Satellite Tagging and Cardiac Physiology Reveal Niche Expansion in Salmon Sharks

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Shark populations are declining globally, yet the movements and habitats of most species are unknown. We used a satellite tag attached to the dorsal fin to track salmon sharks (*Lamna ditropis*) for up to 3.2 years. Here we show that salmon sharks have a subarctic-to-subtropical niche, ranging from 2° to 24°C, and they spend winter periods in waters as cold as 2° to 8°C. Functional assays and protein gels reveal that the expression of excitation-contraction coupling proteins is enhanced in salmon shark hearts, which may underlie the shark's ability to maintain heart function at cold temperatures and their niche expansion into subarctic seas.

Many sharks are threatened by fishing around the world (*1*), and biological knowledge is urgently needed to design management strategies. Sharks have been tracked using short-term acoustic telemetry (*2*) and towed satellite tags, which are attached to large, slow-moving basking and whale sharks (*3*, *4*). Pop-up satellite archival tags (PATs) have also been used to track sharks (*5*, *6*); however, geolocations have root mean square errors of 0.89° of longitude and 1.47° of latitude (*7*). In this study, we used a Smart Position Only Tag (SPOT), designed with a small Argos transmitter, that permits direct attachment to the shark's dorsal fin (Fig. 1). This tag enables the tracking of sharks with near–real-time positions for multiple years (table S1). SPOT tags greatly improve geopositioning for sharks. After applying a filter, 59% of our salmon shark positions having errors under 1 km, based on Argos accuracies (Fig. 1 and table S2).

The movements and behaviors of 48 salmon sharks (total length = 233 ± 9 cm, mean ± SD) were recorded by tagging sharks in Prince William Sound (PWS), Alaska, with two types of electronic tags. SPOT tags (n = 38 sharks) uplinked to Argos satellites provided track lengths of 351 ± 38 days (mean ± SE) and 8715 ± 747 km (13,335 total days) (Fig. 1 and fig. S1). The longest distance traveled by an individual was 18,220 km over 640 days (shark 37380). By double tagging some sharks with SPOT and PAT tags (n = 21) and by tagging some individuals (n = 10) with PAT tags alone, we obtained 5048 days of behavioral and environmental data (mean length 163 ± 14 days). Archival records were obtained from three sharks recaptured after tagging in the vicinity of their release location (table S1). The sharks provided 187,680 measurements of ocean pressure and temperature from the surface to a depth of 832 m, demonstrating their value as platforms for oceanographic observations (Fig. 2).

Salmon sharks undergo a striking seasonal migration from subarctic to temperate and subtropical regions, presumably to forage or give birth to their young (Fig. 1 and fig. S1) (*8*). During summer and autumn, the majority of tagged salmon sharks (all females) were foraging in PWS and the Gulf of Alaska (GOA). In winter, some sharks embarked on their migration to the subtropics, whereas others remained in GOA waters (overwintering). In spring, the migrating sharks' habitat extended as far south as Hawaii (22°N), a new location record for the archipelago (*9*), and from 170°W to the North American continental shelf, covering oligotrophic waters in the subtropical gyre (fig. S2) as well as the productive waters of the California Current.

Salmon sharks have a broad thermal niche, and their subarctic winter habitat demonstrates

