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Elevated sea surface temperatures drive greater seasonal depth use in a baited aggregation of silky sharks *Carcharhinus falciformis*

Collin T. Williams[1,2,*], Ashlie J. McIvor[3], Eloise B. Richardson[1], James Lea[4,5], Chris R. Clarke[6], Jesse E. M. Cochran[1], Alexander Kattan[1], Rupert Ormond[7], Michael L. Berumen[1]

[1]Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, Thuwal 23955, Kingdom of Saudi Arabia

[2]Ocean Sciences and Solutions Applied Research Institute, Education Research and Innovation Foundation, NEOM, Tabuk 49643, Kingdom of Saudi Arabia

[3]Department of Environmental Protection and Regeneration, Red Sea Global, Hanak 48513, Kingdom of Saudi Arabia

[4]Save Our Seas Foundation, Geneva 1201, Switzerland

[5]Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

[6]Danah Divers Marine Research Facility, Beach Palace, Jeddah 23812, Kingdom of Saudi Arabia

[7]Marine Conservation International, South Queensferry, Edinburgh EH30 9RG, UK

ABSTRACT: Conservation plans for pelagic sharks in future climate scenarios are limited by a lack of empirical data on behavioral responses to sustained elevated temperatures. The relatively high sea surface temperatures observed in the Red Sea provide a unique opportunity to investigate how sharks may respond to these thermal extremes. In this study, we examined the space use, diving behavior, and thermal preferences of silky sharks *Carcharhinus falciformis* tagged on coral reefs in the Red Sea (Saudi Arabia). Ten individuals (9 females, 1 male; ~2–2.5 m total length) were single- or double-tagged with smart position and temperature tags and pop-up satellite archival tags. Regional residency was observed up to 267 d, with most sharks dispersing <50 km. Archival tag data sets (n = 5) revealed that sharks spent most of their time in waters of 26–27°C during both warm and cool seasons, corresponding to marked seasonal shifts in shark depth use. During warmer months, sharks predominately occurred within a narrow depth band between 70 and 100 m, which had not been previously documented in this species. When surface temperatures dropped below ~30°C, individuals exhibited surface-oriented behaviors including diel vertical migration and regular movements throughout the mixed layer (0–100 m). These findings suggest that silky sharks may respond to elevated sea surface temperatures by concentrating into narrower depth ranges, which may consequently increase their vulnerability to fisheries exploitation in the Red Sea.

KEY WORDS: Temperature · Climate change · Ocean warming · Behavior · Pelagic sharks · Thermoregulation · Fisheries · Coral reef

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1. INTRODUCTION

The behavioral response of marine species to prolonged and elevated temperatures is an important consideration for conservation planning in warming oceans worldwide (Smith et al. 2023). This is particularly relevant for exploited taxa, such as large-bodied sharks, where climate-driven behavioral shifts may result in increased vulnerability to fisheries mortality (e.g. movement out of protected areas and altered depth use) (Rummer et al. 2022, Waller et al. 2024). Temperature is a well-documented driver of shark

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*Corresponding author: collin.williams@kaust.edu.sa

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movement, often associated with behavioral thermoregulation in which sharks occupy water masses with preferred thermal conditions to regulate their core body temperature (Schlaff et al. 2014, Andrzejaczek et al. 2018, Arrowsmith et al. 2021). In response to elevated surface temperatures, both endothermic and ectothermic sharks are known to alter their space use, dive deeper, spend more time at depth, and, in some instances, exhibit submergence behavior (i.e. remaining below the thermocline for extended durations) (Weng et al. 2005, Skomal et al. 2009, Kessel et al. 2014, Schlaff et al. 2014, Coffey et al. 2017, Andrzejaczek et al. 2018). Yet, our understanding of how many shark species behave at their upper thermal limits for long periods of time (i.e. months to years) remains limited.

With protracted seasonal marine heat waves occurring more frequently in regions such as the Red Sea (Reimer et al. 2024), we can look to these locations for insights into how marine species may respond to projected ocean warming scenarios. The Red Sea is especially well suited for such investigations as it is a semi-enclosed basin characterized by increasingly high sea surface temperatures (SSTs) (Raitsos et al. 2011, Rich et al. 2022). The prevalence of silky sharks *Carcharhinus falciformis* in the Red Sea provides a unique opportunity to examine how pelagic sharks behave at such thermal extremes. The silky shark is a large-bodied shark found throughout the world's tropical and sub-tropical seas. This species is generally considered highly migratory and is capable of >4500 km trans-basin migrations (Curnick et al. 2020, Salinas-de-León et al. 2024), which likely constitute important ecological connections (McCauley et al. 2012). Additionally, silky sharks are capable of diving beyond 1000 m (Curnick et al. 2020), but such behavior is rare. Most individuals are strongly surface-oriented (<50 m depth) and spend most of their time in the mixed layer shallower than the thermocline, with occasional brief dives into the mesopelagic zone (i.e. 200–1000 m depth) (Filmalter et al. 2015, 2021, Hutchinson et al. 2019, Curnick et al. 2020).

Silky sharks are also a major component of pelagic fisheries, representing a high proportion of the global shark meat and fin trade (Clarke et al. 2006, Bonfil 2008, Rigby et al. 2021). Overexploitation has been linked to steep declines of silky shark populations globally (~90%; Baum & Myers 2004, Pacoureau et al. 2021), contributing to the listing of this species as Vulnerable by the International Union for Conservation of Nature (Rigby et al. 2021). In the Red Sea and greater Arabian region, silky sharks are among the most harvested shark species, with population declines driven by targeted and incidental commercial fishery harvest across all life-stages, including neonates and adults of both males and females (Bonfil 2003, Clarke et al. 2013, Spaet & Berumen 2015, Jabado & Spaet 2017). Nearly every Red Sea nation has enacted shark fishing bans or restrictions, yet without adequate enforcement, shark fisheries in the Red Sea persist largely unregulated (Spaet 2018). While management plans specific to silky sharks have not been established in the Red Sea, the species is increasingly valued for regional tourism and shark diving operations, particularly at offshore coral reefs along the coast of Jeddah, Saudi Arabia, where provisioning (i.e. humans feeding sharks) has occurred year-round at a weekly to monthly interval since the 1990s (Clarke et al. 2011, 2013).

Both provisioning and SST influence the occurrence of silky sharks on Red Sea reefs, with sharks utilizing baited sites more frequently and fewer individuals observed during warmer months (July–December) (Clarke et al. 2011, 2013). Acoustic telemetry and dive-based observations have recorded residency of individual silky sharks to specific reefs near Jeddah throughout the year, with some sharks documented over a period of ~2.5 yr (Clarke et al. 2011, 2013). However, most silky sharks in this reef complex (70%) appear to be transient as evidenced by short detection durations of 2 mo or less (Clarke et al. 2011, 2013). Broader movement patterns of these sharks as well as fine-scale environmental drivers of their behavior and depth use in the Red Sea remain unknown.

