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Report

Transequatorial Migrations by Basking Sharks in the Western Atlantic Ocean

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Summary

The world's second largest fish, the basking shark (*Cetorhinus maximus*), is broadly distributed in boreal to warm temperate latitudes of the Atlantic and Pacific oceans from shallow coastal waters to the open ocean [1, 2]. Previous satellite archival tagging in the North Atlantic has shown that basking sharks move seasonally, are often associated with productive frontal zones [3, 4], and may make occasional dives to mesopelagic depths [3, 5]. However, basking sharks are thought to be restricted to temperate latitudes, and the extent to which they exploit deeper-water habitat remains enigmatic. Via satellite archival tags and a novel geolocation technique, we demonstrate here that basking sharks are seasonal migrants to mesopelagic tropical waters. Tagged sharks moved from temperate feeding areas off the coast of southern New England to the Bahamas, the Caribbean Sea, and onward to the coast of South America and into the Southern Hemisphere. When in these areas, basking sharks descended to mesopelagic depths and in some cases remained there for weeks to months at a time. Our results demonstrate that tropical waters are not a barrier to migratory connectivity for basking shark populations and highlight the need for global conservation efforts throughout the species range.

Results and Discussion

We deployed 25 pop-up satellite archival transmitting (PSAT) tags on basking sharks in the western North Atlantic off the coast of Cape Cod, Massachusetts, during the summer and autumn months. In total, 18 (72%) of the tags transmitted data to Argos satellites after deployment periods of 12–423 days (mean = 203 days). Pop-up locations spanned a broad geographic area in the western Atlantic from New England to the coast of Brazil south of the equator (Figure 1). Although eight of these locations were within the well-described range of this species [1, 6–9], the locations of the remaining tags significantly broaden the range of basking sharks to include the subtropical and tropical western Atlantic, including the Sargasso Sea (n = 3), the Bahamas (n = 2), the Puerto Rico Trench (n = 1), the Caribbean Sea (n = 1), and along the South American coasts of Guyana (n = 1) and Brazil (n = 2). Straight-line movements ranged from 120–6480 km (mean = 1904 km); five sharks moved over 2400 km. These distances are considerably longer than movements of basking sharks previously reported in the eastern North Atlantic [3, 5]. Our data represent not only the first documented movement of basking sharks into tropical latitudes but also the first known transequatorial movement of any fish species detected via archival tag technology.

We chose six representative sharks, spanning the likely range of migratory behaviors based on PSAT tag pop-up location, for more detailed analysis of archived data recorded by the tags. Temperature profiles from these sharks revealed remarkable diving behavior in five of the six individuals. These sharks traveled at mesopelagic depths (200–1000 m) for extended periods of time (Figure 2). Some individuals made relatively frequent excursions to the surface (Figure 2D), whereas others remained at depths between 250 and 1000 m for up to 5 months (Figures 2B, 2C, and 2E). The temperature profiles also showed sharks moving through distinct water masses during tag deployment. For instance, temperature profiles of two sharks located off the coast of Brazil at the time of tag pop-up showed the 5°C thermocline at a depth of 300–400 m (Figures 2E and 2F), whereas the 5°C thermocline was found at 750–1000 m for those sharks with tags reporting from the Bahamas (Figure 2B) and the northeast coast of the United States (Figure 2D).

Light levels during many dives were consistently below those required for conventional light-level geolocation. We were therefore unable to determine intermediate positions between tagging and pop-up during large periods of time for many of the sharks. To overcome this problem, we developed a new approach to estimate locations based on matching temperature depth profiles recorded by the tags with climatological temperature profiles from 1° or 4° bins in the western Atlantic Ocean. We then calculated the most probable tracks for six sharks via Kalman filter analysis [10] by combining estimated positions generated by both light-level geolocation and temperature profile analysis. The resulting tracks confirmed that movements of the tagged sharks were more extensive than pop-up locations alone would imply, and maximum estimated distances exceeded 9000 km (Figure 3). One of the sharks, confined to epipelagic waters for most of the tag deployment (Figure 2A), followed a migration pattern similar to that reported in earlier work [4] by overwintering in shelf waters off the coast of South Carolina (track A in Figure 3). Three sharks left coastal Massachusetts waters in early autumn, but instead of traveling south along the continental shelf, these individuals crossed the Gulf Stream and immediately began

