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Movements of three female silky sharks (*Carcharhinus falciformis*) as tracked by satellite-linked tags off the Caribbean coast of Cuba

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Marine Ecology and Conservation in Cuba

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ABSTRACT.—The silky shark, *Carcharhinus falciformis* (Müller and Henle, 1839), is a large circumtropical, oceanic, and coastal-pelagic species whose spatial ecology is not well understood. In Cuba, silky sharks are captured in local fisheries and are subjects for shark-based diving tourism off the Caribbean coast. Our study tracked three female *C. falciformis* (ranging 174–200 cm precaudal length) using satellite-linked tags to characterize the movement patterns and behavioral ecology of this species off the southeast coast of Cuba. Field work was conducted in the Jardines de la Reina (Gardens of the Queen) archipelago and utilized a novel in-water method for attaching pop-up satellite archival tags to free-swimming sharks. Results from both archival and position-only tags suggest the sharks traveled <30 km from the tagging site during the month-long deployments. The depth and temperature ranges recorded for two specimens were 0–640 m and 11.5–27.5 °C. Time-at-depth/temperature data revealed preferences for the upper-mixed layer (down to 150 m) and a temperature range of 24–27 °C. A diel vertical movement pattern was observed with silky sharks spending greater time at depth during the day than at night. Plasticity of vertical habitat utilization was noted with occasional forays to depths in excess of 550 m during both day and night. Daytime forays to surface waters were also observed and were most common during the morning hours between 09:00 and 11:00, possibly due to the ecotourism industry's use of bait during that time to attract sharks to the dive area.

The silky shark, *Carcharhinus falciformis* (Müller and Henle, 1839), is a common cosmopolitan species inhabiting oceanic and coastal-pelagic waters in all tropical oceans (Bonfil 2008). In the western Atlantic Ocean, the range of *C. falciformis* extends from Massachusetts to southern Brazil and includes the Gulf of Mexico (GOM) and Caribbean Sea (Compagno 1984). Despite its large size [to at least 314 cm total length (TL); Bonfil et al. 1993] and ubiquitous nature in warm seas, silky sharks are relatively understudied and many aspects of their life history are poorly known (Castro 2011).

Silky sharks are captured in directed shark fisheries and are an important bycatch in pelagic longline and purse seine fisheries targeting swordfish and tunas (Bonfil 2008, Rigby et al. 2016). The widespread practice of utilizing man-made fish aggregating devices (FADs) in tuna purse seine fisheries to increase catch rates while reducing search time has been shown to increase shark bycatch compared to fishing sets on free-schools of tuna (Gilman 2011). In tuna fisheries using FADs, the silky shark is by far the most commonly captured non-target species and can represent up to 90% of the elasmobranch bycatch (Gilman 2011). Total silky shark mortality for FAD-associated captures has been estimated at 92% (Eddy et al. 2016). In the global shark fin trade, *C. falciformis* ranks among the most important species (Clarke et al. 2005, 2006, Sembiring et al. 2015). As a result of high and sustained levels of fishing pressure across its range, there is growing evidence that silky shark abundance has declined globally in recent decades (Anderson and Juaharee 2009, Rigby et al. 2016). Given its vulnerability to various pelagic fisheries and relatively conservative life history characteristics, *C. falciformis* is listed as "Near Threatened" with a decreasing population trend on the IUCN Red List of Threatened Species (Rigby et al. 2016).

Our knowledge of the movements and migration of silky sharks is largely limited to results from conventional tagging (Kohler et al. 1998), a few published studies deploying satellite tags in the Pacific Ocean (Musyl et al. 2011, Hutchinson et al. 2015), and an acoustic telemetry study from the Red Sea (Clarke et al. 2011). Most of the conventional tagging in US waters has been under the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program and largely confined to shelf edge and pelagic waters of the northern GOM, eastern Florida, and off the mid-Atlantic states (Kohler et al. 1998). Recapture results demonstrate movement northward along the US east coast and exchange between the GOM and the Atlantic Ocean. Published studies using satellite-linked tags on *C. falciformis* have primarily been aimed at assessing post-release mortality, but also have provided some insight into movement patterns. The satellite tagging of juvenile silky sharks (93–145 cm TL, n = 26, 2.6 M:F sex ratio) in the southwest Pacific Ocean revealed diel vertical movement patterns within the upper 100 m of the water column and occasional forays to depths below the thermocline in excess of 300 m (Hutchinson et al. 2015). Larger silky sharks (116–200 cm TL, n = 10, 4.0 M:F sex ratio) tagged with pop-up satellite archival tags (PSATs) in the central Pacific Ocean remained in near-constant temperatures (approximately 26 °C) within the upper mixed layer (approximately 120 m), while their limited vertical movements demonstrated some plasticity, pronounced movements at crepuscular periods, and a correlation between average nighttime depth and lunar illumination (Musyl et al. 2011). In this same study, the potential for significant horizontal movements of the species was observed with a 170 cm TL male demonstrating a linear displacement (LD) of 1273 km while at liberty for 132 d (minimum LD was 138 km for another male specimen after 20 d at large).