In this study, we characterize the space use, diving behavior, and thermal niche of silky sharks in the central Red Sea. We primarily sought to examine the influence of temperature on silky shark movements, with the aim of gaining insights into how this species might respond to higher SSTs associated with global ocean warming. The findings of this study are further intended to advance our understanding of silky shark movements in the Red Sea region specifically and facilitate targeted fisheries enforcement as well as informed spatial planning. Identifying potential behavioral shifts associated with elevated temperatures may play a key role in enabling adaptive strategies to manage silky shark populations and the industries they support (i.e. fisheries and tourism).

2. MATERIALS AND METHODS

2.1. Tagging

Capture and tagging of sharks occurred at an offshore coral reef complex, the Eliza Shoals, located about 50 km north-west of Jeddah, Saudi Arabia (Fig. 1). Tagging efforts were concentrated around an isolated coral reef pinnacle, which peaks at approximately 40 m depth and quickly drops off to depths greater than 800 m. This pinnacle reef is where regional shark provisioning predominantly occurs and is herein referred to as the provisioning site. Sharks were attracted to tagging vessels using chum and small pieces of tuna (e.g. *Auxis thazard* and *Euthynnus affinis*). Once visible from the boat, sharks were captured using pelagic buoy lines that consisted of 2 polyform buoys, 10 m of 6 mm nylon rope, 2.5 m of single-strand 1200 lb monofilament, and 1 m of double-strand 1200 lb monofilament baited with large chunks of *E. affinis* on 3X strength 18/0 in-line circle hooks. Sharks were restrained in the water alongside the boat by securing ropes around the caudal peduncle and mid-section of the body between the dorsal and pectoral fins. All procedures were authorized and regulated by institutional and national animal care use committees (Approval: 18IACUC14).

Sharks were either single- or double-tagged using the following 2 tag types: pop-up satellite archival tags (PSATs) and smart position and temperature (SPOT) tags. The data recorded by PSATs (depth [m], temperature [°C], and light levels for geolocation track reconstruction) were archived within the tags' internal storage until a programmed date when tags released from the animal, floated to the surface and transmitted data via satellite, whereas SPOT tags were utilized exclusively for transmitting location estimates in real-time on each instance the shark's dorsal fin rose above the water surface. PSATs (Wildlife Computers miniPAT-348) were attached using a double-strand loop of 200 lb monofilament encased in silicone tubing with an integrated duo lock snap (size 5) just below the tag. A 6 mm hole was drilled through the anterior lower third of the dorsal fin, the tether was then fed through this hole, looped over the tag, and secured to the snap. The SPOT tags (Wildlife Computers SPOT-258) were mounted to dorsal fins using 3 stainless steel A4 bolts, 2 mm thick rubber washers, stainless steel washers, and locking nuts. PSATs were programmed for 150 d deployments with time series data to be transmitted at a 150 s interval. A 15 s satellite uplink interval was used for SPOT tag transmissions. Time-at-temperature histograms and percent dry timelines were both disabled on the de-

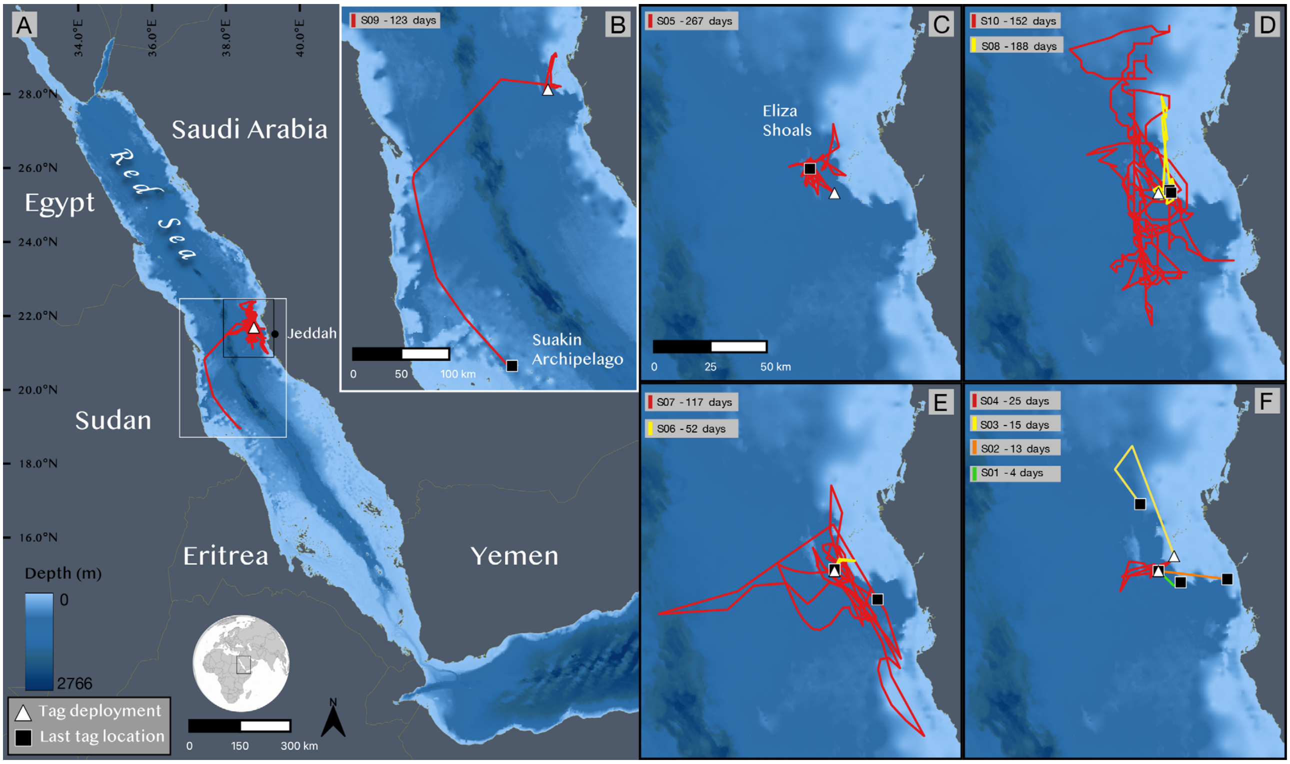

Fig. 1. Satellite-derived movement paths of silky sharks *Carcharhinus falciformis* tagged in the central Red Sea (n = 10). In (A), tracks of all 10 individuals are shown in red, whereas within the inset maps, individuals are distinguished by different track colors: (B) S09; (C) S05; (D) S08, S10; (E) S06, S07; (F) S01, S02, S03, S04. The provisioning site is represented as the tag deployment location (white triangle) for all individuals except for S03, which was tagged on a nearby reef

ployed SPOT tags. When possible, PSAT tags were recovered using an Argos goniometer (Collecte Localisation Satellites, model: RXG-234).