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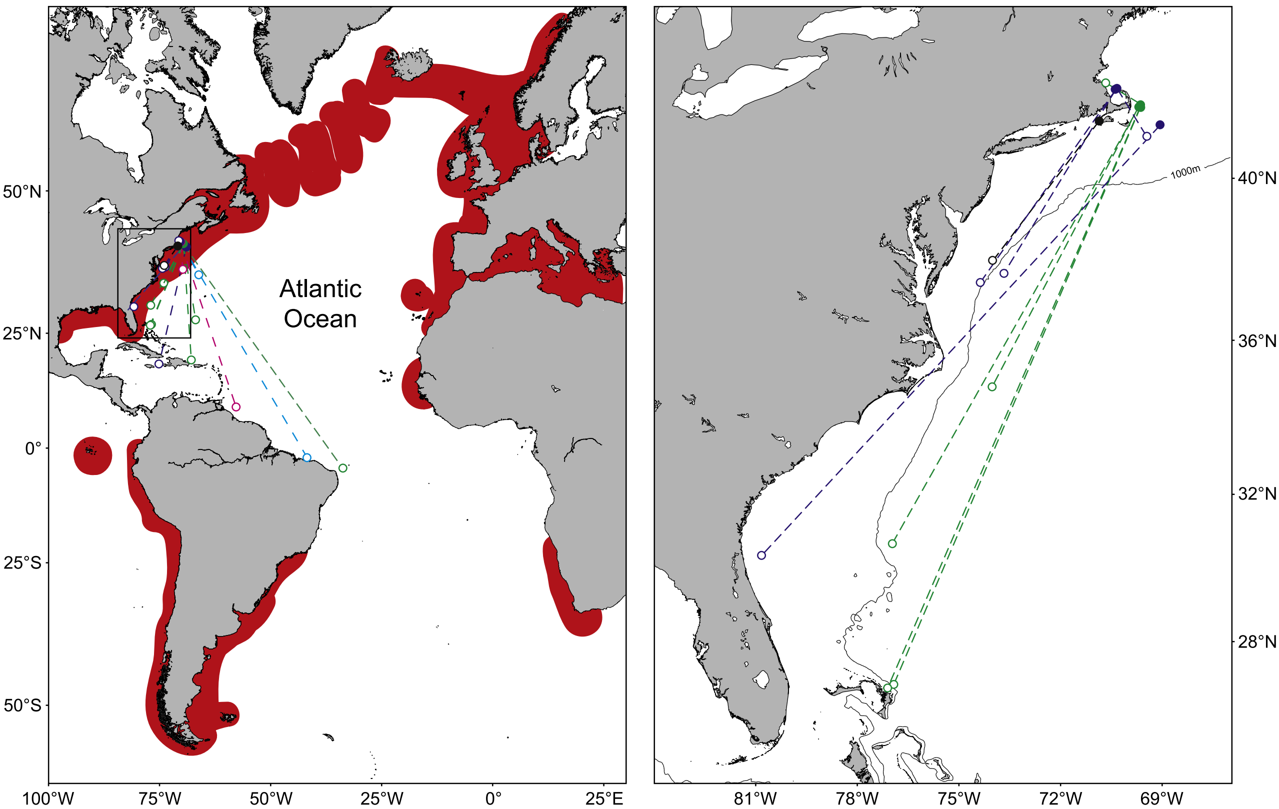

