



Pop-up archival tags reveal environmental influences on the vertical movements of silvertip sharks *Carcharhinus albimarginatus*

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ABSTRACT: Vertical space use informs the ecology and management of marine species, but studies of reef-associated sharks often focus on horizontal movements. We analysed the vertical movements of silvertip sharks *Carcharhinus albimarginatus* using pop-up archival tags deployed on 7 individuals in the Chagos Archipelago, central Indian Ocean. The sharks changed depth predictably with water column thermal structure, moving deeper with seasonal increases in mixed layer depth while occupying a narrow ambient water temperature range around ~27°C. At shorter timescales, higher resolution data from 5 tags showed that silvertip shark depth varied cyclically with surface light levels, increasing during daylight and on nights around the full moon. This matches the diel vertical migrations of many fish species, suggesting that the sharks' light-driven depth changes might relate to foraging. While most vertical movements (>98%) were within the mixed layer, deeper dives to 200–800 m occurred approximately every 3 d. High-resolution data from one recovered tag showed the shark ascending deep (>200 m) dives in 2 sharply defined phases, initially fast then slow. Analysis of dive profiles against dissolved oxygen (DO) data suggested that the shark may have ascended rapidly to escape low DO levels at depth, then reduced its ascent rate by 50–80% once DO levels increased. While a small sample, the electronic tags deployed in this study revealed the silvertip sharks' predictable use of mixed layer waters, narrow thermal range and apparent intolerance of hypoxic conditions. These characteristics may exacerbate the species' vulnerability as oceanic warming and shoaling oxygen minimum zones modify vertical habitat availability.

KEY WORDS: Coral reef · Mini-PAT · Oxygen threshold · Silvertip shark · Spatial ecology · Telemetry · Thermal tolerance · Diving behaviour

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1. INTRODUCTION

Sharks are an important group of marine predators, but both pelagic and reef-associated species are under threat (Baum & Myers 2004, Ferretti et al.

2010, Graham et al. 2010, Worm & Tittensor 2011, Nadon et al. 2012, MacNeil et al. 2020). Population declines of many species have been observed globally, with fisheries impacts (Meekan et al. 2006, Vianna et al. 2016) and habitat degradation (Knip et

al. 2010, Sguotti et al. 2016) identified as key drivers. Sharks are also likely to be impacted by the effects of climate change, including ocean warming and reductions in dissolved oxygen (DO) availability (Chin et al. 2010, Gilly et al. 2013, Rosa et al. 2017).

Knowledge of sharks' spatial ecology improves our understanding of their ecosystem roles (Williams et al. 2018) and vulnerability to threats (Jacoby et al. 2020), and aids in designing conservation strategies (Chapman et al. 2005, Lea et al. 2016, Dwyer et al. 2020). While data on the horizontal movements of sharks provides important insights, a full understanding of the ecology of many species requires information on their vertical space use (Andrzejaczek et al. 2019, 2022). Sharks' vertical movements may be an important dimension of their role in connecting ecosystems and food webs, for example by mediating nutrient transfers between surface, meso- and bathypelagic layers (Roman & McCarthy 2010, Braun et al. 2014, Howey et al. 2016). Vertical space use also influences species' exposure to human threats, including their likelihood of interacting with different fishing gears (Vedor 2021).

Species' vertical space use may be driven by, inter alia, water temperature and thermoregulation needs (Weng et al. 2005, Sims et al. 2006, Campana et al. 2011), DO levels (Carlson 2003, Carlisle et al. 2017) and diel cycles in prey distribution and behaviour (Bost et al. 2002, Baumgartner et al. 2011). Modelling species' vertical space use with respect to environmental factors, such as temperature, oxygen availability and light levels, can therefore provide insights into their ecology and biology, revealing cryptic behaviours such as foraging or aggregating at depth (Cagua et al. 2015, Braun et al. 2019) and physiological constraints such as temperature and DO thresholds (Abascal et al. 2011, Carlisle et al. 2015).

Highly mobile shark species are commonly studied with pop-up satellite archival tags (hereafter PATs), which collect data on depth, temperature and light levels, with the latter used to infer tag position via light-based geolocation. Summary data are programmed to be transmitted via satellite after the tag detaches from the animal, but a full data archive at high resolution (up to 1 Hz) can be downloaded from any physically recovered tags (Block et al. 2011, Hammerschlag et al. 2011, Hussey et al. 2015). Satellite tagging studies have been conducted on many mobile shark species, including oceanic white tip *Carcharhinus longimanus* (Tolotti et al. 2017, Andrzejaczek et al. 2018), blue *Prionace glauca* (Campana et al. 2011), white *Carcharodon carcharias* (Weng et al. 2007, Jorgensen et al. 2012), salmon *Lamna*