2.2. Analysis

Light-based geolocation paths derived from PSATs were constructed with the Wildlife Computers GPE3 model at a speed of 2 m s^{-1}. All other data analysis was conducted using the R software v.4.4.0 (R Core Team 2024). Argos positions obtained from SPOT tags were integrated into PSAT geolocation estimates from the same individual where possible, then filtered for duplicate positions, erroneous locations (e.g. on land), and a swim speed of $\leqslant 2$ m s^{-1} using the 'aniMotum' package (Jonsen et al. 2023). This package was further used to regularize tracks with a 24 h time step random walk state space model that integrated the positioning error ellipse of each location estimate and was sequentially fitted for multiple individuals excluding gaps of $\geqslant 10$ d without transmitted locations. Tracks were visualized in QGIS, while depth and temperature data were visualized in R.

SST values were obtained from the NOAA 1/4° Daily Optimum Interpolation V2 High Resolution data set (Huang et al. 2021). Seafloor depth along shark tracks were extracted with the 'marmap' package (Pante & Simon-Bouhet 2013). Proximity to the provisioning site was calculated using the 'geosphere' package as a straight-line distance between the tagging location and each location along a shark's track (Hijmans 2023). Thermocline depths were calculated using tagged shark dive profiles with a structural change model in the 'strucchange' package (Zeileis et al. 2002). Depth-at-temperature data from archived PSAT data were first aggregated into discrete 24 h profiles, cleaned by averaging duplicate depths and interpolated to 1 m steps. Structural changes in temperature–depth relationships were then detected with a linear model (allowing a maximum of 2 breaks) that tests all possible partitions and selects segmentation of thermocline boundaries that minimizes the Bayesian information criterion.

Seasonal comparisons of shark depth use were conducted between autumn and winter, which correspond to the hottest and coldest Red Sea SST conditions, respectively (Rich et al. 2022). Comparative histograms of shark depth and temperature between autumn and winter were produced by first calculating the percent time that each tagged shark spent within discrete bin limits and then the mean across sharks for each bin to maintain individual weighting. Temperature thresholds corresponding to changes in shark depth were identified with a breakpoint analysis, a Bayesian piecewise regression model run using the 'brms' package that leverages the Stan programming language (Bürkner 2017), similar to that described by Andrzejaczek et al. (2018). Breakpoint values are reported with a 95% confidence interval. Dive periodicity was examined with a spectral analysis by demeaning (i.e. centering) archived depth data and applying a Hamming smoothing window before implementing a fast Fourier transformation (FFT) as described by Carlisle et al. (2011), where peaks in spectral power indicate temporal periodicity of diving behavior.

Generalized additive mixed models (GAMMs) were implemented using the 'gamm4' package to investigate environmental drivers of tagged shark depth. Time series data from recovered tags were subsampled to retain 1 data point every 25 min (non-averaged). A Gaussian error distribution was assumed given the continuous nature of the response variable (shark depth). The model included smooth terms for SST (°C), seafloor depth (m), and proximity to the provisioning site (km), with 10 basis functions for each smooth ($k = 10$). A continuous temporal variable (e.g. month) was not included in the model due to a high correlation with SST in the Red Sea. Diagnostics checks of k-values were completed to ensure models were not under- or overfitted, in addition to sensitivity analyses using higher k-values to confirm robustness. Model performance was evaluated through residual diagnostics (including residual vs. fitted and QQ plots) and by comparing the full model with nested models that excluded individual predictors. Random effects for individual shark IDs were also included to account for repeated measures.

3. RESULTS

3.1. Tag deployments and reporting

A total of 10 mature to near mature silky sharks (190–253 cm total length [TL]; Bonfil 2008) were tagged between 2009 and 2022 (Table 1). Tagging was strongly sex-biased towards females, with 9 females and 1 male tagged (Table 1). Sharks captured prior to 2022 (n = 5) were tagged with either a PSAT or SPOT tag, while those captured in 2022 (n = 5) were equipped with both tag types (Table 1). Track durations among both tag types spanned 4 to 267 d (mean = 95 d) (Table 1).

Tracking data were obtained from all 10 tagged sharks. In total, 11 tags (5 PSAT and 6 SPOT) repre-

Table 1. Collection information for silky sharks *Carcharhinus falciformis* tagged near Jeddah, Saudi Arabia, including fish total length, sex, tag type (pop-up satellite archival tag [PSAT] or smart position and temperature [SPOT] tag), tracking dates (yyyy-mm-dd), track duration, track length, and linear displacement distances. DNR indicates a tag that did not report data. Deployment of each tag type is indicated by Y. Recovered PSATs are denoted by *

ID	Total length (cm)	Sex	PSAT	SPOT	Tag date	Tag pop-up date	Last SPOT location (date)	SPOT locations (n)	Track duration (d)	Track length (km)	Linear displacement (km)
S01	190	F	Y	–	2009-06-20	2009-06-23	–	–	4	13	11
S02	240	F	Y	–	2009-10-17	2009-10-23	–	–	13	30	30
S03	220	M	Y	–	2011-05-21	2011-06-04	–	–	15	104	31
S04	240	F	–	Y	2012-05-06	–	2012-05-30	16	25	103	0.04
S05	200	F	–	Y	2012-05-29	–	2013-02-21	134	267	293	15
S06	199	F	Y	Y	2022-11-06	DNR	2022-12-27	8	52	24	0.7
S07	244	F	Y*	Y	2022-11-07	2023-03-01	2023-03-03	165	117	992	54
S08	237	F	Y	Y	2022-11-07	DNR	2023-05-13	113	188	165	7
S09	210	F	Y	Y	2022-11-08	DNR	2023-03-10	62	123	555	304
S10	253	F	Y*	Y	2022-11-10	2023-04-10	DNR	0	152	2268	12

senting 956 d of data were available for analysis. While 4 tag failures occurred (3 PSAT and 1 SPOT), successfully reporting SPOT tags yielded high-resolution Argos location estimates with a 32 h mean interval between transmitted locations, and physical recovery of 2 PSATs provided ~10 million depth and temperature time-series data points at a 3 s interval. Time series of temperature and depth data were only available from PSAT deployments on 3 individuals for subsequent analysis (i.e. spectral, breakpoint, and GAMM).