Off Cuba, silky sharks are captured on both longline and drift net gear (NPOA-Sharks 2015). In a 1-yr survey (October 2010–November 2011) of the pelagic longline fishery of Cuba's northwest coast, the silky shark was the fifth-most abundant shark species landed (by number), out of 15 shark species observed (Aguilar et al. 2014). More recently, a nearly 5-yr (October 2010–April 2015) monitoring program of the same fishery documented *C. falciformis* as the second-most abundant pelagic shark species landed, exceeded only by the longfin mako, *Isurus paucus* Guitart, 1966 (NPOA-Sharks 2015). Silky sharks are often found off the north coast of Cuba associated with schools of little tunny, *Euthynnus alletteratus* (Rafinesque, 1810), and Cuban tuna fishermen consider the sharks to be helpful in herding the tunny into dense schools that make fishing easier (R Hueter, unpubl data). Off the south coast of Cuba, silky sharks are one of several target species for recreational scuba diving with sharks (Gallagher and Hammerschlag 2011, Puritz 2017). Shark-based ecotourism is a growing worldwide activity providing significant revenue for local economies (Gallagher and Hammerschlag 2011), and in Cuba, on both the north and south coasts, shark diving tourism is well established (Figueredo-Martín et al. 2010, NPOA-Sharks 2015).

Despite the silky shark's commercial importance in fisheries and ecotourism, our knowledge of this shark's movement patterns and behavioral ecology in Cuban waters, and in the western Atlantic region as a whole, is extremely limited. The goal of the present study was to use satellite-linked tagging methods to study the movements and behavior of silky sharks off Cuba and provide some range information to resource managers for effective management and conservation of this species.

Methods

Study Area.—Field work for the present study was conducted in the Jardines de la Reina (Gardens of the Queen) archipelago in the provinces of Camagüey and Ciego de Ávila, Cuba (Fig. 1). The 135 km long archipelago off Cuba's Caribbean coast is composed of numerous islets, shoals, and reefs, and lies between the Gulf of Ana María and the Gulf of Guacanayabo. Jardines de la Reina comprises one of the largest marine protected areas in Cuba. In 1996, about 950 km^2 of the area were placed into a special protection category by the Cuban government and the area was designated as a National Park in 2010, making it the largest marine reserve in the Caribbean Sea (Hernández Fernández et al. 2016, Puritz 2017).

PSAT Tags.—On 11 February, 2015, researchers using scuba dove the El Farallón dive site off the southern tip of Cayo Caballones (20.829°N, 78.982°W; Fig. 1). About a dozen silky sharks were attracted to the dive boat with teleost chum prior to the dive. The sharks were predominantly large (>2 m TL) females, with some males, and most stayed within the upper 6 m of the water column. We used a unique method to attach satellite tags to the free-swimming sharks, without the use of a hook, net, rope, or spear. Two snorkelers approached a shark of suitable size (>2 m TL) and sex (large females were preferred to gain insight into reproduction) and one of them (co-author NLF) grabbed the free-swimming animal by the extreme upper tip of the caudal fin, exerting just enough pressure to slow the shark's swimming and cause the animal to relax into a near-vertical, head-down position. With a firm pinch maintained on the caudal fin, the snorkeler steadily moved his other outstretched hand down the ventral surface of the shark, gently stroking the shark's abdomen, and slowly rotated the shark into a normal horizontal position. Although similar in effect to tonic immobility (TI; Kessel and Hussey 2015), the shark was never turned upside-down during the procedure. While the second snorkeler assisted as necessary to keep the shark relaxed and restrained, the first snorkeler brought the shark to the surface for