Figure 1. Basking Shark PSAT Locations Compared to Known Distribution

Left: tagging locations of basking sharks in coastal waters of Massachusetts (solid circles) and subsequent pop-up locations (open circles) of PSAT tags deployed in June (black symbols), July (green symbols), August (magenta symbols), September (dark blue symbols), and October (cyan symbols) in 2004 to 2006. Known basking shark distribution range is indicated by red shading.
Right: boxed region from left panel, enlarged to show tagging and pop-locations along the eastern coast of the United States.

making dives to depths of 800–1000 m. One of these three traveled as far south as the Puerto Rico Trench by October before heading north to the Bahamas (track B in Figure 3), whereas the other two were either in tropical waters north of Puerto Rico or had crossed into the Caribbean Sea by early January (tracks C and D in Figure 3). A fifth shark had traveled as far south as the coast of Venezuela by late January (track E in Figure 3). Perhaps the most intriguing result was the observation that two sharks made significant excursions into the tropical South Atlantic Ocean. The shark that moved the longest distance in

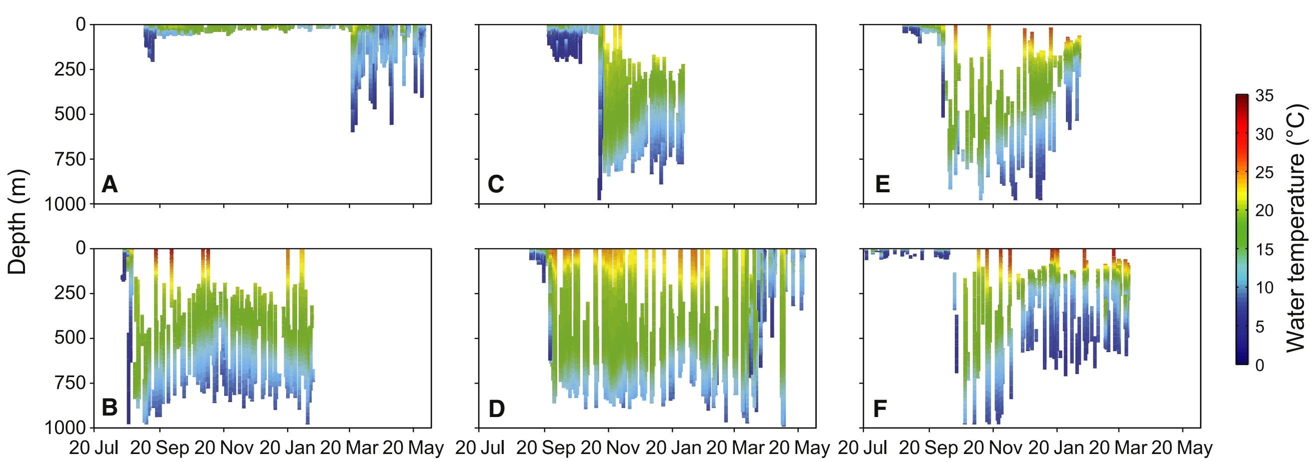

Figure 2. Basking Shark Vertical Behavior

Profiles showing ambient water temperatures as a function of depth recorded by PSAT tags on six basking sharks from the time of tag deployment until tag pop-up in Virginia coastal waters (A and D), the Bahamas (B), the northern Caribbean Sea (C), off the coast of Guyana (E), and off the coast of Brazil (F). Tags were deployed in 2004 (C), 2005 (A, B, and F), and 2006 (D and E).