3.2. Horizontal movements

The sharks tagged in this study rarely utilized open ocean habitats and exhibited residency for upwards of 267 d in the Eliza Shoals coral reef complex where tagging occurred (Fig. 1). No sharks were tracked for a full year, but collections and tracking indicated silky shark occurrence in the Eliza Shoals region during all seasons (Table 1, Fig. 1). Sharks predominantly utilized areas within 50 km of their capture location (89% of transmitted locations indicated dispersal <50 km), but 3 individuals (S07, S09, and S10) undertook occasional forays farther away, mostly within 80 km of their tagging site (Figs. 1 & 2). Only 1 individual (S09) dispersed away from the east-central Red Sea, crossing the basin to Sudan near Dungonab Bay before moving southward into the Suakin Archipelago >300 km from its tagging location (Fig. 1). While total track lengths of tagged sharks reached more than 2000 km, linear displacement distances (i.e. straight-line distance from the tagging location to the last transmitted location) spanned from <1 to 304 km (Fig. 2).

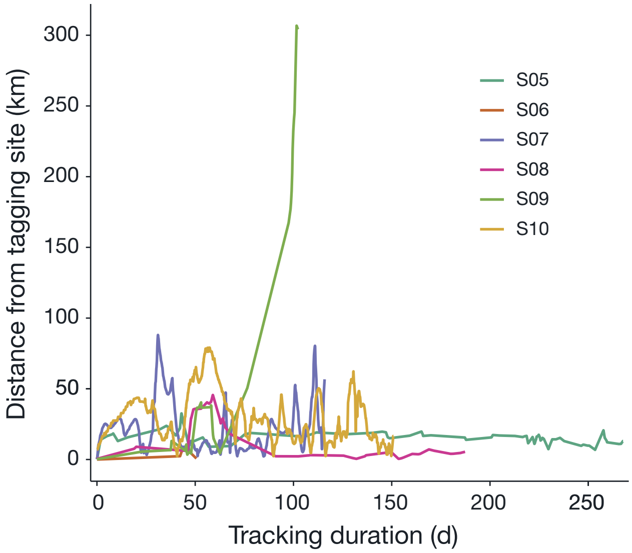

Fig. 2. Dispersal of silky sharks *Carcharhinus falciformis* in the Red Sea with >50 d tracking durations (n = 6) shown as the distance of each individual from the tagging site through time

3.3. Depth and temperature

Sharks occupied depths ranging from the surface down to 585 m (Fig. 3), while use of mesopelagic habitats (200–1000 m depth) was often infrequent and brief (i.e. <10 min; Fig. 3). Pronounced changes in depth use were observed between autumn and winter, corresponding to distinct seasonal stratification of the water column (Table 2, Figs. 4 & 5). Shark dive profiles revealed a seasonal (upper) thermocline in autumn (mean depth 75 m) and a permanent (lower) thermocline (mean depth 103 m) that

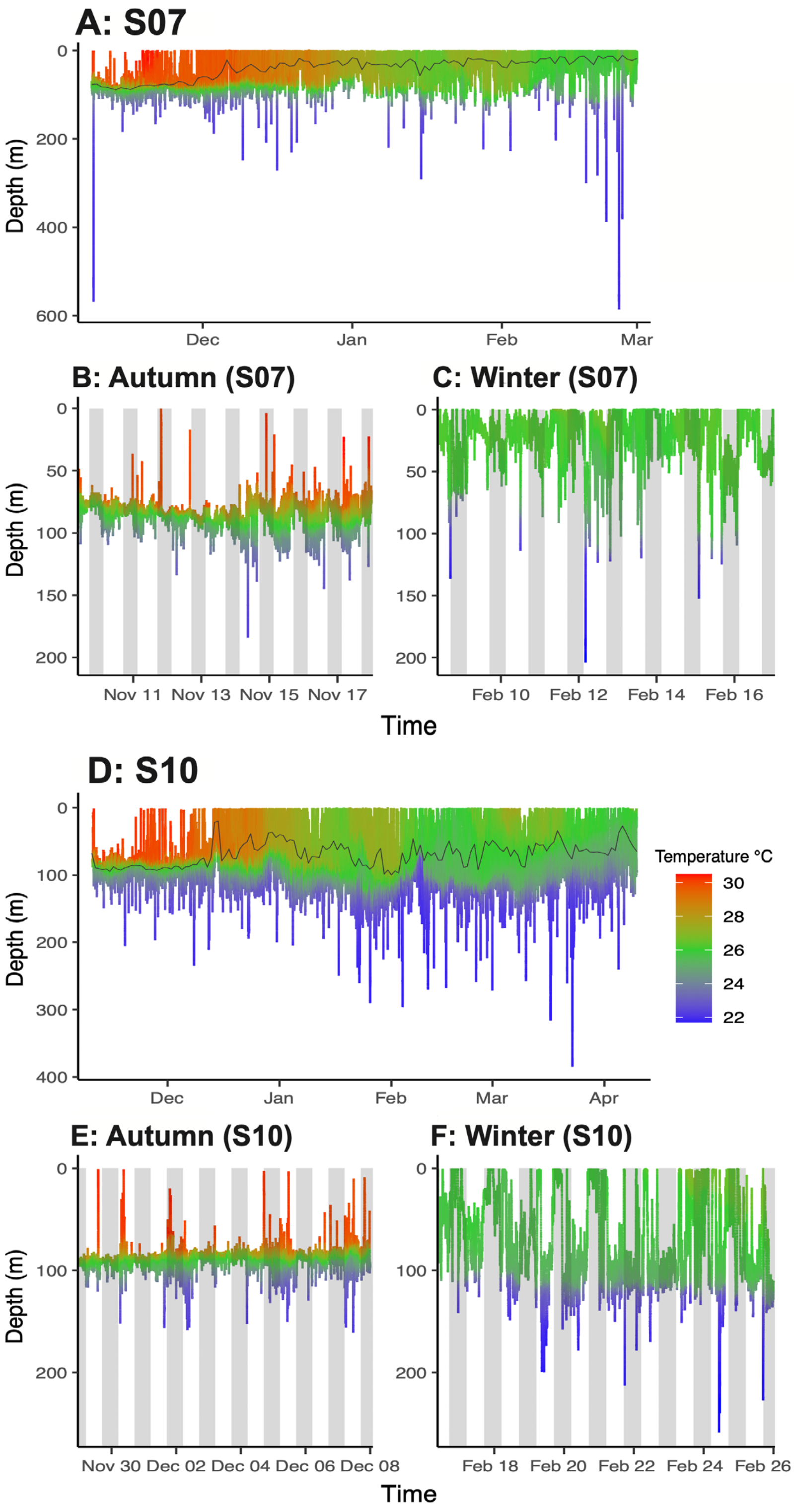

Fig. 3. Three-second resolution dive profiles of 2 individual silky sharks *Carcharhinus falciformis* (S07 and S10) in the Red Sea. (A,D) Vertical movements across the entire tag deployment duration. B,C,E,F represent temporal subsets during (B,E) autumn and (C,F) winter. Color denotes temperature of each dive profile. The overlain black line in A ,D indicates mean daily dive depth. Shaded vertical bars in B,C,E,F mark the time between sunset and sunrise (i.e. nighttime hours)

persisted across seasons. In autumn months, sharks exhibited depth-restricted submergence behavior, spending most of their time (70%) within a relatively narrow depth band (70–100 m) between the 2 thermoclines and only undertaking brief movements above the upper thermocline into shallower, warm water. In contrast, during winter months after the upper thermocline dissipated, sharks were strongly surface oriented (0–10 m), but frequently undertook dives to ~100 m predominantly occurring in the mixed layer above the lower thermocline (88% of time spent at 0–100 m) (Figs. 3–5). Spectral analysis revealed a strong peak of diving periodicity at 24 h (i.e. a strong repeating depth pattern on a daily interval) in the winter that was much less pronounced in autumn, indicating seasonal patterns of diel vertical migration (DVM), with this behavior primarily exhibited in the winter (Fig. 6).

