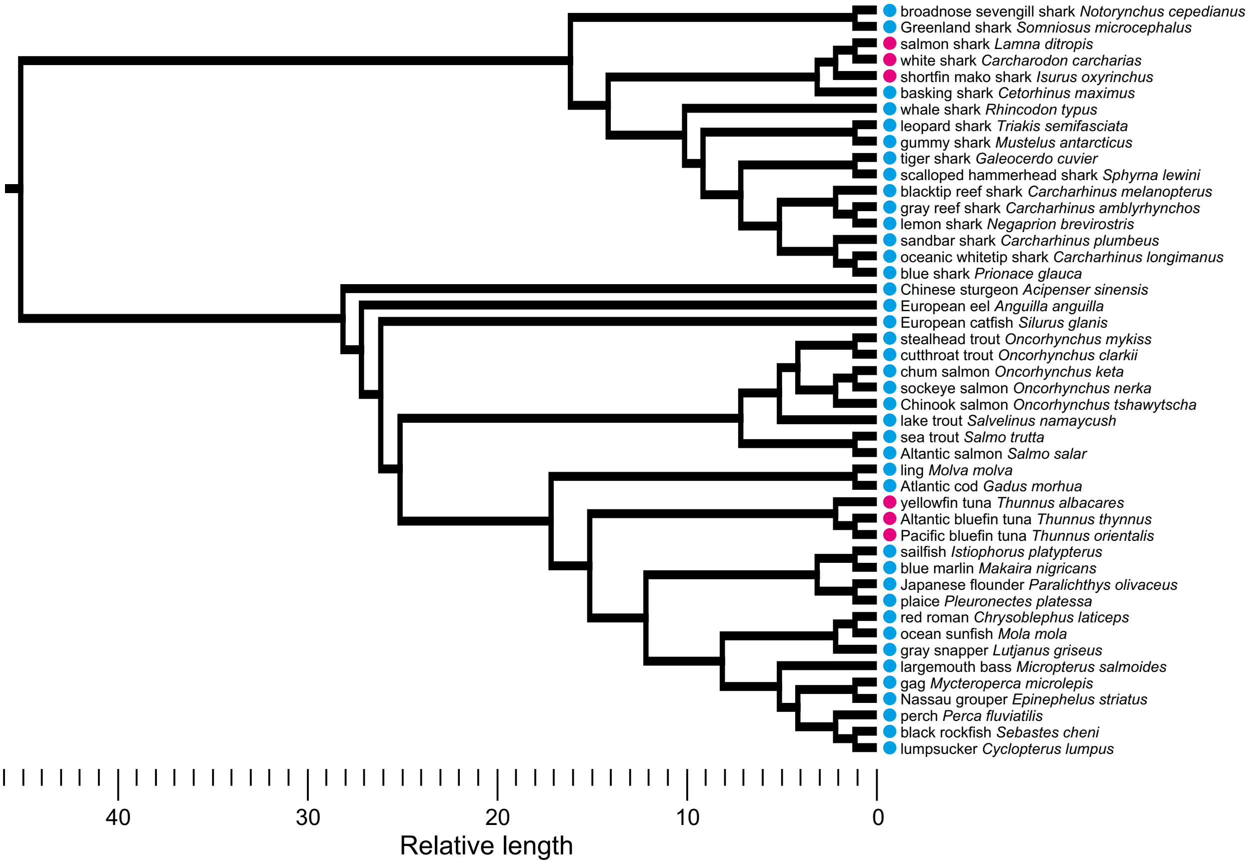

Fig. S1. Phylogenetic tree used in the comparative analysis of swim speed and the cost of transport. Pink and light blue circles represent fishes with and without RM endothermy, respectively.