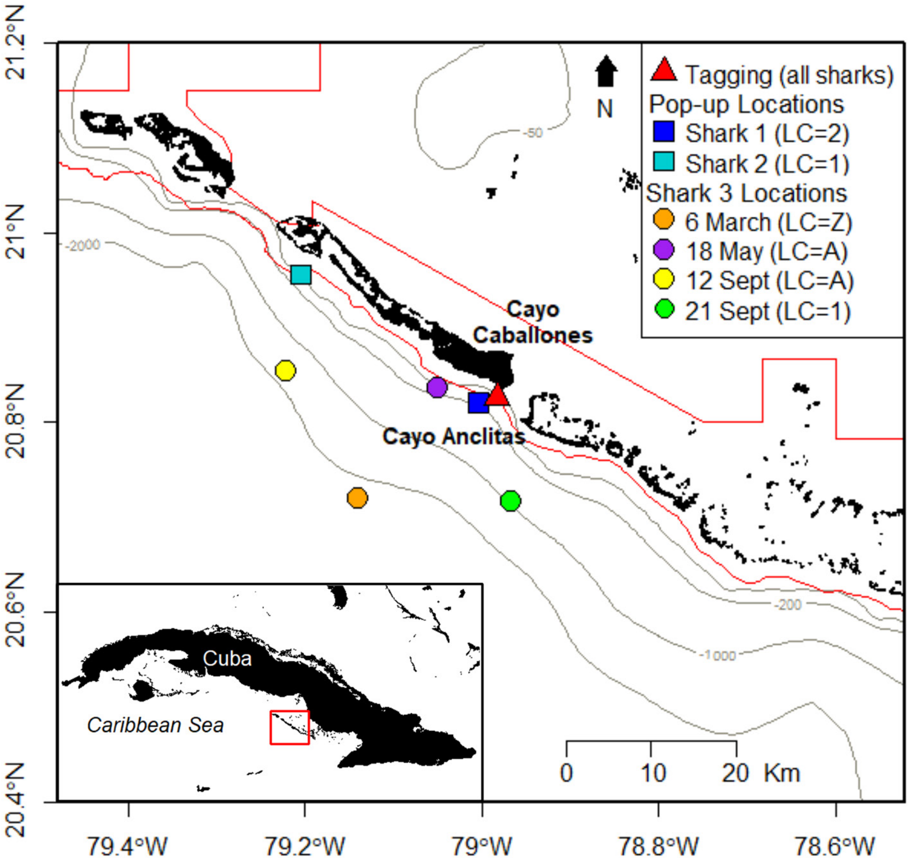

Figure 1. Jardines de la Reina study area and locations of tagging (triangle), pop-up of MiniPAT tags (squares), and SPOT tag transmissions (circles) for three female silky sharks, *Carcharhinus falciformis,* off the southeast coast of Cuba. Bathymetric contours (gray traces) for 50, 200, 1000, and 2000 m depths are shown. The Cuban National Park boundary is displayed as a red trace in the larger map. Estimated error radii for each location class (LC): LC3, <250 m; LC2, 250–500 m; LC1, 500–1500 m; LC0, >1500 m; LCA, B, and Z, no estimates provided (CLS 2016).

measurement and tagging by two researchers on scuba (Fig. 2). Shark length [precaudal length (PCL)] was measured with a measuring tape and a small scalpel cut was made to the shark's skin just below the base of the first dorsal fin, eliciting no reaction by the relaxed shark. A MiniPAT (Wildlife Computers, Redmond, WA) pop-up satellite tag was then attached to the shark using either a plastic (Domeier; 20 × 14 mm; Wildlife Computers) or stainless steel (Type SSD; 34 × 8.5 mm; Hallprint Pty, Ltd, South Australia, Australia) anchor inserted below the skin through the scalpel cut. The tag was attached to a 15-cm tether composed of stainless steel wire rope with a load capacity of 23 kg (Type 18-8; McMaster-Carr, Santa Fe Springs, CA). Upon insertion of the anchor, the shark reacted by swimming vigorously away.

The satellite tags archived temperature, pressure, and light level measurements at 3-s intervals and summarized these data into 12-hr periods to facilitate data transmission. Tags were programmed to detach from the sharks after either 90 or 120 d, float to the sea surface, and transmit summaries of their archived data via the Argos satellite system. The MiniPAT's time-at-depth (TAD) and time-at-temperature (TAT)

Figure 2. Non-invasive in-water procedure during the present study's deployment of MiniPATs on silky sharks, *Carcharhinus falciformis*. The photograph shows the measuring of a shark immediately prior to tag attachment.

histograms were programmed into the following ranges: 0, >0–2, >2–5, >5–15, >15–30, >30–50, >50–100, >100–200, >200–300, >300–400, >400–500, and >500 m; and 0–3, >3–6, >6–9, >9–12, >12–15, >15–18, >18–21, >21–24, >24–27, >27–30, >30–33, and >33 °C. These tags also were programmed to transmit a time series of depth and temperature readings (at a frequency of 300 or 450 s) through the Argos system.

A clear inert anti-fouling coating (Propspeed™, Propspeed USA, Miami, FL) had been applied to the MiniPATs excluding the sensors and release pins. To prevent tag destruction from extreme pressure, we used a mechanical release device (RD1800; Wildlife Computers) that would cut through the tether at depths exceeding 1800 m, releasing the tag. As an additional failsafe (e.g., in the event of a mortality), the tags were programmed to release from the tether if they remained at a near constant depth (±2.5 m) for 72 continuous hours. The tether, excluding the RD device portion, was protected with heat shrink tubing (3M, Two Harbors, MN).