SST values along shark tracks fluctuated seasonally, ranging from 29 to 31°C in autumn and 25 to 29°C in winter (Fig. 3). Silky sharks encountered water temperatures that ranged from 21.6 to 31.0°C, but spent the largest proportion of their time (32%) in water of 26–27°C across all seasons and 74% of their time between a wider, but still relatively small, thermal range of 25–28°C (Table 2, Fig. 4). In both autumn and winter, tagged sharks predominantly occurred within 26–27°C (24 and 35% of time in autumn and winter, respectively). However, during warmer autumn months, tagged sharks also spent a considerable portion of time (23%) at temperatures above 29°C, corresponding to short forays above the upper thermocline, which contrasts from winter months when just 1% of time was spent at >29°C. Based on seasonal differences in thermocline depths, daily utilization of the mixed layer for breakpoint analysis was calculated as the percent time

Table 2. Comparative seasonal metrics of depth and temperature, including the mean depth and temperature of time series records from all tagged sharks, the percent of time sharks spent shallower than the thermocline (autumn: 75 m; winter: 100 m), and the mean daily sea surface temperature (SST) of shark locations as indicated by the NOAA high-resolution data set. Variance is denoted by standard deviation

	Autumn	Winter
Mean depth (m)	79.8 ± 23	49.6 ± 38
% Time above thermocline	15.9 ± 23	86.3 ± 18
Mean temperature (°C)	27.1 ± 1.8	26.5 ± 1.4
Mean daily SST (°C)	30.2 ± 0.4	27.1 ± 1.0

shallower than depths of 75 m in autumn and 100 m in winter. Breakpoint analysis revealed that SST at and above 29.1 ± 0.03°C resulted in a sharp decrease in the use of the upper water column (i.e. <75 m) such that sharks spent more time at depth when surface waters experienced elevated temperatures (Figs. 3 & 7). The percent of time tagged sharks spent in the mixed layer was notably diminished at SSTs >30°C (13%), relative to SSTs ≤30°C (83%). For behavioral comparisons between autumn and winter, seasons were demarcated by the day that SST dropped below the resulting value from the breakpoint analysis

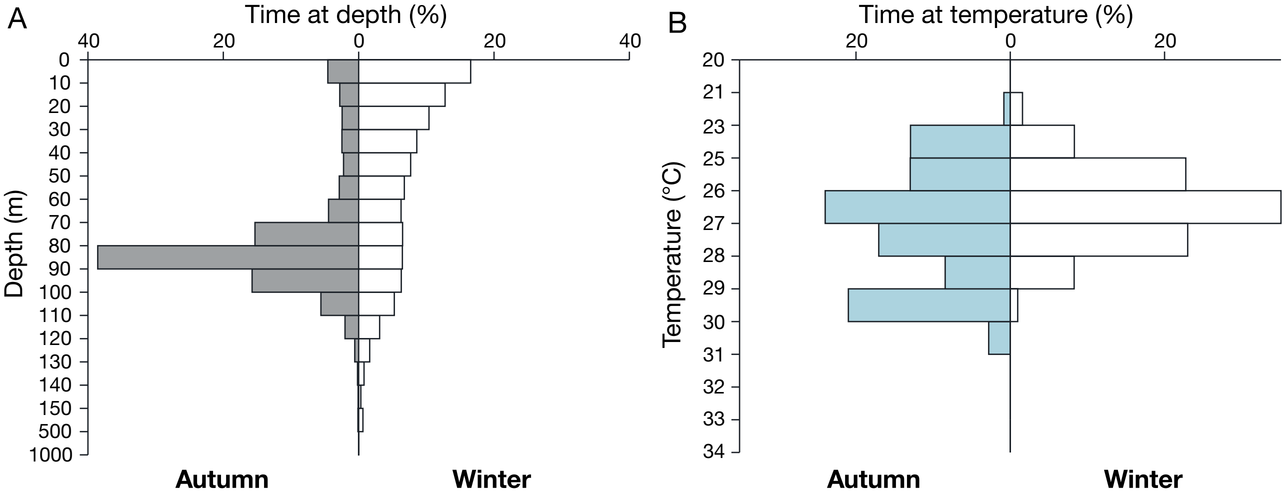

Fig. 4. (A) Time at depth and (B) time at temperature for autumn and winter derived from pop-up satellite archival tags deployed on silky sharks *Carcharhinus falciformis* in the Red Sea. Histograms represent the mean percentage of time spent in specific depth and temperature bins among sharks (n = 5), with wider bars indicating more time spent between a given range of values. Color is used to differentiate seasons

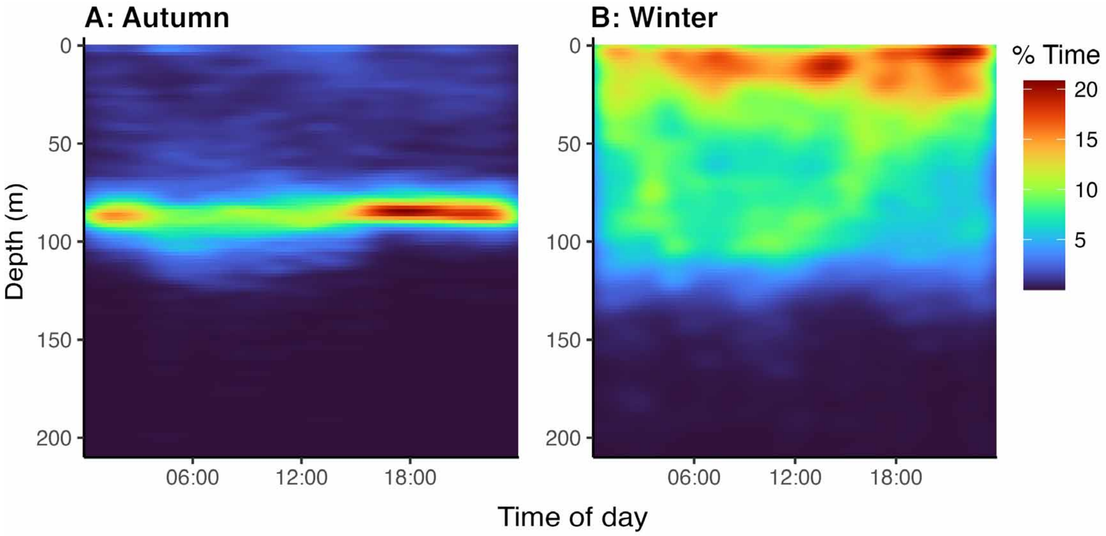

Fig. 5. Daily patterns of silky shark *Carcharhinus falciformis* (n = 3) depth use in (A) autumn and (B) winter seasons in the Red Sea. Density plots represent time series depth records from the entire deployment period of all sharks (S02, S07, S10), rather than just a single day. The color scale corresponds to the percent of time that tagged sharks spent at a given depth