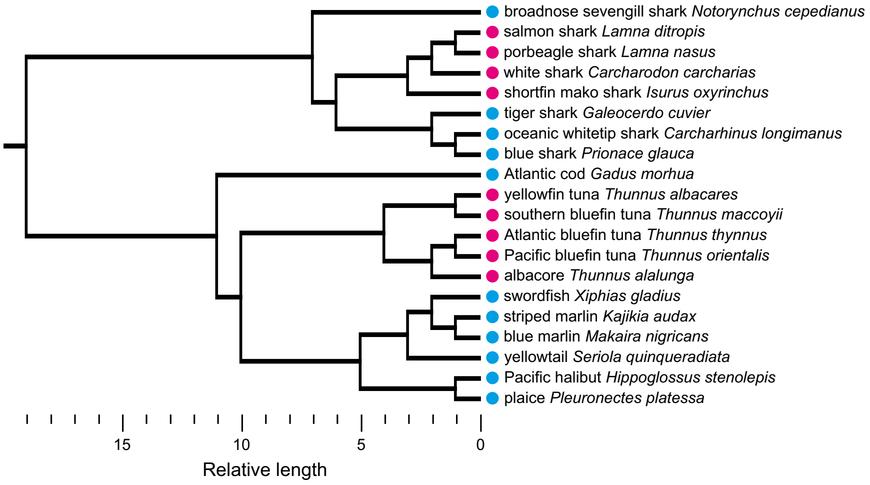

Fig. S2. Phylogenetic tree used in the comparative analysis of migration range. Pink and light blue circles represent fishes with and without RM endothermy, respectively.

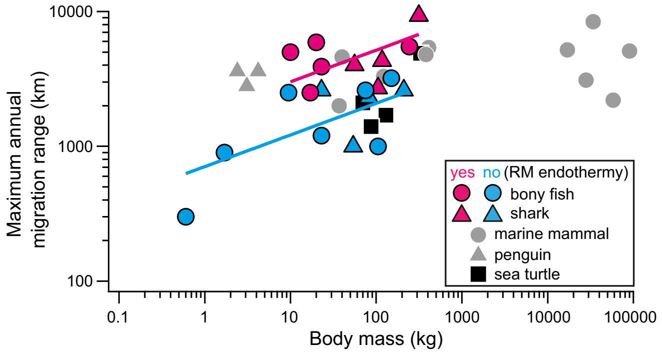

Fig. S3. The maximum annual migration ranges of various vertebrate swimmers as a function of body mass. Fishes with and without RM endothermy (pink and light blue, respectively) are shown with their phylogenetically informed regression lines (see main text for equations). For comparison, marine mammals, penguins (gray), and sea turtles (black) are also shown.

Table S1. Cruising speed of fishes recorded in the wild, and their energetics estimated for that speed

Group	Species	RM endothermy	Body length, m	Body mass, kg	Swim speed, $m \cdot s^{-1}$	Body temp, °C	Basal metabolic rate, W	Routine metabolic rate, W	Cost of transport, $J \cdot kg^{-1} \cdot m^{-1}$	Method	Source
Shark	Broadnose sevengill shark *Notorynchus cepedianus*	No	2.13	50	0.48	16	5.4	8.2	0.34	Acoustic tracking 2D	1
	Greenland shark *Somniosus microcephalus*	No	2.98	263	0.34	2	11.5	14.6	0.16	Speed sensor	2
	Salmon shark *Lamna ditropis*	Yes	2.15	155	1.09	25 (13)[†]	38.1	82.5	0.49	Speed sensor	This study
	White shark *Carcharodon carcharias*	Yes	3.60	428	2.25	26 (15)[†]	102.9	250.7	0.26	Acoustic tracking 2D	3
	Shortfin mako shark *Isurus oxyrinchus*	Yes	1.10	16	1.86	22 (18)[†]	6.7	32.5	1.09	Acoustic tracking 3D	4
	Basking shark *Cetorhinus maximus*	No	4.00	400	1.08	13	29.0	46.9	0.11	Boat	5
	Whale shark *Rhincodon typus*	No	6.00	2200	0.85	25	236.3	313.3	0.17	Pitch	6
	Leopard shark *Triakis semifasciata*	No	1.19	7.7	0.34	18	1.2	1.9	0.73	Acoustic tracking 2D	7
	Gummy shark *Mustelus antarcticus*	No	0.88	2.3	0.33	16	0.36	0.67	0.89	Acoustic tracking 2D	1
	Tiger shark *Galeocerdo cuvier*	No	3.57	266	0.69	26	38.8	56.0	0.31	Speed sensor	8
	Scalloped hammerhead shark *Sphyrna lewini*	No	0.57	0.76	0.46	26	0.23	0.64	1.84	Tailbeat	9
	Blacktip reef shark *Carcharhinus melanopterus*	No	1.20	11.9	0.52	29	2.9	5.9	0.95	Speed sensor	This study
	Gray reef shark *Carcharhinus amblyrhynchos*	No	1.57	26.1	0.59	28	5.6	10.4	0.67	Speed sensor	This study
	Lemon shark *Negaprion brevirostris*	No	1.71	27	0.63	22	4.2	7.9	0.46	Speed sensor	10
	Sandbar shark *Carcharhinus plumbeus*	No	0.83	5.2	0.42	22	1.0	2.2	0.99	Acoustic tracking 2D	11
	Oceanic whitetip shark *Carcharhinus longimanus*	No	2.09	97	0.71	25	15.2	27.1	0.39	Speed sensor	This study
	Blue shark *Prionace glauca*	No	2.52	105	0.44	22	14.0	19.7	0.43	Speed sensor	12
Bony fish	Chinese sturgeon *Acipenser sinensis*	No	2.97	198	1.10	20	22.2	41.0	0.19	Speed sensor	13
	European eel *Anguilla anguilla*	No	0.81	1.18	0.42	13	0.17	0.38	0.76	Acoustic tracking 2D	14
	European catfish *Silurus glanis*	No	1.21	10.3	0.36	18	1.5	2.5	0.68	Acoustic tracking 2D	15
	Stealhead trout *Oncorhynchus mykiss*	No	0.79	5.0	0.71	13	0.61	1.9	0.53	Acoustic tracking 2D	16
	Cutthroat trout *Oncorhynchus clarkii*	No	0.49	1.01	0.22	12	0.14	0.29	1.32	Acoustic tracking 2D	17