Transmitted data for each tag were downloaded via the Argos website and processed using the manufacturer's software (DAP Processor 3.0). The data were exported as csv and pxp files and visually inspected using Igor Pro software (v6.3.4.1). Plots were constructed in either Igor Pro or SigmaPlot (v10.0). For analyzing the shark's horizontal movements, MiniPAT data were uploaded to the Wildlife Computers Data Portal (http://my.wildlifecomputers.com) for processing with GPE3 software. This statistical processing tool runs exclusively on the tag manufacturer's internet server and utilizes the tag data and corresponding sea surface temperature (SST) and bathymetry reference data as inputs into its gridded hidden Markov model, which generates the most likely animal location and a distribution of likelihoods as an indicator of location quality. The model provides an overall score as an indicator of how well the model fits the observed data. We ran the model with varying inputs of the animal speed parameter to generate a fit with an optimal score and realistic maximum likelihood track (MLT). To evaluate differences between day/night TAD distributions, we performed two-sample Kolmogorov-Smirnov (K-S) tests. Mean depths between day and night were compared with Welch's unequal variances *t*-test. Statistical analyses were performed by using the stats package for R (R Development Core Team 2015).

Smart Position or Temperature Transmitting Satellite Tag (SPOT).—On 11 February, 2015, a third silky shark was captured using a hand-line deployed from the stern of the Cuban research vessel Itajara at the El Farallón dive site. The fishing gear consisted of a monofilament mainline with a double-strand monofilament leader (both 700 lb test) and 9/0 nickel-plated swivel terminating with an 18/0 circle hook with zero offset and baited with barracuda, *Sphyraena barracuda* (Edwards, 1771). Upon capture, the shark was pulled aboard the boat and secured on deck for measurements and satellite tagging, during which its gills were irrigated with seawater via a hose inserted into the mouth. The shark was tagged with a SPOT tag that provides near real time estimates of the shark's position (model SPOT5 fin mount version; Wildlife Computers). Attachment of the SPOT required drilling four ¼-in holes using a predrilled template on the upper portion of the shark's first dorsal fin. The tag was secured with hardware provided by the tag manufacturer (four lengths of nylon-threaded, round bar stock fastened with stainless steel nuts with nylon locking inserts, and washers) and a neoprene-lined backing plate positioned on the opposite side of the fin. SPOT tags contain a saltwater switch that activates the tag when above the water's surface, enabling it to transmit a coded data stream to an orbiting satellite. The Argos Centers calculate the transmitter's position by measuring the Doppler shift of its transmit frequency. Each position is coded with a location class (LC = 3, 2, 1, 0, A, B, and Z) with LC = 3 having the highest accuracy (error of <250 m) and LC = Z resulting in no location without Auxiliary Location Processing (CLS 2016).

Results

PSAT Tagging.—The first silky shark (Shark 1), a 200-cm-PCL female, was satellite-tagged at the El Farallón dive area at 09:37 hrs (local time) on 11 February, 2015. The 90-d PSAT detached prior to the programmed date and began transmitting on 21 March, 2015. The initial Argos transmission came from a location off Cayo Caballones (20.82°N, 79.00°W), 2.4 km west-southwest from the tagging location (Fig. 1). Approximately 68% and 62% of the tag's histogram and time series data, respectively, were received for the 34-d track before the tag's battery power fell below the minimum threshold required for transmission, 16 d after pop-up. A second silky shark (Shark 2), a 174-cm-PCL female, was satellite-tagged in the same dive area at 12:14 hrs on 11 February, 2015. The 120-d tag also detached early and began transmitting on 19 March, 2015. The first Argos transmission received was from a location northwest of Cayo Caballones (20.96°N, 79.21°W), 27.3 km west-northwest from the tagging site (Fig. 1). Transmitted data were received over a period of 23 d, with approximately 81% and 87% of the histogram and time series data, respectively, received for the 32-d track before the tag's battery failed. Efforts to recover the detached tags in the field were unsuccessful.