ditropis (Weng et al. 2005, Carlisle et al. 2011), porbeagle *L. nasus* (Francis et al. 2015), basking *Cetorhinus maximus* (Doherty et al. 2019), sixgill *Hexanchus griseus* (Coffey et al. 2020), tiger *Galeocerdo cuvier* (Heithaus et al. 2007, Afonso & Hazin 2015), silky *Carcharhinus falciformis* (Curnick et al. 2020), whale *Rhincodon typus* (Araujo et al. 2019), mako *Isurus* spp., thresher *Alopias* spp. (Block et al. 2011) and Greenland sharks *Somniosus microcephalus* (Stokesbury et al. 2005). These studies have provided many insights into the vertical lives of the species studied, such as residency to the relatively warm surface mixed layer (Tolotti et al. 2017), ontogenetic differences in depth use (Afonso & Hazin 2015) and the characteristics of diving behaviour (Howey et al. 2016). Nominally resident species, such as reef-associated sharks, are more commonly studied with passive acoustic telemetry, with movements inferred from detections of acoustically tagged animals within an array of acoustic receivers. While acoustic tagging can also provide depth and temperature data (e.g. Vianna et al. 2013, Espinoza et al. 2015a), its collection relies on animals being within detection range, and continuous high-resolution data can be difficult or impossible to acquire. Much of the research on reef-associated sharks to date has, therefore, focussed on quantifying aspects of horizontal space use such as habitat associations, movement networks and home ranges (e.g. Donaldson et al. 2014, Espinoza et al. 2015b, White et al. 2017, Jacoby et al. 2020).

To date, few studies have used PATs to study the vertical space use of reef-associated sharks (Andrzejaczek et al. 2022). This may be driven by the high cost of the individual tags relative to their perceived utility for species thought to exhibit relatively restricted movements and diving behaviours. Compared to pelagic taxa, PATs have so far been deployed sparingly on reef-associated species: on a single silvertip shark *Carcharhinus albimarginatus* in Fiji (Bond et al. 2015), 16 grey reef sharks *C. amblyrhynchos* in the Marshall Islands (Bradley et al. 2019) and 6 Caribbean reef sharks *C. perezi* in Belize (Chapman et al. 2007), as well as 12 reef manta rays *Mobula alfredi* near the Chagos Archipelago (Andrzejaczek et al. 2020). However, the high-resolution depth and temperature time series generated by the PATs have allowed these studies to generate physiology and behavioural insights beyond the capabilities of acoustic telemetry. These include describing a much larger vertical and thermal niche than previously suspected for Caribbean reef sharks (Chapman et al. 2007), observing oscillatory and deep-diving behaviour in reef manta rays (Andrzej-

jaczek et al. 2020) and providing direct evidence of offshore mesopelagic diving in silvertip sharks (Bond et al. 2015).

In the current study, we used PATs to investigate the vertical space use of silvertip sharks. Silvertip sharks are a large, mobile, reef-associated species, with a wide but fragmented distribution throughout the Indo-Pacific (Compagno 1984). They are listed as Vulnerable by the IUCN (Espinoza et al. 2021) and populations appear to have been seriously impacted by fishing in several parts of the species' range (Meekan et al. 2006, Graham et al. 2010, Ferretti et al. 2018). Silvertip sharks are reported to dive up to 800 m (Compagno 1984), and a short deployment of a PAT on a silvertip shark in Fiji found that the animal occupied a depth range of 0–380 m, with a mean depth of ~60 m and an average water temperature of 26.3°C, cooler than the shallows (Bond et al. 2015). Similarly, a 2012 survey around the Chagos Archipelago, using baited remote underwater video, found that while silvertip sharks were present across a broad depth range (15–80 m), they were at higher abundance, relative to grey reef sharks, at deeper sites (Tickler et al. 2017). This apparent deeper depth distribution may have biased earlier attempts to model silvertip shark abundance and population trends based on shallow visual surveys or fishing (e.g. Ferretti et al. 2018), and better knowledge of their spatial ecology might better inform abundance surveys and analyses used to infer their conservation status. Additionally, the silvertip shark has been relatively under-studied compared with its smaller congener, the grey reef shark, and improved knowledge of its spatial ecology could help to better inform its conservation management.

Here, we analyse data from PATs deployed in 2013 and 2014 on 7 silvertip sharks within the large marine protected area (MPA) that surrounds the Chagos Archipelago in the central Indian Ocean. The overall goal of this study was to describe the vertical space use of silvertip sharks in relation to physical drivers including sea surface temperature (SST), water column structure and solar and lunar illumination, to better predict temporal variations in its susceptibility to fishing gears (e.g. surface longlines) and to identify any thermal or other constraints that might provide insight into this species' vulnerability to ocean warming under climate change. We examined temporal variation in the depth use of sharks relative to SST and the depth of the surface mixed layer (MLD), since both have been shown to drive vertical space use in other mobile ectothermic shark species (Campana et al. 2011, Howey et al. 2016). We

also investigated the influence of diel and lunar cycles, which have both been shown to predict depth use in multiple species, including the grey reef shark (Vianna et al. 2013), silky shark (Curnick et al. 2020), blue shark (Queiroz et al. 2010) and blacktip reef shark *C. melanopterus* (Papastamatiou et al. 2018). Lastly, we investigated the relationship between diving behaviour and water column stratification (temperature, DO), which are known to influence the diving behaviour of other species that make mesopelagic excursions (such as the oceanic whitetip shark; Howey et al. 2016).