Table S1. Cont.

Group	Species	RM endothermy	Body length, m	Body mass, kg	Swim speed, $m \cdot s^{-1}$	Body temp, °C	Basal metabolic rate, W	Routine metabolic rate, W	Cost of transport, $J \cdot kg^{-1} \cdot m^{-1}$	Method	Source
	Chum salmon *Oncorhynchus keta*	No	0.65	3.3	0.75	15	0.47	1.7	0.70	Speed sensor	18
	Sockeye salmon *Oncorhynchus nerka*	No	0.67	2.5	0.67	11	0.30	1.0	0.60	Acoustic tracking 2D	19
	Chinook salmon *Oncorhynchus tshawytscha*	No	0.84	6.2	0.64	15	0.82	2.3	0.57	Acoustic tracking 2D	20
	Lake trout *Salvelinus namaycush*	No	0.58	2.14	0.69	21	0.44	1.6	1.10	Acoustic tracking 2D	21
	Sea trout *Salmo trutta*	No	0.20	0.062	0.14	11	0.012	0.030	3.50	Acoustic tracking 2D	22
	Altantic salmon *Salmo salar*	No	0.15	0.025	0.09	11	0.0053	0.012	5.68	Acoustic tracking 2D	23
	Ling *Molva molva*	No	0.60	0.6	0.08	8	0.074	0.10	2.02	Acoustic tracking 2D	24
	Atlantic cod *Gadus morhua*	No	0.40	0.8	0.29	5	0.082	0.22	0.95	Acoustic tracking 2D	25
	Yellowfin tuna *Thunnus albacares*	Yes	0.80	11.7	1.24	28 (23)[†]	4.2	19.4	1.34	Acoustic tracking 3D	26
	Altantic bluefin tuna *Thunnus thynnus*	Yes	2.46	240	2.00	25 (13)[†]	50.9	146.0	0.30	Acoustic tracking 3D	27
	Pacific bluefin tuna *Thunnus orientalis*	Yes	1.00	22.6	1.37	25 (16)[†]	7.4	30.8	0.99	Acoustic tracking 3D	28
	Sailfish *Istiophorus platypterus*	No*	1.34	20	0.64	22	3.3	6.9	0.54	Acoustic tracking 2D	29
	Blue marlin *Makaira nigricans*	No*	2.20	85	0.50	28	15.7	23.9	0.56	Speed sensor	30
	Japanese flounder *Paralichthys olivaceus*	No	0.52	2.2	0.31	14	0.31	0.75	1.09	Speed sensor	31
	Plaice *Pleuronectes platessa*	No	0.42	0.68	0.24	7	0.079	0.18	1.12	Acoustic tracking 2D	32
	Red roman *Chrysoblephus laticeps*	No	0.32	0.48	0.14	19	0.11	0.21	3.16	Acoustic tracking 2D	33
	Ocean sunfish *Mola mola*	No	1.15	87	0.60	16	8.8	19.4	0.37	Speed sensor	34
	Gray snapper *Lutjanus griseus*	No	0.33	0.69	0.57	29	0.24	1.2	3.04	Acoustic tracking 2D	35
	Largemouth bass *Micropterus salmoides*	No	0.40	0.93	0.12	6	0.10	0.17	1.50	Acoustic tracking 2D	36
	Gag *Mycteroperca microlepis*	No	0.66	3.8	0.14	18	0.62	0.92	1.74	Acoustic tracking 2D	37
	Nassau grouper *Epinephelus striatus*	No	0.73	6.0	0.53	27	1.5	3.9	1.22	Acoustic tracking 2D	38
	Perch *Perca fluviatilis*	No	0.26	0.26	0.10	18	0.059	0.11	4.26	Acoustic tracking 2D	39

Table S1. Cont.