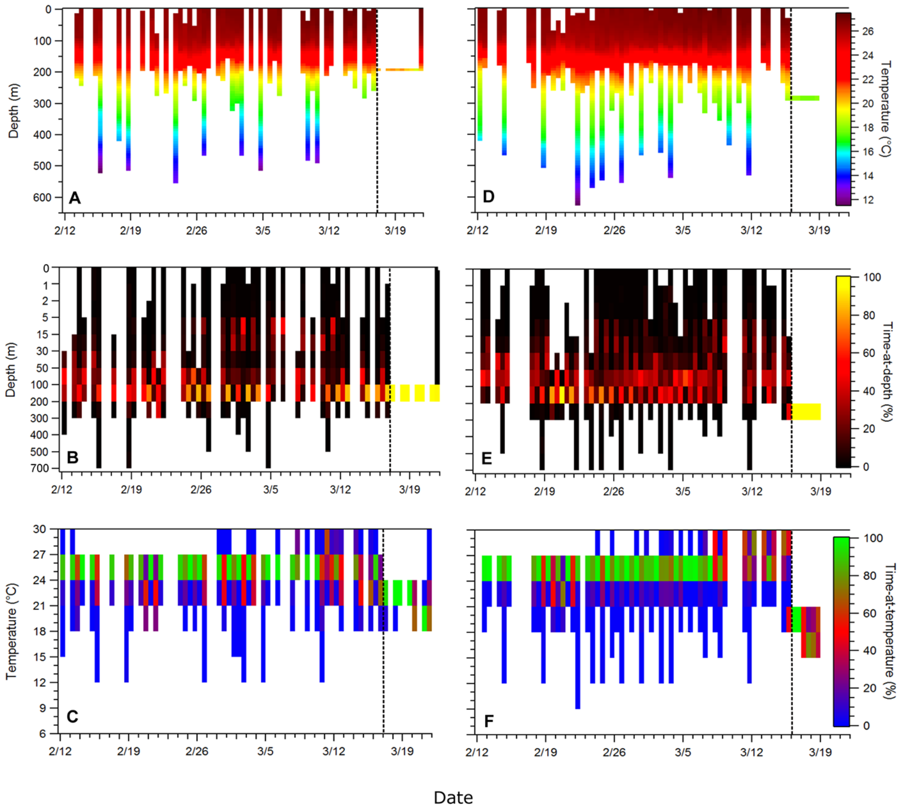

Figure 3. Use of vertical habitat for two satellite-tagged silky sharks, *Carcharhinus falciformis*. (A) Daily depth-temperature profile for Shark 1. (B) Daily time-at-depth utilization for Shark 1. (C) Daily time-at-temperature for Shark 1. Panels D, E, and F contain the same information for Shark 2. Broken lines indicate the approximate point of tag detachment. Gaps represent periods where no data of that type were received.

The GPE3 model was able to generate MLTs for the two silky sharks tagged with MiniPATs (Sharks 1 and 2). Both tracks showed an offshore, southerly loop of movement away from the archipelago (maximum distance of 346 km from the tagging site) before returning to the study area. However, one of the two sharks tagged with a MiniPAT was resighted and photographed at the El Farallón dive site on 4 March, 2015 (21 d after tagging). It is unclear which of the two sharks this was, but this confirmed resighting conflicted with the GPE3-generated MLTs of both Sharks 1 and 2, which were calculated to be 150 and 115 km, respectively, south of the dive site on that particular day. Given this inconsistency and that the pop-up locations of both tags were close to the tagging locations (<28 km; Fig. 1), it is unlikely these MLTs were accurate representations of the sharks' movements. Therefore, we do not show them here. In instances where track duration is short and actual horizontal movement away from a tagging site is limited, the error associated with the light-based method for PSAT data often exceeds the true displacement of the sharks (Musyl et al. 2011, Braun et al. 2015).

Vertical Movements from PSATS.—Overall recorded depth and temperature ranges were 0–632 m and 11.5–27.4 °C for Shark 1, and 0–640 m and 11.6–27.5 °C

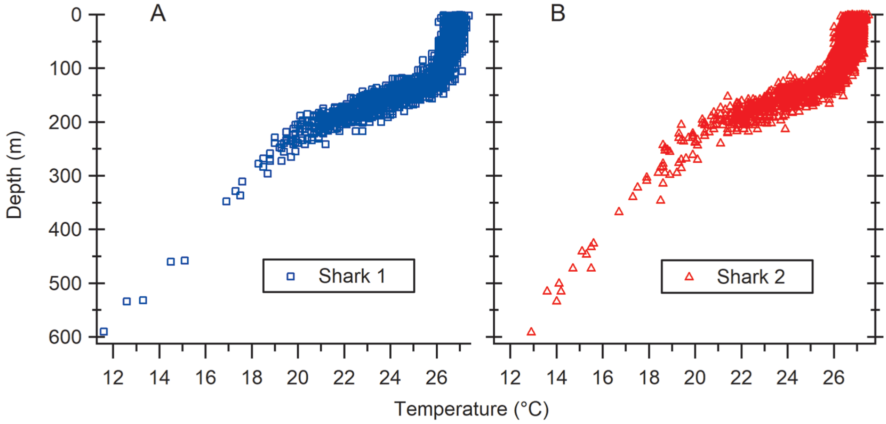

Figure 4. Depth-temperature profiles from time series data for two silky sharks, *Carcharhinus falciformis*. (A) Shark 1. (B) Shark 2. Depth scales are identical in the two graphs. Sharks 1 and 2 occupied water with similar temperature structure. The mixed layer extends down to approximately 150 m.

for Shark 2 (Fig. 3). A comparison of TAD plots for the two sharks revealed a similar pattern of vertical habitat usage. Sharks 1 and 2 spent 95.7%, 97.8% and of their time, respectively, in the epipelagic zone (0–200 m) (Fig. 3B, E). The sharks spent a comparatively small amount of time in near-surface waters ≤5 m depth, at 2.8% and 3.3% for Sharks 1 and 2, respectively (Fig. 3B, E). Both silky sharks demonstrated a relatively narrow temperature preference with Sharks 1 and 2 spending 75.4% and 78.0% of their time, respectively, in the 24–27 °C range (Fig. 3C, F). This temperature range corresponded to the mixed layer, which extended down to approximately 150 m in the area the sharks occupied during these deployments (Fig. 4).