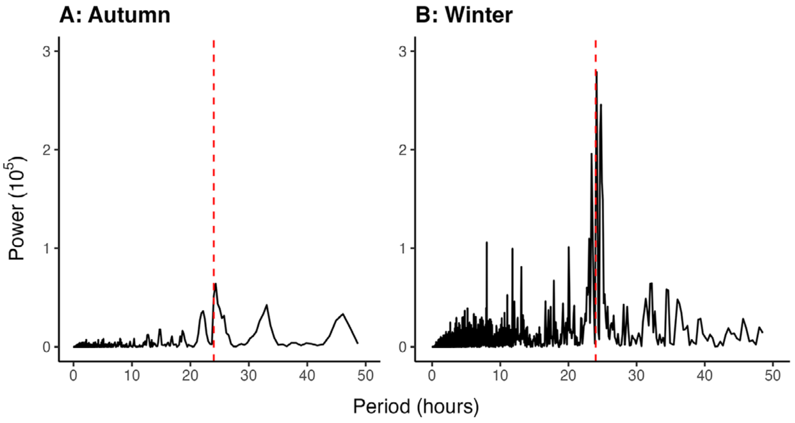

Fig. 6. Periodograms from fast Fourier transformation (FFT) spectral analysis of silky shark depth use (n = 3) for (A) autumn and (B) winter. The *x*-axis shows possible cycle lengths in hours, while the *y*-axis represents how strong a repeating depth pattern is at each cycle length. Higher peaks mark clearer, recurring changes in depth. The dashed red line is a 24 h reference for daily cycles

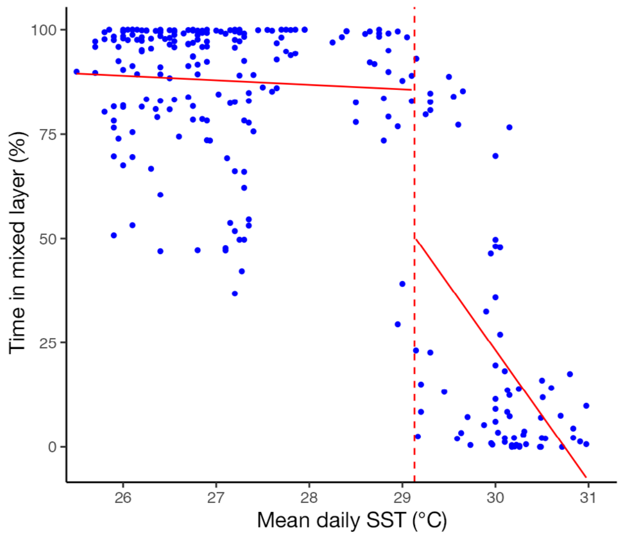

Fig. 7. Relationship between tagged shark (n = 3) presence in the mixed layer each day (depth <75 m in autumn and <100 m in winter) and the mean daily sea surface temperature (SST; °C) at their location. Solid red lines denote a Bayesian piecewise regression model representing data on either side of a breakpoint value, which is depicted here as a dashed red line. Figure modeled after Fig. 4 of Andrzejaczek et al. (2018)

(29.1°C, 10 December 2022), which occurred just before the winter solstice (22 December 2022). The percentage of time sharks spent in the mixed layer was significantly greater during cooler winter months (86%) than the warmer surface temperatures recorded in autumn (16%) (Fig. 4, Table 2; Wilcoxon rank-sum test: $W = 896$, $p < 0.001$). The short tracking duration (15 d) of the only male tagged in this study (S03) precluded sex-based behavioral comparisons, but the vertical behavior of this male was consistent with seasonal depth use patterns exhibited by tagged females (i.e. movement throughout the upper mixed layer when SST was <29.1°C). While similar patterns of seasonal depth use were observed among all sharks in this study with available depth–temperature data (5 PSATs; 3 with time-series profiles), this small sample size limits inferences into the vertical behavior of other tagged individuals (i.e. those equipped with SPOT tags) and the wider population of silky sharks in the Red Sea.

SST, sea floor depth, and distance from the provisioning site all influenced the recorded depth of silky sharks in variable, non-linear relationships (Table 3, Fig. 8). Random effects due to individual sharks also explained a small portion of observed variability (1.23%), although the low sample size available for this analysis (n = 3) limited detection of individual-level variations. SST had the strongest, most pronounced effect accounting for more than half of all variation in diving behavior (51.42%), with high temperatures driving greater depth use at a threshold approximately corresponding to the 29.1°C breakpoint value (Table 3, Fig. 8). Neither sea floor depth nor distance from the provisioning site influenced shark depth in a consistent way (Fig. 8), and these factors explained only a small percentage of variation in shark depth use (4.25 and 0.82%, respectively; Table 3).

Table 3. Statistical outputs of generalized additive mixed models (GAMMs) representing the effect of sea surface temperature (SST), seafloor depth, and distance from provisioning site on silky shark *Carcharhinus falciformis* depth, including the estimated degrees of freedom (edf) and the percent of variability in depth explained by each predictive variable (% exp. var.)