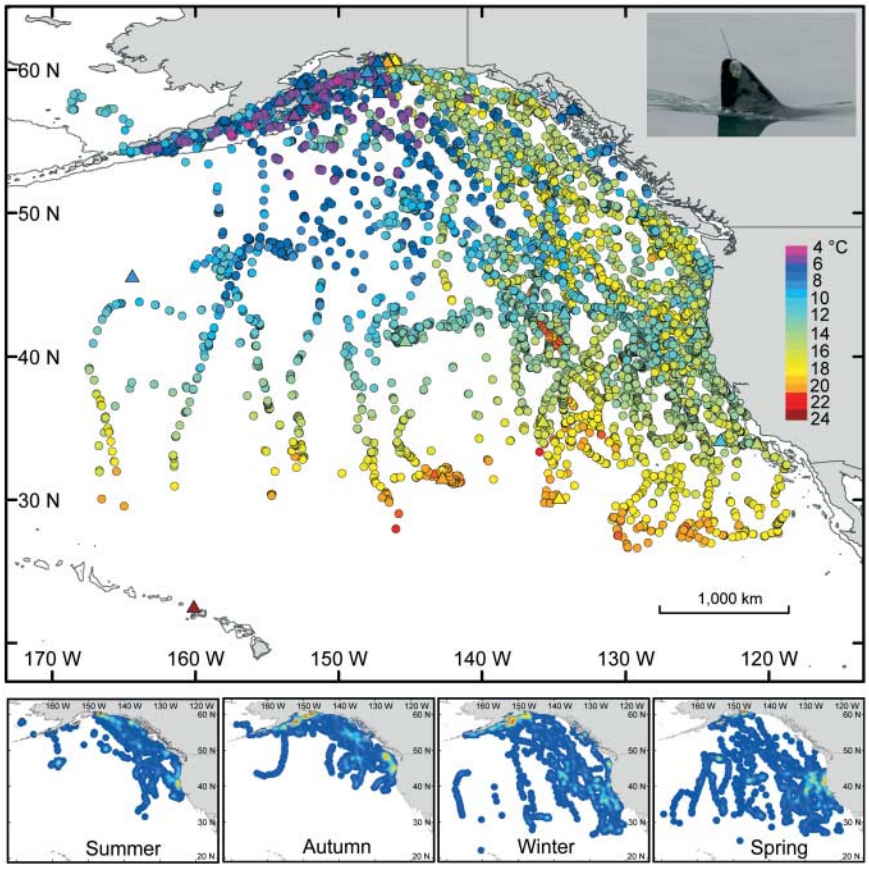

Fig. 1. Movements of salmon sharks in the eastern North Pacific. (**Top**) Salmon sharks occupy a broad region of the eastern North Pacific. Animals were tagged in Alaskan waters in July 2002, August 2003, and July 2004. Circles indicate SPOT positions and triangles indicate PAT satellite endpoint positions. (Inset) Photo of a salmon shark with a SPOT3 tag on the dorsal fin. (**Bottom**) Kernel density plots reveal extensive seasonal migrations. Salmon sharks used habitats in PWS and GOA most heavily in the summer and autumn, with some individuals overwintering in Alaskan waters. Sharks expanded their range southward in the winter and spring, encompassing a wide range of habitats from Hawaii to the North American coast.

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their tolerance of cold waters (Fig. 2). They inhabited waters from 2° to 24°C, spending much of their time (68 ± 6%) in waters cooler than 10°C and 72 ± 3% of their time in waters shallower than 50 m (Fig. 3). The sharks (n = 26) often remained in subarctic waters during winter, where they occupied depths from 0 to 368 m in an unstratified water column (Fig. 2A) with ambient temperatures of 2° to 8°C. PAT tags (n = 13) showed occupancy of these waters for mean durations of 53 ± 7 days and up to 96 days (690 total days), with 98 ± 1% of the time in water shallower than 150 m. Periods of submergence occurred, sometimes associated with temperature inversions, causing gaps in SPOT records (Fig. 2B). Salmon sharks are known to eat salmon (*10*) and herring (*11*). Whereas salmon are abundant in PWS during the summer and autumn, herring live there all year (*12*) and may be a prey species for sharks that overwinter. These data reveal that salmon sharks are major apex predators in Alaskan waters in all seasons, and this information could improve ecosystem models of PWS (*13*).