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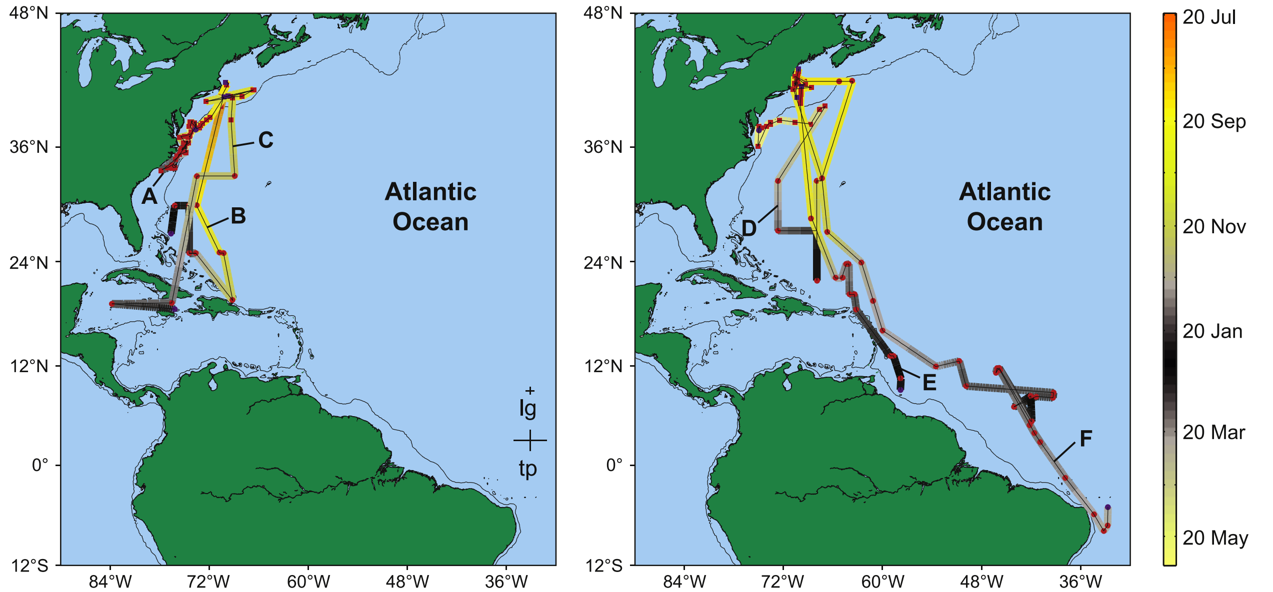

Figure 3. Basking Shark Movements Derived from Light-Based and Temperature Profile Geolocation Methods

Most probable movements of six basking sharks determined from light-level geolocation (red squares) or temperature profiles (red circles), along with location of tag deployment (purple squares) and tag pop-up (purple circles). Color gradients of individual movement tracks represent date, and track labels correspond to individual temperature profiles in Figure 2. Bars in left panel show mean latitudinal and longitudinal errors for light-level geolocation (lg) and temperature profile geolocation (tp).

our study remained in shelf waters off Cape Cod through the end of September before moving rapidly across the Gulf Stream, through the Sargasso Sea, and past the Windward and Leeward Islands in late November and early December. By January, this shark was offshore in the vicinity of the Amazon River mouth, where it remained for approximately one month before resuming a southward migration parallel to the coast of Brazil until tag pop-up in early May (track F in Figure 3).

The longstanding observation that basking sharks disappear during winter months has prompted researchers to hypothesize that seasonal declines in zooplankton force them to hibernate in deep offshore waters because feeding is no longer energetically profitable [11]. Prior to this study, PSAT tagging and energetics calculations dispelled some of this mystery by showing that basking sharks move seasonally in the North Atlantic to remain feeding yet are restricted to temperate latitudes [3, 4, 12]. However, the bulk of that tagging was conducted in the eastern Atlantic Ocean, where relatively stable environmental conditions mediated by the Gulf Stream may limit the extent to which basking sharks need to move during winter months to find sufficient food. In contrast, we found that basking sharks in the western Atlantic Ocean, which is characterized by dramatic seasonal fluctuations in oceanographic conditions, migrate well beyond their established range into tropical mesopelagic waters.