We divided the binned histogram data for the two sharks into 12-hr blocks of time that roughly corresponded to day (07:00–19:00 hrs) and night (19:00–07:00 hrs). The differences between day and night TAD distributions were not significant (K-S test: $P = 0.869$), but were indicative of a diel vertical migration (DVM) pattern. During the day, Sharks 1 and 2 spent 91.0% and 86.6% of their time, respectively, at depths >50 m compared to 57.6% and 53.2% of time at those depths during the night. An examination of mean hourly depths from time series data further highlighted the diel pattern in vertical movements (Fig. 5). For Shark 1, the mean nighttime depth [71.4 (SD 46.0) m] was significantly shallower than the mean daytime depth [138.1 (SD 62.3) m] ($P < 0.0001$). For Shark 2, mean nighttime depth [60.3 (SD 46.7) m] was also significantly shallower than daytime depth [111.3 (SD 62.9) m] ($P < 0.0001$). The overall mean depths were 86.1 and 106.6 m for Sharks 1 and 2, respectively. Plotted time series of depth data similarly demonstrated a DVM pattern, but also revealed a crepuscular activity pattern and plasticity of vertical habitat utilization (Fig. 6). Forays to depths in excess of 550 m were observed during both the day and night. During the daytime, upward movements into the near-surface waters were also noted (Fig. 6). These daytime forays toward the surface (≤5 m depth) were most common during the hours of 9:00–11:00 hrs (Fig. 7).

SPOT Tagging.—The third satellite-tagged silky shark (Shark 3), a 183-cm-PCL female, was fitted with a SPOT tag and released on 11 February, 2015. Only four

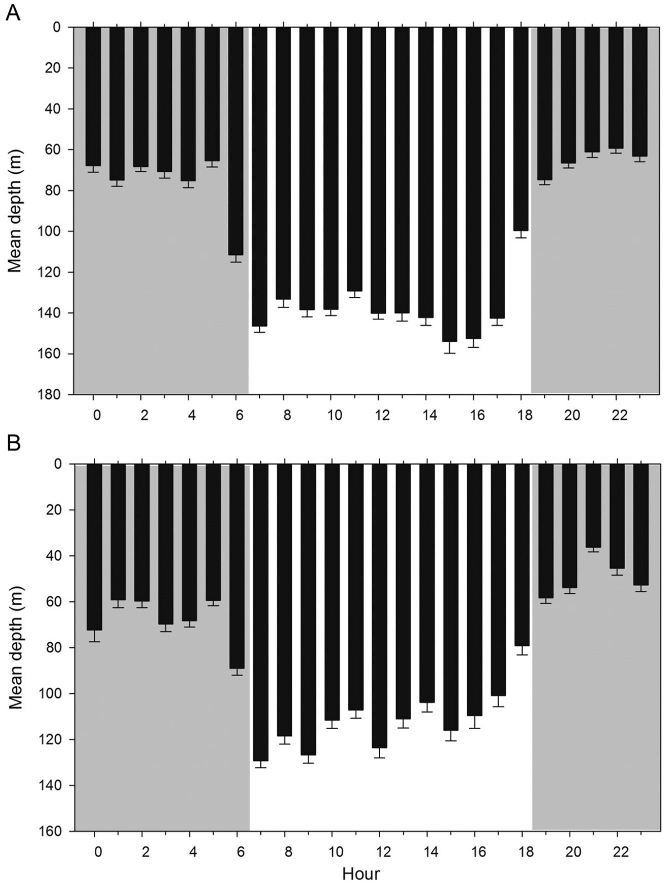

Figure 5. Mean depth by hour of the day from time series data for two satellite-tagged silky sharks, *Carcharhinus falciformis*. (A) Shark 1. (B) Shark 2. The division between shaded (night) and unshaded (day) areas approximates the times of sunrise and sunset. Error bars represent the standard error of the mean.

Argos locations were obtained from this tag (Fig. 1). The first was from a series of weak transmissions from multiple satellite passes during the first week of March 2015, that required auxiliary Argos processing to generate a single location (LC = Z; 20.72°N, 79.14°W), about 20.2 km southwest of the tagging site. The second location (LC = A; 20.84°N, 79.05°W) was from 18 May, 2015, approximately 7.0 km west-northwest of the tagging site. The third location (LC = A; 20.85°N, 79.22°W) was from 12 September, 2015, a distance of 24.8 km west-southwest of the tagging site. The fourth location (LC = 1; 20.72°N, 78.97°W) was from 21 September, 2015, a distance of 13.3 km south of the tagging site. Additionally, a resighting of this SPOT-tagged shark at the tagging site (El Farallón) on 10 March, 2015, was reported and confirmed through photographs.