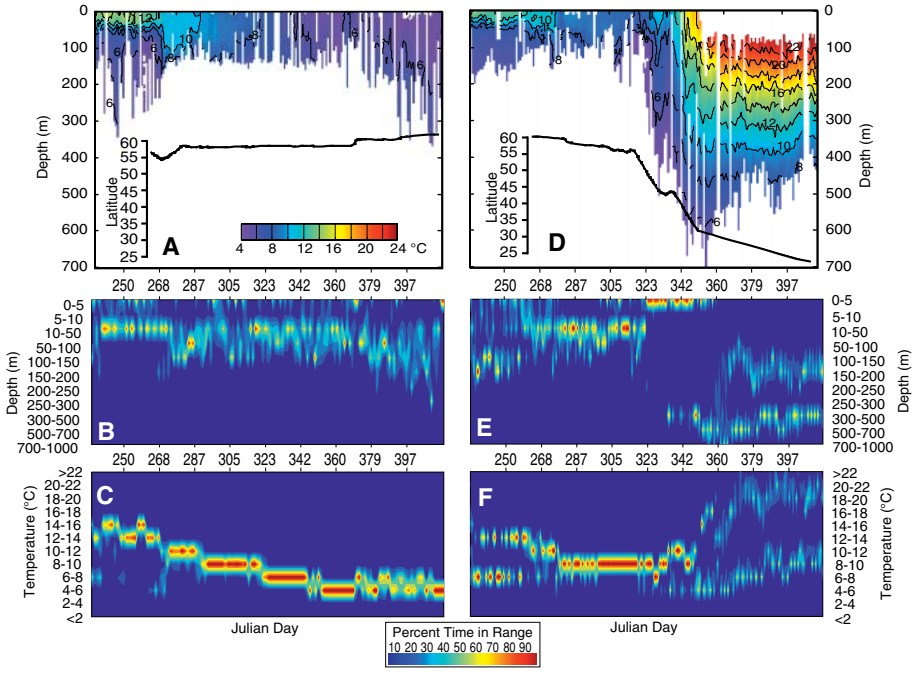

Fig. 2. Subarctic and subtropical depth and temperature preferences of salmon sharks. (**A**) Depth and temperature profiles of the water column along the track of a shark (41670) that overwintered in the GOA. The stratified summer water column cooled, and the thermocline dissipated in the autumn. Black lines show latitude. (**B** and **C**) Contour plots made from discrete measurements from PAT tags of (B) time-at-depth and (C) time-at-temperature show a preference for the shallow mixed layer through November, followed by deeper diving when an inversion developed in December and mixed layer waters cooled to 5° to 6°C. (**D**) The thermal profile slice along the track of a shark (41675) moving from Alaska to the subtropics shows an increase in temperature and strong thermal stratification. (**E**) Depth and (**F**) temperature preferences of the shark show a bimodal pattern in the warm subtropical gyre.