2. MATERIALS AND METHODS

2.1. Study area

The Chagos Archipelago comprises a group of atolls, islands and seamounts in the central Indian Ocean, centred on ~6.5° S, ~72° E (Fig. 1). The majority of the 640 000 km² Exclusive Economic Zone which surrounds the Archipelago, currently the British Indian Ocean Territory, is a no-take MPA, excepting a 3 nautical mile zone around the military base on Diego Garcia. Since the creation of the MPA in 2010, all commercial fishing and other extractive activities have been prohibited, and due to its geographical isolation and protected status, the reefs and surrounding waters are considered a valuable location at which to investigate the ecology of both reef and pelagic sharks under conditions of very low anthropogenic disturbance (Hays et al. 2020). The area's climate is defined by 2 monsoon seasons: the summer (northwest) monsoon from December to March, characterised by light west-northwesterly winds, warmer temperatures and more rainfall, and the winter (southwest) monsoon from June to September, with stronger south-easterly winds and cooler, drier weather. Periods in between the monsoons tend to have calm weather with light and variable winds.

2.2. PATs

Seven PATs (MiniPAT-247 model tags, Wildlife Computers) were used in this study. Since data recovery from PATs via the Argos satellite network is constrained by tag battery life and satellite coverage, a range of configurations of data resolution and deployment time was used to increase the likelihood of obtaining useable data (Table 1). The PATs were programmed to record ambient depth, temperature and

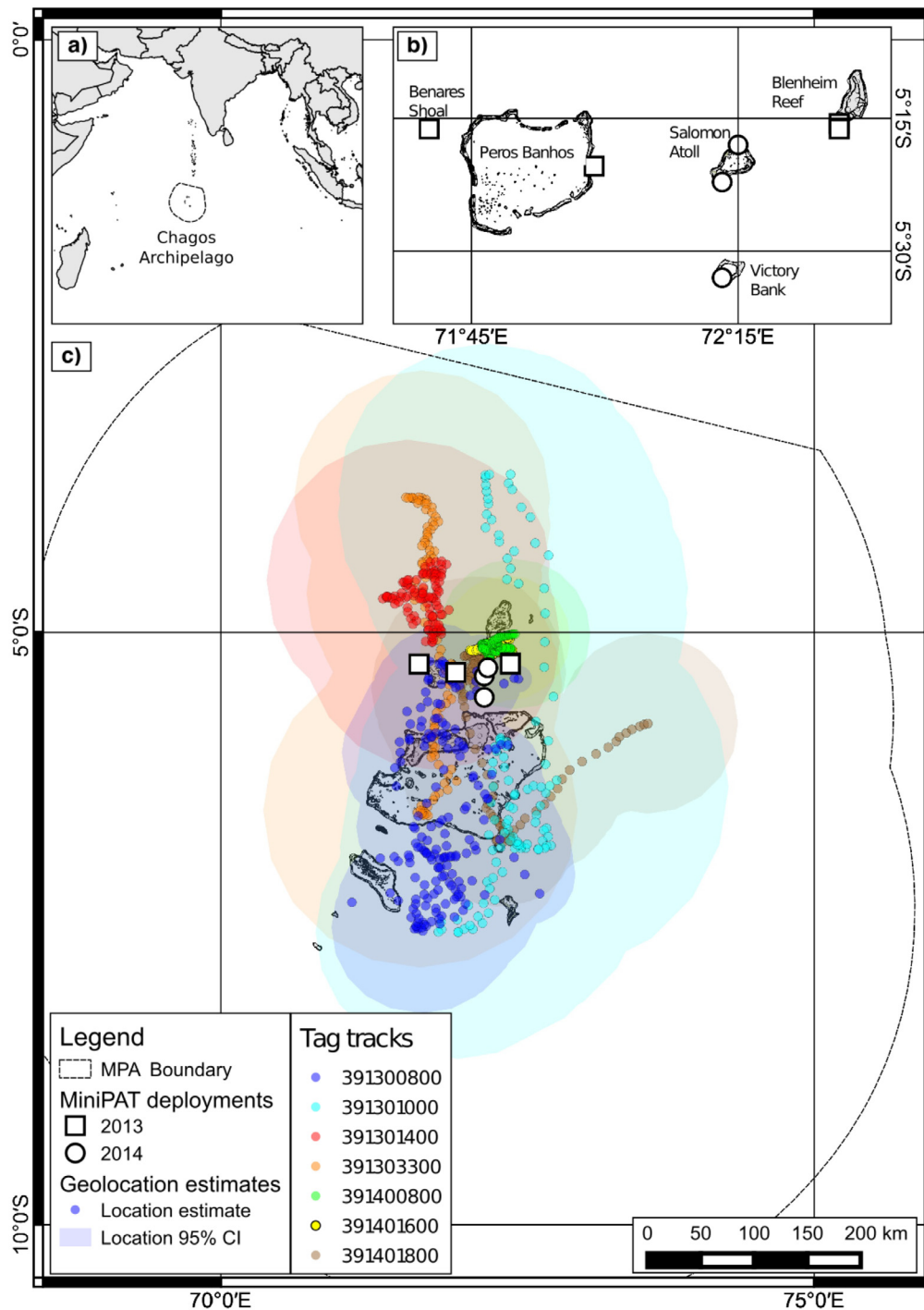


Fig. 1. Study area showing (a) location of the Chagos Archipelago and marine protected area (MPA, dashed line) in the Indian Ocean; (b) locations of 7 pop-up satellite archival tag (PAT) deployments on silvertip sharks in 2013 (squares, n = 4) and 2014 (circles, n = 3); and (c) daily geolocation-based position estimates and their 95% confidence areas, for all 7 tags colour coded by tag ID as per legend