Group	Species	RM endothermy	Body length, m	Body mass, kg	Swim speed, $m \cdot s^{-1}$	Body temp, °C	Basal metabolic rate, W	Routine metabolic rate, W	Cost of transport, $J \cdot kg^{-1} \cdot m^{-1}$	Method	Source
	Black rockfish *Sebastes cheni*	No	0.21	0.157	0.06	21	0.044	0.073	7.71	Acoustic tracking 2D	40
	Lumpsucker *Cyclopterus lumpus*	No	0.43	3.2	0.20	8	0.32	0.67	1.05	Acoustic tracking 2D	41

*These species have cranial endothermy, in which eye and brain temperatures are elevated. See the terminology section in *SI Materials and Methods* for details.

†Body temperature is different from the ambient water temperature (shown in parentheses) in fishes with RM endothermy.

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Table S2. Maximum annual migration range of vertebrate swimmers

Group	Species	Elevated body core temperature	Body mass, kg	Maximum migration range, km	Distal positions on migration path	Method	Source
Shark	Broadnose sevengill shark *Notorynchus cepedianus*	No	54	1,000	S44°00′ E147°30′ S35°00′ E151°00′	Pop-up tag	1
	Salmon shark *Lamna ditropis*	Yes	117	4,300	N58°00′ W152°00′ N26°00′ W120°00′	Argos tag	2
	Porbeagle shark *Lamna nasus*	Yes	105	2,700	N44°00′ W69°00′ N20°00′ W62°00′	Pop-up tag	3
	White shark *Carcharodon carcharias*	Yes	315	9,300	S37°00′ E15°00′ S22°00′ E113°50′	Pop-up tag	4
	Shortfin mako shark *Isurus oxyrinchus*	Yes	56	4,000	N46°00′ W44°00′ N10°00′ W48°00′	Argos tag	5
	Tiger shark *Galeocerdo cuvier*	No	210	2,600	S11°00′ E132°00′ S24°00′ E111°00′	Argos tag	5
	Oceanic whitetip shark *Carcharhinus longimanus*	No	82	2,300	N30°00′ W76°00′ N18°00′ W58°00′	Pop-up tag	6
	Blue shark *Prionace glauca*	No	23	2,600	N34°00′ W46°00′ N49°00′ W22°00′	Argos tag	7
Bony fish	Atlantic cod *Gadus morhua*	No	1.7	900	N58°00′ E11°20′ N52°00′ E02°00′	Archival tag	8
	Yellowfin tuna *Thunnus albacares*	Yes	17	2,500	N33°00′ W119°00′ N17°00′ W137°00′	Archival tag	9
	Southern bluefin tuna *Thunnus maccoyii*	Yes	20	5,900	S38°00′ E140°00′ S31°00′ E75°00′	Archival tag	10
	Atlantic bluefin tuna *Thunnus thynnus*	Yes	244	5,500	N24°00′ W73°00′ N47°00′ W16°00′	Pop-up tag	11
	Pacific bluefin tuna *Thunnus orientalis*	Yes	23	3,900	N25°00′ W113°00′ N37°00′ W152°00′	Archival tag	9
	Albacore *Thunnus alalunga*	Yes	10	5,000	N30°00′ W180°00′ N45°00′ W126°00′	Archival tag	12
	Swordfish *Xiphias gladius*	No*	150	3,200	N41°50′ W65°40′ N14°00′ W75°00′	Pop-up tag	13
	Striped marlin *Kajikia audax*	No*	75	2,600	S34°10′ E172°20′ S14°00′ E158°00′	Pop-up tag	14
	Blue marlin *Makaira nigricans*	No*	105	1,000	N27°50′ W95°30′ N19°30′ W92°60′	Pop-up tag	15
	Yellowtail *Seriola quinqueradiata*	No	9.5	2,500	N28°40′ E124°10′ N46°30′ E141°00′	Archival tag	16
	Pacific halibut *Hippoglossus stenolepis*	No	23	1,200	N59°00′ W141°00′ N54°50′ W158°30′	Pop-up tag	17
	Plaice *Pleuronectes platessa*	No	0.6	300	N57°30′ E03°50′ N54°40′ E04°00′	Tidal location	18
Marine mammal	Humpback whale *Megaptera novaeangliae*	Yes	34,000	8,400	S65°21′ W64°58′ N08°39′ W83°43′	Photo ID	19
	Blue whale *Balaenoptera musculus*	Yes	90,000	5,100	N19°00′ W106°00′ N52°00′ W147°00′	Argos tag	20
	Gray whale *Eschrichtius robustus*	Yes	17,000	5,200	N26°40′ W113°20′ N54°20′ W164°50′	Radio tag	21
	North Atlantic right whale *Eubalaena glacialis*	Yes	58,000	2,200	N31°10′ W80°50′ N44°30′ W62°50′	Argos tag	22
	Bowhead whale *Balaena mysticetus*	Yes	28,000	3,100	N62°00′ W178°00′ N74°00′ W105°00′	Argos tag	23
	Northern fur seal *Callorhinus ursinus*	Yes	40	4,600	N60°00′ W171°00′ N33°00′ W122°00′	Argos tag	24
	Antarctic fur seal *Arctocephalus gazella*	Yes	37	2,000	S54°00′ W38°00′ S43°30′ W60°00′	Argos tag	25
	Northern elephant seal *Mirounga angustirostris*	Yes	410	5,400	N37°06′ W122°20′ N41°00′ E174°00′	Argos tag	26
	Southern elephant seal *Mirounga leonina*	Yes	380	4,800	S54°40′ E158°60′ S57°00′ W120°00′	Argos tag	27
	Hooded seal *Cystophora cristata*	Yes	122	3,300	N75°00′ W13°00′ N51°00′ W55°00′	Argos tag	28