Parameter	edf	*F*	p	% exp. var.
SST	8.691	200.7	<0.001	51.42
Seafloor depth	7.333	19.04	<0.001	4.25
Distance from provisioning site	8.14	10.14	<0.001	0.82

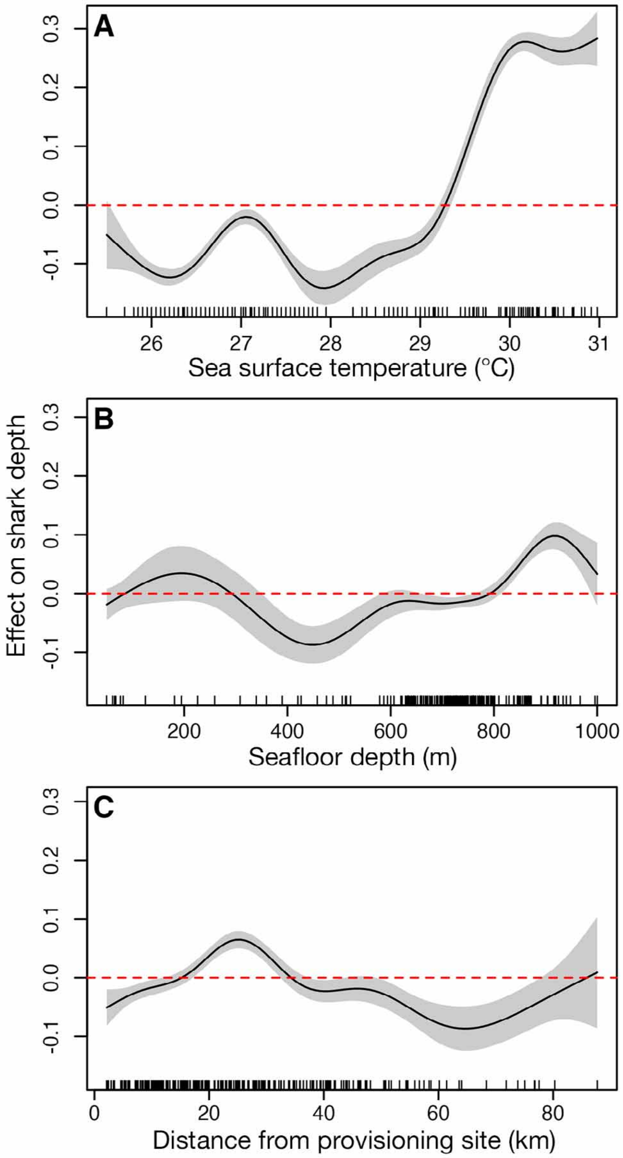

Fig. 8. Generalized additive mixed models (GAMMs) illustrating partial effects (smooth terms) of (A) sea surface temperature, (B) seafloor depth, and (C) distance from provisioning site, on depth use by silky sharks *Carcharhinus falciformis* in the Red Sea. Grey shading represents 95% confidence intervals. Red dashed lines serve as a reference to null effects of the smooth terms on shark depth. Black ticks along each *x*-axis are rug marks indicating individual data points

4. DISCUSSION

This study is the first to describe previously undocumented patterns of depth use by silky sharks in response to seasonally elevated mixed layer temperatures. While the current data set was small (n = 10) and strongly biased towards female silky sharks (n = 9 females, n = 1 male) at a provisioning site in the Red Sea, it provides the first evidence of protracted and pronounced submergence behavior for silky sharks, in which individuals occupied a narrow depth band (70–100 m depth) of cooler water (~26°C) below the upper thermocline during periods of elevated SST (>29.1°C). This thermally driven pelagic habitat compression documented here could have significant implications for silky shark vulnerability to fisheries and corresponding management plans.

Previous investigations of silky shark movements in the Red Sea suggested that individuals dispersed away from central Red Sea reefs during the warmest periods of the year, inferred from reduced detections using surface-based methods (e.g. diver surveys and acoustic telemetry on shallow reefs) (Clarke et al. 2011, 2013). Our study revealed that this reduction in silky shark observations during seasonally elevated surface temperatures was likely not driven by dispersal, but rather, sharks remained in the area and sought thermal refuge at greater depths (70–100 m) beyond traditional methods of detection. These findings indicate that while silky sharks are generally categorized and managed as migratory species (Rigby et al. 2021), Saudi Arabian authorities may have the opportunity to manage silky sharks as a regionally resident reef species where localized enforcement and spatial protections could potentially have a greater effect on the population. Regional variations in space use have been documented for other carcharhinid sharks (e.g. *Carcharhinus amblyrhynchos*), where a greater portion of individuals in certain regions are more dispersive than in other areas where they are found to be relatively resident (Barnett et al. 2012, Heupel & Simpfendorfer 2015, White et al. 2017). The present study further emphasizes the value of location-specific tracking data sets to inform conservation planning (e.g. marine reserve design), as regional behavioral plasticity may be associated with varied depth use and thermal stratification of the water column.

With SST predicted to increase across ocean basins globally, the preferred thermal niche of silky sharks in surface waters is likely to be altered (Cheng et al. 2022, Rummer et al. 2022, Reimer et al. 2024). Previous tagging of silky sharks has indicated a thermal preference to waters ranging from 24 to 29°C with marked utilization of upper mixed layer depths when SST is <30°C (Hueter et al. 2018, Hutchinson et al. 2019, Curnick et al. 2020). At the upper end of this thermal range (SST ~29°C), silky sharks have been shown to display slightly greater depth use (e.g. 25–50 m), but remain mostly within the mixed layer (i.e. depths above 85 m in the west-central Pacific Ocean) and still regularly utilize surface waters (Hutchinson et al. 2019). Our study demonstrated that when SSTs are sustained above previously documented thermal preferences (i.e. 29°C), silky sharks can exhibit submergence behavior, seeking thermal refuge below the mixed layer (i.e. Red Sea depths below 75 m in autumn) within a narrow intermediate layer of the water column (i.e. between the upper mixed layer and deep-water mass). If this behavior is indicative of how the species may respond to projected ocean warming, the reduction of 3-dimensional space occupied by silky sharks may increase their susceptibility to overharvesting by making it easier to capture more individuals with less effort (Waller et al. 2024). For silky sharks, fishery threats may be even further exacerbated by elevated SSTs that concentrate sharks below the mixed layer by increasing vertical overlap with commercial longline set depths (~100 m; Nishida et al. 2003). Similar concerns of increased vulnerability to fisheries have been expressed in relation to climate-driven ocean deoxygenation, which also concentrates sharks into a narrower depth range (Vedor et al. 2021, Waller et al. 2024). There are relatively fewer *in situ* data on shark depth-use responses to sustained surface thermal conditions consistent with projected ocean warming scenarios (Rummer et al. 2022), and further investigation is needed to understand if the behaviors documented in this study could be expected to occur among other species and regions.