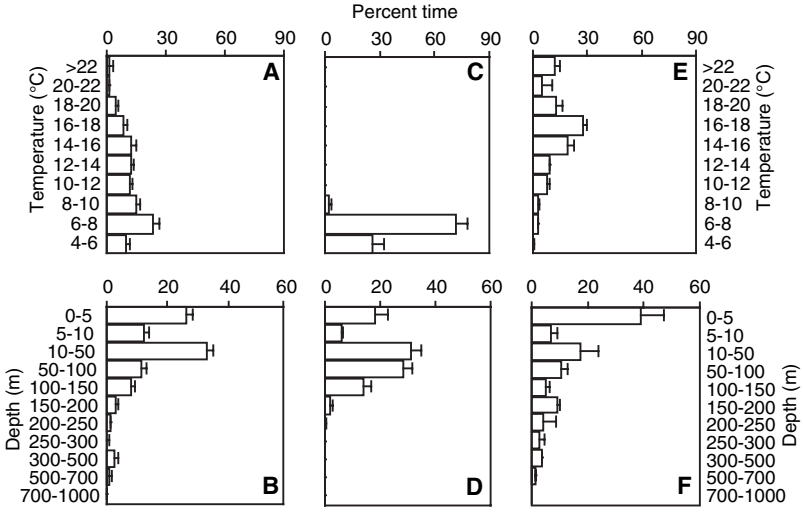

Fig. 3. Thermal and depth habitats of salmon sharks and blue sharks. (**A**) Thermal habitat for 22 PAT-tagged salmon sharks shows a broad thermal niche of 4°C to 24°C. Some sharks experienced temperatures that ranged as low as 2° to 4°C. (**B**) Salmon sharks spent 72 ± 3% of their time in the top 50 m. (**C**) PAT-tagged salmon sharks remaining in northern waters after the dissipation of the thermocline (n = 13) occupied 4° to 8°C waters and (**D**) occupied depth habitat predominantly shallower than 150 m. (**E**) Blue sharks (n = 15) preferred a warmer thermal environment, spending 44 ± 7% of their time in temperatures of 14° to 18°C, and had (**F**) depth preferences with greater time near the surface than salmon sharks. Error bars indicate SE.

Upon migrating to the subtropical gyre, salmon sharks (n = 19) encountered warmer waters (18° to 24°C) with increased thermal stratification (Figs. 1 and 2). PAT data (n = 4, averaging 43 ± 9 days) indicate distinct bimodal diving behaviors, with one occupancy peak in the upper thermocline (100 to 200 m) at temperatures from 18° to 20°C and another below the thermocline (300 to 500 m) in 6° to 8°C waters. In these warm waters, salmon sharks remained submerged for long durations, possibly because of a physiological limitation, causing considerable gaps in SPOT records. Sharks that moved into the eastern Pacific along the continental shelf (n = 12) occupied water with temperatures of 7° to 18°C and foraged from the surface to 356 m.

For comparison, we tagged blue sharks (n = 27; total length 197 ± 23 cm, mean ± SD) in the eastern North Pacific (figs. S3 and S4 and table S3), producing track lengths averaging 114 ± 14 days (2970 total days). Blue sharks in the eastern North Pacific inhabit pelagic and neritic waters from 104° to 157°W and 4° to 37°N. Blue sharks carrying PAT tags (n = 15) spent 74 ± 6% of their time in waters of 14° to 27°C, with 67 ± 5% of their time above 50 m in the upper mixed layer. They encountered sub-10°C temperatures only on brief dives beneath the thermocline, which made up 6 ± 2% of their records (Fig. 3E). Over the range tracked, the occupancy of waters cooler than 10°C was significantly greater for salmon sharks than for blue sharks (Mann-Whitney test, W = 30.5, P = 0.001).

The distribution of salmon sharks and their prolonged occupation of subarctic waters indicate a capacity to sustain cardiac performance at cold temperatures. Salmon sharks are members of the family Lamnidae, renowned for their endothermic physiology (*14*). High metabolic rates combined with extensive counter-current heat exchangers (*14*) enable this species to maintain body temperatures up to 21.2°C above water temperature (*15*). As in all endothermic fishes, the oxygen demands of warm metabolically active tissues are supplied by a heart

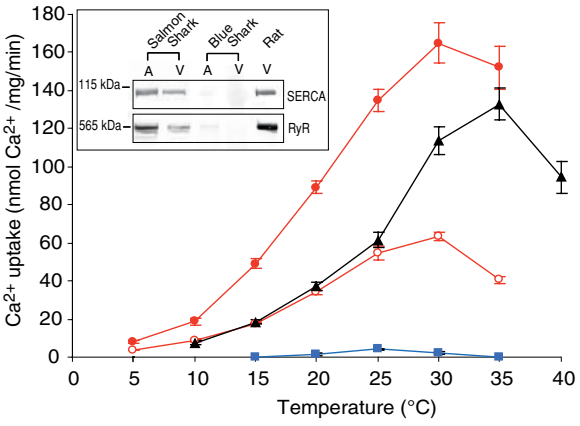

Fig. 4. Rate of SR Ca^{2+} uptake in salmon shark heart. Temperature dependence of Ca^{2+} uptake catalyzed by SERCA2 in microsomes from salmon shark atrium (red solid circles), salmon shark ventricle (red open circles), rat ventricle (black triangles), and blue shark atrium (blue squares). Values represent mean ± SE of experiments performed with preparations from at least four individuals. Absence of the appearance of error bars indicates that the error bars are smaller than symbol. (Inset) Immunoblot analysis of atrial (A) and ventricular (V) microsomes using a SERCA2-specific or RyR-specific polyclonal antibody.

operating at ambient temperature (*16*). We hypothesize that, similar to the *Thunnus* lineage (*17*), an increased expression of the proteins required for excitation-contraction coupling in the heart may underlie the ability to maintain cardiac contractility in the cold. This physiological trait may be a key specialization enabling thermal and geographic niche expansion into productive subarctic seas.