Table S2. Cont.

Group	Species	Elevated body core temperature	Body mass, kg	Maximum migration range, km	Distal positions on migration path	Method	Source
Penguin	Macaroni penguin *Eudyptes chrysolophus*	Yes	4.2	3,600	S49°30′ E70°30′ S51°00′ E122°00′	Archival tag	29
	Northern rockhopper penguin *Eudyptes moseleyi*	Yes	3.1	2,800	S37°50′ E77°36′ S44°00′ E110°00′	Archival tag	29
	Eastern rockhopper penguin *Eudyptes filholi*	Yes	2.4	3,600	S49°30′ E70°30′ S49°00′ E121°00′	Archival tag	29
Sea turtle	Leatherback turtle *Dermochelys coriacea*	Yes	330	4,900	N47°00′ W55°00′ N3°00′ W47°00′	Argos tag	30
	Green turtle *Chelonia mydas*	No	130	1,700	N35°22′ E33°40′ N31°26′ E16°00′	Argos tag	31
	Hawksbill turtle *Eretmochelys imbricata*	No	87	1,400	N18°10′ W68°30′ N15°00′ W81°00′	Argos tag	32
	Loggerhead turtle *Caretta caretta*	No	70	2,100	N35°22′ E33°40′ N34°30′ E10°40′	Argos tag	31

*These species have cranial endothermy, in which eye and brain temperatures are elevated. See the terminology section in *SI Materials and Methods* for details.

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Table S3. Fitting of nonphylogenetic regression models

Model	R^2	AIC	ΔAIC	wAIC
Swim speed ~ Body mass + Body temp + Endothermy	0.70	−6.3	0	0.78
Swim speed ~ Body mass + Endothermy	0.67	−3.7	2.6	0.21
Swim speed ~ Body mass + Body temp	0.61	4.6	10.8	<0.01
Swim speed ~ Body mass	0.54	9.7	16.0	<0.01
Swim speed ~1	0	43.6	49.9	<0.01
COT ~ Body mass + Body temp + Endothermy	0.90	−48.1	0	0.89
COT ~ Body mass + Body temp	0.88	−43.8	4.3	0.10
COT ~ Body mass + Endothermy	0.85	−32.3	15.8	<0.01
COT ~ Body mass	0.82	−25.4	22.7	<0.01
COT ~1	0	50.4	98.5	<0.01
Migration range ~ Body mass + Endothermy	0.68	−1.7	0	>0.99
Migration range ~ Body mass	0.37	10.3	12.0	<0.01
Migration range ~1	0	17.4	19.1	<0.01

The best models are shown in bold. wAIC, Akaike weight.