light level at 15 s intervals, and were set to detach at 120, 180 or 270 d (Table 1). Tags were programmed to transmit their depth and temperature data, summarised as time-at-depth (TAD) and time-at-temper-

ature (TAT) histograms, in 6 or 24 h intervals. The histogram data were reported as the proportion of time spent in each of 12 pre-defined depth or temperature bins during each 6 or 24 h period (Tables S1

and S2 in the Supplement at www.int-res.com/articles/suppl/m717p085_supp.pdf). A subset of tags was programmed to transmit depth and temperature time series sampled at 5 or 7.5 min intervals (Table 1). Tags also reported summarised light level data for geolocation purposes, daily temperature-at-depth profiles (PDT), minimum and maximum depth in each reporting period (MinMaxDepth), and daily estimates of MLD. The PDT data contain the minimum and maximum temperature recorded at either 8 or 16 depth steps, set dynamically between the minimum and maximum depth recorded on a given day. Prior to deployment, each tag was prepared with anti-fouling paint (Trilux 33; International Paint LLC) and attached to a custom-made titanium dart using 15 cm of 180 kg monofilament leader (Moimoi). The leader material was protected from abrasion with a layer of Spectra (Honeywell Advanced Fibres and Composites) and covered with a length of heat-shrink tubing.

2.3. Tag deployment

In total, 7 silvertip sharks were tagged around the Chagos Archipelago in February–March 2013 (4 tags) and March 2014 (3 tags). Tags were deployed on sharks caught around the Peros Banhos and Salomon Atolls and near the submerged features at Benares Shoals, Blenheim Reef and Victory Bank (Fig. 1b). Sharks were captured using barbless 16/0 circle hooks, attached to a wire leader (1 m of 3 mm steel wire rope) joined to 2 m of 10–15 mm polypropylene line with a swivel, and terminated with a large longline branch hanger ('tuna clip'). These hook sets were baited with pieces of squid and deployed either singly, clipped to a weighted polypropylene drop line, or in sets of up to 10 at a time clipped at 15 m intervals to a floating polypropylene surface line. Once a shark was hooked, it was brought alongside the tagging vessel and a soft tail rope was secured just anterior to the caudal fin. Animals larger than approximately 1.5 m were left in the water and turned ventral side up to induce tonic immobility (Kessel & Hussey 2015). Smaller individuals were lifted onto a large padded vinyl mat and restrained. While sharks were out of the water, their gills were irrigated using a perforated plastic pipe attached to a seawater pump, and their eyes were covered with a wet cloth to further reduce stress. The PATs were attached externally by inserting the beta-dine-coated dart into the dorsal musculature just below the dorsal fin. The dart was inserted at a shallow angle relative to the axis of the shark's body, from the

Table 1. Summary of pop-up satellite archival tag deployments on silvertip sharks in the Chagos Archipelago in 2013 and 2014 (dates are d/mo/yr). Maximum depth estimates were obtained from daily temperature and depth summaries or directly from tag series data. PCL: precaudal length; FL: fork length; TL: total length. TS: time series; MLD: mixed layer depth

Tag ID	Shark metadata			Deployment			Pop-off			Tag programming				Tag reporting			
	Sex	PCL (cm)	FL (cm)	Date	Lat. (°S)	Long. (°E)	Date	Lat. (°S)	Long. (°E)	Days planned	Days active	% active	Histogram interval (h)	Max. depth (m)	Days data	TS data	MLD data
1 391300800 ^a	-	141	155	12/02/13	5.34	71.98	11/08/13	5.32	72.00	180	180	100	24	594 ± 6	179	✓	✓
2 391301000	-	122	134	16/03/13	5.26	72.44	27/07/13	5.91	71.35	270	133	49	24	488 ± 4	87	×	✓
3 391301400	-	122	134	12/03/13	5.27	72.44	06/07/13	5.26	71.67	180	116	64	6	760 ± 4	104	×	✓
4 391303300	-	113	124	22/03/13	5.27	71.67	04/07/13	5.24	71.66	180	105	58	24	792 ± 4	105	×	✓
5 391400800 ^b	F	129	139	24/03/14	5.37	72.22	22/07/14	5.04	73.02	120	120	100	24	464 ± 4	102	✓	×
6 391401600 ^c	F	110	124	25/03/14	5.30	72.25	30/07/14	5.29	71.72	180	127	71	6	400 ± 4	107	×	✓
7 391401800 ^b	F	109	120	27/03/14	5.55	72.22	06/07/14	4.87	74.12	180	101	56	24	328 ± 4	86	×	✓