Our results shed further light on the apparent winter disappearance of this species [11]. Whereas the basking sharks occupied productive surface waters in temperate regions from late spring through early autumn, in winter months most of the individuals we tagged traveled the majority of the time (81%) at mesopelagic depths in tropical waters where the species has managed to avoid detection by humans to date. The seasonal decline of copepod abundance at higher latitudes in the western North Atlantic provides a rationale for southward migration of basking sharks to winter residence locations in highly productive shelf areas off the southeastern United States [4, 12]. However, there seems little justification for moving as far as the Southern Hemisphere based on energetics requirements alone.

Extensive migrations may be linked to the reproductive biology of basking sharks. The lack of pregnant females and neonates observed to date suggests that these individuals may be spatially or bathymetrically segregated [1, 13]. Females may spend spring and summer feeding in temperate shelf waters of the northwest Atlantic before migrating to tropical waters that provide stable conditions for gestation and parturition as well as suitable nursery habitat for neonates. Unfortunately, it was not possible to sex most of the tagged sharks, and we were therefore unable to determine whether males and females showed different movement patterns. Alternatively, basking sharks may be making ocean basin-scale migrations to mate or give birth in yet unknown locations in either the South Atlantic Ocean or, perhaps, the Pacific Ocean. A recent study of sequence variability in the mitochondrial DNA control region of basking sharks found worldwide panmixia that likely results from a historical population bottleneck or female-mediated gene flow [14]. Although these authors suggested that the low genetic diversity they documented argues for a significant population bottleneck in the recent past, our data raise the possibility that there may also be migratory connectivity of basking sharks on global spatial scales.

Basking sharks are currently listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora and categorized as Vulnerable on the IUCN Red List of Threatened Species [15]. Although the total number of basking sharks remaining in the world's oceans is not known, a recent estimate suggests that the effective global population size of the species is less than 10,000 individuals [14]. Our results have important conservation implications because tropical waters should no longer be considered a barrier to demographic or genetic connectivity among basking shark subpopulations. Global coordination of conservation efforts will therefore likely be necessary to rebuild basking shark populations throughout the species range.

Experimental Procedures

Tagging

Twenty-five basking sharks were tagged with pop-up satellite archival transmitting (PSAT) tags off the coast of Cape Cod, Massachusetts, in September 2004 (n = 2), June to October 2005 (n = 17), and September 2006 (n = 6). The PSAT tags, which recorded depth, temperature, and light levels at 10–15 s intervals, were programmed to release during the months of December, January, February, April, June, and September after periods ranging from 129 to 361 days. Of the 18 tags that reported, one tag shed prematurely (12 days), one reported 263 days late off of Massachusetts (total period of 423 days), one was found on a stranded shark in Rhode Island, and the balance popped up and immediately relayed data as programmed. Additional materials and methods are described in the Supplemental Data available online.

Geolocation

Geolocation estimates were generated with light-level data from the PSAT tags when available. When light levels were too low to provide an accurate geoposition, we estimated daily positions by comparing temperature profiles recorded by the PSAT tags with seasonal depth temperature profiles extracted from climatological data in the western Atlantic Ocean (see Supplemental Data). Geolocation estimates from both light-level data and temperature profiles were corrected or verified with weekly sea surface temperature (SST) data from the National Oceanic and Atmospheric Administration Geostationary Satellite (GOES) satellites. Light-level data provided an estimate of longitude and latitude that was then corrected by matching near-surface temperatures measured by the tags with the closest latitude at which the same SST value was measured by the GOES satellites. Location estimates from temperature depth profiles were considered acceptable if the near-surface water temperature for the estimated position measured by the PSAT tag was within $\pm 1.5^{\circ}$C of the corresponding weekly SST value in the box measured by the GOES satellites; otherwise, the data point was rejected from subsequent analyses. We used light-level geolocation data only if estimates from both techniques were available for the same day. Raw location data were then filtered with the KFtrack R package described in Supplemental Data to provide a most probable track for each of the six sharks.

Supplemental Data

The Supplemental Data include Supplemental Experimental Procedures and two figures and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)00978-6.

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