We measured the activity and expression of SERCA2, the sarcoplasmic reticulum (SR) Ca^{2+} adenosine triphosphatase (ATPase), which is a protein important for the maintenance of intracellular Ca^{2+} stores vital for beat-to-beat contractions. Salmon shark atrial SR vesicles have a high Ca^{2+} uptake rate, which is an order of magnitude greater than the rate for blue sharks (Fig. 4). SERCA2-dependent Ca^{2+} uptake could be measured at temperatures as cold as 5°C in salmon shark atrial and ventricular SR. The increase in the rate of Ca^{2+} uptake in the atrial tissues for each 10°C increase in temperature (Q_{10} values, 15° to 25°C) were 2.6 ± 0.4 (mean ± SE) and 4.8 ± 0.02 for salmon shark and blue shark, respectively. Ca^{2+} uptake was negligible in blue shark ventricular SR, so for comparison, we measured Ca^{2+} uptake rates in rat ventricular SR. At temperatures below 25°C, the activity of the SERCA2 enzyme in salmon shark ventricle microsomes was equivalent to that of rat ventricle vesicle preparations. Activity in the salmon shark vesicles dropped below that of the rat vesicles above 25°C. Q_{10} values (15° to 25°C) of ~3.3 for Ca^{2+} uptake in ventricular tissues were similar in salmon shark and rat.

Analysis of SR protein content showed high expression of SERCA2 and SR Ca^{2+} release channel (RyR2) proteins in salmon shark cardiac tissues (Fig. 4, inset) and in other sharks of the family Lamnidae (fig. S5). Densitometry indicated a 1.29 ± 0.72–fold greater SERCA2 expression in rat ventricle compared with salmon shark ventricle. The cold tolerance of salmon sharks may be directly related to this increased expression of SERCA2 and RyR2, which are crucial for maintaining rhythmic contractions of myocytes, cardiac output, and oxygenation of endothermic tissues. Enhanced SR CA^{2+} uptake and increased expression of SERCA2 has been shown to be a cardioproductive mechanism in hibernating mammals that are also resistant to cardiac dysfunction at cold temperatures (*18*).

Direct satellite telemetry from the dorsal fins of sharks reveals subarctic-to-subtropical migrations of salmon sharks over multiple years. The species' cardiac specializations and endothermy underlie its remarkable capacity to occupy a subarctic niche. Satellite tracking technologies can be used to rapidly map shark habitats worldwide, an objective that is critical to their future protection.

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Materials and Methods
Figs. S1 to S5
Tables S1 to S3
References

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EGFR Activation Mediates Inhibition of Axon Regeneration by Myelin and Chondroitin Sulfate Proteoglycans

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Inhibitory molecules associated with myelin and the glial scar limit axon regeneration in the adult central nervous system (CNS), but the underlying signaling mechanisms of regeneration inhibition are not fully understood. Here, we show that suppressing the kinase function of the epidermal growth factor receptor (EGFR) blocks the activities of both myelin inhibitors and chondroitin sulfate proteoglycans in inhibiting neurite outgrowth. In addition, regeneration inhibitors trigger the phosphorylation of EGFR in a calcium-dependent manner. Importantly, local administration of EGFR inhibitors promote significant regeneration of injured optic nerve fibers, pointing to a promising therapeutic avenue for enhancing axon regeneration after CNS injury.

Failure of successful axon regeneration in the CNS is attributed not only to the intrinsic regenerative incompetence of mature neurons, but also to the environment encountered by injured axons (*1*–*7*). The inhibitory activity is principally associated with components of