^aTag 391300800 was physically recovered, allowing the full on-board data archive to be downloaded (15 s interval time series)
^bTags 391400800 and 391401800 transmitted time series data, sampled from the on-board data archive at 5 and 7.5 min intervals, respectively
^cTag 391401600 comprised both a pop-up satellite archival tag and a Vemco V16 acoustic tag

tail towards the head, to minimise drag from the tag. In all cases, precaudal, fork and total (TL) lengths were measured to the nearest cm, a fin clip from a pectoral fin was taken for DNA analysis and a muscle punch was taken for stable isotope analysis. One shark (Tag 6, ID 391401600) was tagged with both a PAT and an acoustic tag (V16 model tag, Vemco). The acoustic tag was inserted into the abdominal cavity of the shark via a small incision made posterior to the pectoral fins and just off the ventral midline (Haulsee et al. 2016) and closed with a single non-absorbable nylon suture (3-0, 24 mm) using a reverse cutting needle (Ethicon). Animals were also tagged externally with a conventional 'spaghetti' type identification tag, so that tagged animals could be identified if recaptured. The conventional tag was inserted into the dorsal musculature on the side opposite the PAT anchor to avoid entanglement between the tags. All sharks were tagged and released within 5 min.

2.4. Tag recovery and data pre-processing

Six of the 7 PATs were not recovered after releasing from their sharks, but transmitted subsets of their data via the Argos satellite network. The remaining tag (Tag 1, ID 391300800; see Table 1) was physically recovered after drifting to the Kenyan coast after release and provided a 180 d data set of depth and temperature measurements at 15 s intervals. Raw data transmitted by the PATs via the Argos satellites were processed using Wildlife Computers' Data Analysis Program (Wildlife Computers). This resulted in daily summaries of TAD, TAT, PDT, SST, MinMaxDepth and light levels. Data times in UTC were converted to the local time zone (UTC+5). Four tags generated data summaries at 24 h intervals, of which 2 also transmitted portions of their time series data, sampled at 5 and 7.5 min intervals (see Table 1); the remaining 2 tags generated data summaries at 6 h intervals, at 00:00, 06:00, 12:00 and 18:00 h.

Five of the 7 tags also reported MLD estimates based on the depth and temperature data (see Table 1). For the 2 tags that did not provide MLD estimates, we used the method of Kara et al. (2000) to generate estimates of the isothermal layer depth (approximating the MLD) directly from the tag data, by analysing temperature changes with depth. Briefly, the Kara algorithm searches the depth–temperature profile from the surface downwards until it finds a point at which the change in temperature with depth exceeds a defined threshold; in this case, 1.5°C (Kara et al. 2000). The isothermal layer depth is defined as the depth at which

the difference between the ambient temperature and the inferred mixed layer temperature first exceeds this threshold (Kara et al. 2000). The 1.5°C temperature change threshold was chosen after calibrating the Kara algorithm against MLD estimates from the tags.

The reported summary TAD and TAT histograms (proportion of TAD and TAT) used different bin boundaries to summarise the data from different tags (Tables S1 & S2). To enable us to calculate pooled summary statistics for all tag data, we first recalculated the histogram data for each tag based on a common set of depth and temperature bins. This allowed us to directly compare, and average, the proportion of time spent in each depth or temperature bin across tags. All data histograms were re-calculated using the depth and temperature histogram bin boundaries for Tag 1, with maximum depth and temperature values set to 1000 m and 34°C, respectively (Tables S1 & S2). Where a tag's data used different histogram bins from Tag 1, TAD and TAT were recalculated based on the new bin boundaries on the assumption that time spent between 2 given depths or temperatures in the original histogram was uniformly distributed.

Daily geolocation position estimates for the tags were generated based on light-level data and SST using the method of Teo et al. (2004). This algorithm uses changing ambient light levels to identify local times of dawn and dusk and calculate day length (related to latitude) and time of local noon (related to longitude) (Hill & Braun 2001). Light-based geolocation position estimates were then validated by comparing *in situ* SST measurements from the tag with remote-sensed SST distributions (Teo et al. 2004). The resulting position estimates were refined using a state-space model which takes into account additional data on local cloud cover and bathymetry (Block et al. 2011, Winship et al. 2012). Daily estimated positions and associated errors (95 % CIs) were generated for each tag track.

Data from the V16 acoustic tag were collected using an array of Vemco acoustic receivers (VR2 type) deployed around the reefs in the northern part of the Chagos Archipelago in 2013 and 2014 (Fig. 1). The methods used to deploy, anchor and retrieve the acoustic receivers have been described in detail in earlier studies (Carlisle et al. 2019, Tickler et al. 2019, Williamson et al. 2021)

2.5. Data analysis

All statistical analysis was performed using R statistical software (v.3.5.1; R Core Team 2018). Homo-

geneity of variance for parametric tests (*t*-test and ANOVA) was determined using Levene's test. The results of statistical tests were considered statistically significant at $p < 0.05$.