Discussion

We present here a novel method for tagging large sharks, one that likely causes a minimum of physiological stress for the animal, but still allows for accurate

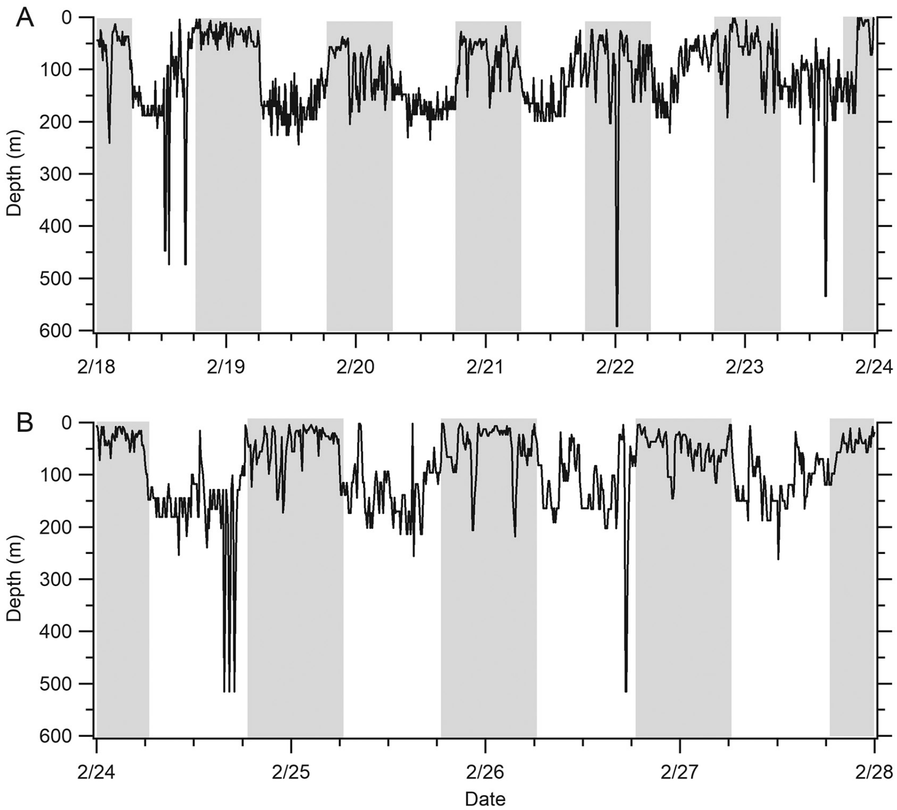

Figure 6. Time series of depth readings for a satellite-tagged silky shark, *Carcharhinus falciformis*. (A) Depth profile for Shark 1 during a 6-d period in February 2015. (B) Depth profile for Shark 1 during a 4-d period in February 2015. Measurements were recorded at 7.5-min intervals. Shaded areas approximate nighttime and are based on known times of sunrise and sunset for Cayo Anclitas.

measurements and application of tags. Our study is only the second to report the deployment of satellite-linked tags on sharks in Cuban waters, after the first on a longfin mako, *I. paucus* (Hueter et al. 2017). The mako study used a traditional hooking, tagging, and release technique, as did the SPOT-tagging of one silky shark in the present study. However, the in-water capture, tagging, and release technique used on two silky sharks in our study, without a hook, net, rope, spear, or other such capture or tagging equipment, is a first. The innovative use of a tail grab and pinch to relax the free-swimming shark, followed by upright cradling of the animal and stroking its abdomen while the tag was applied, differs from most techniques employing TI. Our study animals were never inverted ventral side up (Kessel and Hussey 2015), although their initial head-down position might have induced a form of TI, which can occur whenever an animal is placed in an "unnatural" posture (Watsky and Gruber 1990). An important question is why the tail pinch was effective in slowing and relaxing a free-swimming shark. Because we used this technique on large female sharks, it is possible this treatment might have simulated some aspect of precopulatory behavior in this species (H Pratt, Mote Marine Laboratory, pers comm), triggering submission

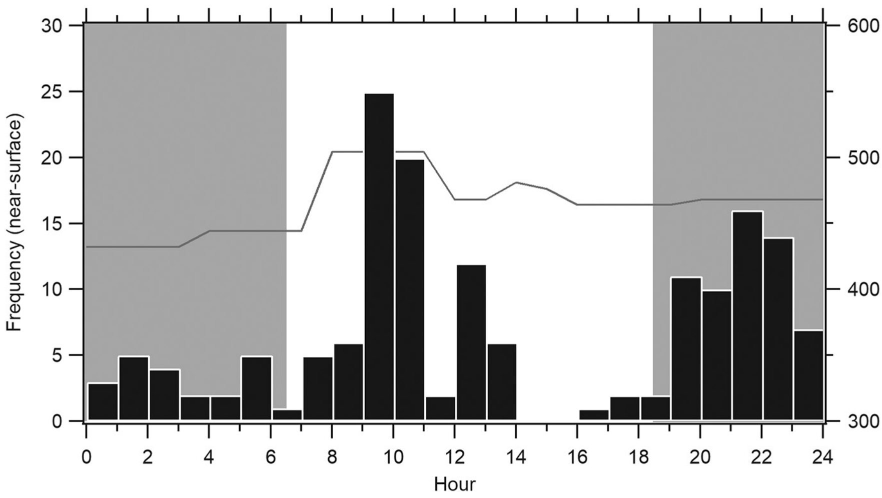

Figure 7. Frequency of near-surface data points from PSAT time series data. Data points correspond to depths ≤5 m for silky sharks, *Carcharhinus falciformis,* 1 and 2 combined. The total number of depth measurements per hour is shown as a gray trace corresponding to the right axis. The division between shaded and unshaded areas approximates the times of sunrise and sunset.

by these females. With caution the technique should be tried on males as well as other shark species to test this hypothesis.