The behaviors of silky sharks at elevated temperatures in the Red Sea are likely associated with multiple biological factors. Sharks tagged in this study spent most of their time in a narrow temperature range (26–27°C), despite seasonal changes in SST, suggesting that sharks targeted water masses at different depths to remain within preferred thermal conditions. These movements may be indicative of thermoregulation, which is a major driver of diving behavior for ectothermic shark species in pelagic environments (Skomal et al. 2009, Schlaff et al. 2014, Meekan et al. 2015, Arrowsmith et al. 2021, Watanabe et al. 2021). However, the observed variation in seasonal depth use by silky sharks in the Red Sea (i.e. deeper occupancy in warmer seasons) could additionally be the result of targeting prey that also exhibit seasonal patterns in depth distribution. Silky sharks forage on a wide range of smaller prey species (e.g. small tunas, flying fish, squid, and swimming crabs; Duffy et al. 2015) which incur lower thermal inertia (i.e. their body temperature assimilates more quickly to external conditions; Peralta-Maraver & Rezende 2021) and are likely to be more influenced by seasonal changes in thermal stratification of the water column. It is also possible that Red Sea silky sharks target multiple prey assemblages at different depths (e.g. at the surface and below the mixed layer), which could explain the short forays into surface waters with elevated temperatures (SST >30°C) during autumn and DVM exhibited in winter as sharks may target discrete vertical habitats based on prey availability. Future biologging investigations that include intramuscular thermistors would help distinguish foraging from thermoregulatory behavior (Dolton et al. 2023).

Reproduction is another factor that may influence the movements of silky sharks and encourage them to remain within a locality, which is especially relevant in the Red Sea where mature females are prevalent (Clarke et al. 2013). The long-distance horizontal migrations commonly undertaken by silky sharks (Curnick et al. 2020, Schaefer et al. 2021, Salinas-de-León et al. 2024) likely incur a significant energetic cost. By remaining resident, female silky sharks in the Red Sea may be able to allocate more energy towards other biological processes, including reproduction. As such, the shark movements observed in this study may be the result of a physiological trade-off between migration and gestation. Multiple lines of evidence suggest that silky shark reproduction occurs in the Red Sea (e.g. the presence of juveniles and pregnant females; Bonfil 2003, Spaet & Berumen 2015), but temporal patterns of reproduction remain undefined. The Red Sea may provide ideal conditions for shark gestation, as elevated temperatures can accelerate embryonic development and reduce the time of gestation in sharks (Schlaff et al. 2014). In addition, the aggregation of silky sharks where tagging was undertaken is sexually segregated, with a large number of females (Clarke et al. 2013), and female sharks are hypothesized to aggregate in warm regions for physiological benefits that may consequently enable sexual maturity to be attained at younger ages (Robbins 2007, Schlaff et al. 2014). Female silky sharks may therefore be employing seasonal submergence as a strategy to withstand thermal extremes, enabling them to remain within the relatively warm waters of the Red Sea year-round where they can accelerate reproductive processes. However, occupancy in higher temperatures during gestation may result in reduced fitness of offspring (e.g. smaller size at birth and lower energy reserves; Wheeler et al. 2021), which could have population-level consequences despite the individual-level maternal benefits.

The occurrence of year-round provisioning (i.e. shark feeding by humans) at the site where sharks were tagged in this study complicated analyses of shark occurrence relative to environmental factors, as this anthropogenic food source could be another possible influence on shark movements. With documented overfishing of lower-trophic prey species in the Red Sea (Kattan et al. 2017), it is possible that silky sharks adjust their movements to withstand elevated seasonal temperatures and remain nearby provisioning sites instead of traveling in search of foraging opportunities. Provisioning has been associated with changes in depth use through increased utilization of surface waters by whitetip reef sharks *Triaenodon obesus* (Fitzpatrick et al. 2011), yet an understanding of how it affects vertical movements of sharks more generally remains quite limited (Gallagher et al. 2015). The atypical behavior of silky sharks in this study is characterized by extensive use of greater depths, which is likely not driven by the provisioning that occurs at the surface. We further demonstrated that tagged shark depth use was not associated with their proximity to the area in which provisioning occurred. Sharks may also respond to provisioning by exhibiting a greater degree of residency (Clua et al. 2010, Mourier et al. 2021). While silky sharks in the Red Sea display residency to specific reefs, there is also growing evidence to suggest variable effects of provisioning among species with some sharks that show no pattern of returning to or spending more time at provisioning sites (Abrantes et al. 2018, Séguigne et al. 2023, Niella et al. 2024). These diminished effects of provisioning on shark behavior stem from the small contribution of anthropogenic food sources to overall shark diets and the strong influence of environmental and biological factors on their movements (e.g. thermal conditions and the pursuit of natural prey resources) (Abrantes et al. 2018, Matley et al. 2025). Additionally, large female silky sharks (⩾2 m TL) are known to aggregate and exhibit residency (dispersing <50 km) to areas with dynamic current regimes and high prey availability, indicating use of such environments independent of provisioning (Carlisle et al. 2019, Curnick et al. 2020, Whitehead et al. 2022). These movement patterns are distinct from juveniles and males of this species, which are much more dispersive (Hutchinson et al. 2019, Curnick et al. 2020, Filmalter et al. 2021), and further suggest that the residency exhibited by tagged female silky sharks in this study is not unique to areas of provisioning. Quantifying the influence of provisioning on silky shark movements in the Red Sea remains a challenge because such activities began due to an existing aggregation of sharks. It is accordingly unclear whether the residency of silky sharks to the Jeddah region is a strategy by certain individuals to remain near the provisioning site year-round or if this is a naturally resident population that has adapted its depth use to withstand seasonally high temperatures in the Red Sea.

Regardless of the associated biological drivers, female silky sharks tagged in this study remained resident during seasonally elevated temperatures in surface waters by employing submergence behavior for extended periods of time. Whilst this study was conducted in a relatively small area of the Red Sea and was limited by a small sample size (n = 10) with a strong female bias (n = 9), the results suggest that sharks may respond to continued ocean warming by condensing their habitat use into narrower depth bands. Further research remains necessary to better characterize the specific physical features influencing shark movement in the Red Sea (Spaet et al. 2017), where other elasmobranchs have also exhibited greater depth use (e.g. new depth records for *C. altimus* and *Rhinobatos punctifer* at 886 and 486 m, respectively: Frappi et al. 2023, 2024), so that more widely applicable insights can be obtained. For example, the hottest seasonal temperatures of Red Sea surface waters coincide with the intrusion of Gulf of Aden intermediate water (Guo et al. 2022). This influx of water yields a particularly stratified water column in the Jeddah region containing an intermediate water mass (i.e. a distinct, uniform layer between the upper mixed layer and deep water) with thermal conditions (~26°C) seemingly preferred by silky sharks tagged in the Red Sea (Zarokanellos et al. 2017). It is possible that the findings of this study are only applicable to similarly stratified oceans where sharks can seek thermal refuge in an intermediate water mass. This would indicate that in less stratified oceans, when mixed layer temperatures rise above a relevant threshold, silky sharks may still need to migrate horizontally to remain within their preferred thermal conditions. Nevertheless, the Red Sea provides an excellent microcosm of how silky sharks may respond to the higher ocean temperatures expected with global climate change. More detailed investigations of shark behavior, including a larger sample size and additional tagging of male silky sharks in the Red Sea, will likely enable more predictive and actionable conservation strategies to be developed for future climate scenarios.

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