2.5.1. Shark horizontal movements

Shark tracks and associated error ellipses based on the 95% CIs of estimated longitude and latitude were overlaid on a map of the MPA to visualise shark movements with respect to their tagging locations, the atolls of the Chagos Archipelago and the MPA boundary. Data from the single shark tagged with both a PAT and a passive acoustic tag was also used to investigate variation in geolocation errors over time. Methods and results for this exploratory analysis are included in Section S2 in the Supplement.

2.5.2. Individual tag depth versus water column temperature profiles

To compare data across all 7 tags, we aggregated all TAD and TAT histogram data to 24 h periods, averaging across shorter 6 h summaries where necessary. For each tag, we calculated the median, interquartile range (IQR) and 95% range for depth and temperature for each daily summary by linearly interpolating within the depth and temperature bin ranges to estimate the depth or temperature value for each quantile. Where upper bin boundaries for depth and temperature were open (i.e. >500 m or >32°C, respectively; Tables S1 & S2), they were assumed to be 1000 m and 34°C, respectively.

We reconstructed water column thermal profiles, or bathythermographs, over time from each tag's daily depth and temperature profiles, i.e. PDT records. We created the bathythermograph data from each tag's PDT records by first averaging the minimum and maximum temperatures for each depth step reported in the PDT and then interpolating temperature linearly between the depth steps to infer the temperature at 2 m intervals. This produced a depth-temperature raster with 2 m vertical resolution for each tag and date; i.e. if a tag reported mean temperatures of 28°C at 10 m and 26°C at 18 m, the temperature was assumed to be 27.75°C at 12 m, 27.50°C at 14 m, etc. In this way, each 2 m increment in the daily depth-temperature profile was assigned a temperature intermediate between the reported values for the large depth steps. For the single tag for which high-resolution (15 s) pairs of depth and tem-

perature records were available (Tag 1, ID 391300800), bathythermograph data were obtained by averaging the temperature records within 2 m depth bins, i.e. 0–2, 2–4 m, etc. for each 24 h period. We plotted each bathythermograph and superimposed the median depth \pm IQR to visualise the relationship between shark depth and the water column thermal structure over time. We calculated the Pearson correlation between the median daily depth of the sharks and the daily estimates of MLD to quantify the strength of the relationship.

2.5.3. Median depth and temperature by month for all sharks

Using the standardised TAD and TAT histogram data, we pooled the data across tags by day and calendar month and calculated the overall median depth and temperature for each day. We then compared trends in the sharks' median daily depth and ambient temperature, by calendar month, with median MLD and SST, respectively, using box plots. As the variance of the observations varied significantly between months, variation in mean depth by calendar month was tested using Welch's ANOVA, using the 'oneway.test()' function, with pairwise comparisons between months made using Tukey's test in the 'games_howell_test()' function.

2.5.4. Diel and lunar variations in depth and temperature

For the 5 tags with data recorded either as 6 h histograms or as a time series (see Table 1), we aggregated depth and temperature data by date and diel period (TOD), classified as 'day' if data were recorded between approximately 06:00 and 18:00 h local time; otherwise, 'night'. Lunar phase (new, waxing, full, waning) was assigned to each record based on date, using the function 'lunar.phase()' in the R package 'lunar' (Lazaridis 2022). For the data stored as histograms, summary depth and temperature statistics (median, IQR and 95% range) were calculated for each period for each date using the same interpolation methodology as described above for the 24 h histograms. Quantile values for the time series data were calculated using the R base function 'quantile()'. We also calculated the mean percentage of time (\pm 95% CI) that sharks spent below depth thresholds (75, 100, 150 m) and temperature thresholds (25, 22, 18°C), overall and by diel period. Day vs.

night differences in the mean proportions of time spent below these temperature and depth thresholds were tested using *t*-tests.

To test for an effect of time of day and lunar phase on shark median depth, independent of seasonal changes in overall depth, we first calculated the difference between the median depth in each period (day or night) and a rolling 30 d median depth for each tag. ANOVA was then used to test for significant effects of time of day and lunar phase, and the interaction between them, on seasonally adjusted median depth. We used Tukey's test to determine any significant differences in levels of interaction between time of day and lunar phase.

2.5.5. Mixed modelling of median depth against environmental factors

We modelled the median daily depth of each shark against environmental factors for the 5 tags with TOD data using generalised linear mixed-effects modelling (GLMM; Bolker et al. 2009) with Gaussian error structure and identity link function, implemented in the function 'lme()' in the R package 'nlme' (Pinheiro et al. 2018). The data set included 962 date–TOD depth records for 481 d of data. Fixed predictors were MLD (in m), SST (in °C), lunar phase (moon: new, waxing, full, waning) and TOD, with tag ID (identifying individual sharks) included as a random effect. We also tested the interaction between TOD and moon to test the hypothesis that depth changes were related to light levels in the water column; i.e. to test for an effect of moonlight levels at night. The significance of the random intercept (1|TagID) was tested using the methodology of Zuur et al. (2009). Akaike's information criterion corrected for sample size (AICc) and log-likelihood scores of a model without random effects were compared to those of a mixed model in which the random effect term was included. The significance of the additional random effect term was evaluated based on the likelihood ratio test (LRT) in the function 'anova()'. Collinearity between the fixed predictors was checked by calculating generalised variance inflation factors (GVIFs) using the 'vif.lme()' function from the package 'spida15' (Monette 2012). The GVIF values were all ≤ 1.01 , indicating low collinearity between predictors (Table S3).