Within a 25-hr period on 16–17 March, both MiniPAT tags began recording depth readings that remained essentially constant, at approximately 190 m for Shark 1 and 280 m for Shark 2 (Fig. 3). After approximately 72 hrs at these constant depths, both tags came to the surface and began transmitting. The reason for the tags staying at constant depth, triggering their pop-up, is unclear. It is unlikely the sharks, which appeared to be behaving normally, both died in this narrow time frame and sank to the bottom with their attached tags. On the other hand, if the intact tag-tether units were shed, by the sharks' active attempts to rub the tags on structure and/or the tether anchors working their way out through the skin, it is possible the tag units would have settled on the bottom in the area where they were shed. The tags' constant depth failsafe, which was programmed for 3 d, would then have been activated to release the positively buoyant tags from the negatively buoyant tethers, allowing the tags to surface and begin transmitting. Again, this scenario seems improbable given the narrow time frame of events involving both tags. Because our field work was conducted at an active dive site and the sharks appeared to return to the area during their time at-large, we cannot rule out the possibility that diver interference was involved with the early detachment of both tags. If this were the case, how the tags would have settled at 190 and 280 m depths, when the depth at the dive site was 50–100 m, is unclear, but deep water is not far away from the dive site (Fig. 1) and drift of the slowly sinking tags could have carried them to those depths. We also cannot rule out fisher removals of the tags, although fishing is highly restricted inside the Jardines de la Reina marine protected area. We have no direct evidence to support either scenario of human interference.

Whether or not the in-water tagging technique contributed in some way to the premature pop-up of the tags is unknown. Once the tag darts were inserted, both sharks quickly swam off, preventing confirmation of the darts' positions in the muscle. However, in both cases a scalpel cut in the skin was made and the darts were inserted with the proper orientation (points flexed in towards the body) through the cuts deeply into the muscle, to the depth of the exposed tagging needle, as with more traditional methods.

Results from the MiniPAT tags generated two unreliable tracks of only about 1-mo duration each. The four SPOT tag locations received from one shark spanned >7 mo after tagging yet ranged only 7–25 km from the tagging site. In addition, resightings of two tagged sharks were noted at the tagging site 3–4 wks after tagging. These data suggest that adult female silky sharks inhabiting the Jardines de la Reina archipelago do not travel appreciable horizontal distances, but longer-term studies with more individuals are needed to confirm this. Future research could use acoustic telemetry to understand better the local-scale movements of sharks of both sexes within and outside of the reserve.

The PSAT tags reported mesopelagic dives to at least 640 m, the deepest descent documented for this species to date. Previously, fisheries catch data have been used to estimate that silky sharks are found to at least 500 m (Bonfil 2008), while satellite tagging studies have demonstrated dives to just over 300 m (Hutchinson et al. 2015). Vertical movements of the PSAT-tagged sharks displayed a diel pattern of spending greater time at depth during the day than at night, contrary to female silky sharks (n = 14) studied on reefs in the Red Sea (Clarke et al. 2011). However, the Jardines de la Reina sharks' daytime forays toward the surface, primarily during the morning hours between 09:00 and 11:00, bore some similarity to the behavior of the Red Sea sharks. As both locations are baited dive sites, these daytime excursions to surface waters are likely correlated with diving ecotourism operations that use provisioning to attract sharks. Sharks are a principal attraction for Jardines de la Reina tourists, many of whom are willing to return for the diving there and pay higher prices for the experience (Figueredo-Martín et al. 2010). The effects of provisioning on sharks have been investigated, with most studies (e.g., Maljković and Côté 2011, Hammerschlag et al. 2012, Brunnschweiler and Barnett 2013) concluding that it does not significantly alter normal animal behavior and health, although other studies have questioned this conclusion (e.g., Fitzpatrick et al. 2011). In general, the conservation benefits of diving ecotourism can outweigh the negative impacts (Heyman et al. 2010) and the economic value of shark diving tourism can be substantial (Huveneers et al. 2017). With this in mind, the Cuban government is moving toward increasing the country's activities in shark dive ecotourism (NPOA-Sharks 2015). Our preliminary findings indicate that properly managed diving tourism can co-exist and even enhance the opportunities for shark research in Cuba, with a common goal of achieving sustainable, healthy shark populations in this island nation.

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