Model building was performed using forward selection following the method of Kock et al. (2013), starting from a null model with random effect only and adding and combining predictors sequentially.

The explanatory power of each model was evaluated using AICc, and an LRT was used to compare the best models at each level of complexity (single-variable, 2-variable, etc.). This approach was favoured over more complex machine-learning approaches (e.g. boosted regression trees; Elith et al. 2008), in order to both find the most parsimonious model and maintain ease of interpretation. Model residuals were tested for over-dispersion using the 'testDispersion()' function in the 'DHARMA' package (Hartig 2022) and temporal autocorrelation was checked using the 'ACF()' function in base R, using the option 'resType = "normalized"'. There was no evidence of over-dispersion (Fig. S1), but a plot of residuals against time and the ACF plot both showed evidence of temporal autocorrelation (Figs. S2 & S3). We added a second-order autoregressive term using 'CorARMA()' with the parameter 'p' set to 2 and rechecked the ACF plot to confirm that the autocorrelation had been correctly accounted for (Fig. S3). The model selection process was then re-run with the 'CorARMA()' term included, with models ranked by AICc as before. A summary table of all model variants tested was generated using the 'model.sel()' function in the package 'MuMIn' (Bartoń 2022). For models within 4 points of the lowest AICc (i.e. $\Delta\text{AICc} < 4$), we used the 'rsquaredGLMM()' function in 'MuMIn' to calculate marginal R^2 (R^2_m) and conditional R^2 so that the variance explained by fixed and fixed-plus-random predictors could be compared (Schielzeth & Nakagawa 2013). Diagnostic plots (residuals vs. fitted values, scale-location, residuals against time and *Q–Q* plots) were used to visualise the fit of the final model selected and check that assumptions of normality were not violated.

2.5.6. Investigation of individual diving behaviour (Tag 1, ID 391300800)

The depth–time series from the recovered PAT (Tag 1, ID 391300800) contained 180 d of continuous 15 s interval depth records, allowing individual dives to be identified in the time series. The threshold for dives below the mixed layer was assumed to be 100 m since this was the maximum MLD found in the data, and the sharks spent >98% of their time above this depth. Detailed analyses focussed on mesopelagic dives below 200 m, since depth–time plots of these deeper dives showed 2 distinct phases in the ascent portion of the dives, marked by a sharp reduction in ascent rate (hereafter transition point, *sensu* Howey et al. 2016), which warranted further investigation.

We defined a custom window function (Section S3 in the Supplement) to identify the time and depth of discontinuities in the ascent trajectory of each dive (i.e. transition points). A transition point was defined as an instantaneous reduction in ascent rate of at least 50%, before and after which the ascent rate had been relatively constant for at least one minute. The window function was initialised at the start of each dive's ascent (i.e. after the deepest point) and then moved through the remaining depth–time series in increments of 15 s (i.e. one time-step in the tag data). The date, time and depth of qualifying points in the dive profiles were recorded. To visualise the transition point dives, we standardised the time axis of each dive profile by defining the transition point of each depth–time series as $t = 0$ and calculated the mean depth at each (relative) time step across all dive profiles.

Temperature data for each dive were obtained directly from the tag data. Climatological DO values for the study area were downloaded from the NOAA World Ocean Atlas (WOA, <https://www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl>; monthly means, 1° latitude–longitude resolution). The WOA data provide average vertical DO profiles at 5 m to 50 m resolution. The vertical resolution of the data set decreases with depth: 25 m resolution from 100–500 m; 50 m resolution from 500–1500 m. To generate DO profiles for each dive, we first interpolated vertically within each WOA record to obtain DO values at 10 m intervals. We then interpolated horizontally and temporally between locations and dates in the WOA DO data to estimate values for the locations and dates of the shark's individual dives. An approximate location for each dive was assumed from the tag's geolocation estimate for the corresponding day. Given the low spatial resolution of the WOA data, the accuracy of the geolocation estimates was not thought to be a significant additional source of error in estimating DO values for the dives. Spatial interpolation between dive locations and the grid centroids in the WOA data set was performed with the R package 'akima', using a cubic-spline interpolation based on the method of Akima (1978). We assumed that the monthly averages in the WOA data corresponded to the 15th day of each month, and we then used a linear interpolation to estimate DO values on the date of each dive.

We investigated potential relationships between the diving behaviour and local environmental conditions by calculating Pearson correlation coefficients between the depth of the ascent rate change for each dive and, separately, the depth of the local oxygen minimum zone (OMZ), depth of the 2.5 ml l⁻¹ DO iso-

pleth, time spent below 100 m (i.e. below the mixed layer), maximum depth of the dive, time spent in waters cooler than 18°C and depth of 18°C isotherm. The 18°C temperature threshold was chosen for these analyses since the silvertip sharks spent >98% of their time in waters warmer than this temperature (see Table 2). A DO level of 2.5 ml l⁻¹ was assumed as a threshold for respiratory stress in a species like the silvertip shark based on levels reported in the literature for active ram-ventilating shark species, including mako sharks *Isurus oxyrinchus* (Vetter et al. 2008), bonnethead *Sphyrna tiburo* and blacknose sharks *Carcharhinus acronotus* (Carlson & Parsons 2001). We estimated the depth of the upper bound of the local OMZ at each dive location by analysing the gradient of the DO–depth curve, assuming that DO declines relatively steeply from the surface to the start of the OMZ but stabilises at that depth (Sewell & Fage 1948).

To better visualise the relationships between average DO and temperature profiles across dives as well as the depth of the transition points, we calculated the mean (\pm CI) temperature and estimated DO at 10 m intervals across all dives and then plotted these data against depth. We then superimposed on the depth axis the mean, CI and IQR of the transition point depths.

We also investigated whether the depth at which changes in ascent rate occurred was associated with rates of increase in DO levels, rather than absolute values. For the ascent phase of each dive, we calculated the rate of ascent (m s⁻¹) at each recorded 15 s time interval, based on the depth change since the previous depth–time record, and estimated the corresponding vertical rate of change in DO concentration (in ml l⁻¹ m⁻¹ of ascent) at the assumed dive location. We pooled these data for all dives and calculated the mean vertical ascent rate (\pm CI) for rates of change in DO concentrations of <-0.01, -0.01 to +0.01, +0.01 to +0.03, and >+0.03 ml l⁻¹ m⁻¹.

3. RESULTS

3.1. Overview of tag deployments

A total of 7 silvertip sharks ranging from 145 to 185 cm TL (mean \pm 95% CI: 158.4 \pm 10.0 cm) were tagged with PATs between 12 February 2013 and 27 March 2014 (Table 1), and 770 daily data records were obtained from the 7 tags (mean: 126 \pm 20 d; range: 101–180 d; Table 1). Two satellite tags released at their pre-programmed time (120 and 180 d

after deployment); the remaining 5 tags released prematurely between 101 and 127 d after deployment (49–71 % of the programmed time; Table 1). The maximum depth (\pm measurement error) recorded on these tags ranged from 328 ± 4 to 792 ± 4 m (Table 1).

3.2. Horizontal movements of the sharks based on geolocation estimates

The geolocation-based position estimates indicate that it is unlikely that any of the tagged sharks left the MPA, with the daily location estimates for each tag suggesting that the sharks spent most of their time close to the Chagos Archipelago reef system (Fig. 1c). However, care should be taken in interpreting the track information, as the 95 % CIs for each shark's daily position estimates were very large relative to the estimated distances moved by the sharks (Fig. 1c), indicating the low precision for the position estimates. A preliminary investigation of geolocation errors relative to position fixes from passive acoustic telemetry is reported in Section S2.

3.3. Variation in the median depth and ambient water temperature occupied by silvertip sharks

Daily median depth for all tagged sharks ranged from 4.0 to 77.2 m (mean: 36.5 ± 0.84 m). The median daily depth for each tagged shark matched the contours of the relatively warm surface mixed layer (Fig. 2a–g), with sharks spending 50 % of their time in the lower part of the mixed layer (Fig. 2a–g). The Pearson correlation score between shark median daily depths and the MLD, pooled for all tags, was 0.77 (Fig. 2h), and the relationship between shark median depth and MLD appeared consistent across tags and years (Fig. 3a). Daily MLD ranged from 18 to 98 m. MLD was shallowest in May (median 38 m, 95 % range 24–51 m) and deepest in August (median 82 m, 95 % range 68–90 m; Fig. 3a).

There was significant monthly variation in the sharks' median depth (Fig. 3a; Welch's ANOVA, $F_{6,764} = 134.3$, $p < 0.001$), with the post hoc test showing that sharks moved shallower in April, May and June than in February, July and August (Table S4) as the MLD shoaled (Fig. 3a). In contrast, the daily median water temperature occupied by sharks varied comparatively little. Daily median temperature averaged $27.2 \pm 0.1^\circ\text{C}$ overall (range: 26.8 – 27.6°C ; Fig. 3b). Local SST, in contrast, varied by up to 3°C during the deployment periods (Fig. 3b).

The median depth occupied by the sharks varied on shorter timescales between day and night and between lunar phases at night-time (Fig. 4). ANOVA revealed significant effects of time of day ($F_{1,954} = 454.16$, $p < 0.001$), lunar phase ($F_{3,954} = 7.28$, $p < 0.001$) and the interaction between time of day and lunar phase ($F_{3,954} = 10.63$, $p < 0.001$). Analysis of between-group differences using Tukey's test showed that sharks were significantly deeper during daylight overall, by ~ 11 m, and night-time depths were greater by up to 6.1 m when there was a full moon (Fig. 4, Table S5).

3.4. Time below depth and temperature thresholds

The sharks in the study spent an average of $5.1 \pm 0.5\%$ of their monitored time below 75 m, $1.5 \pm 0.1\%$ below 100 m and only $0.3 \pm 0.1\%$ of their time (< 5 min d^{-1}) below 150 m (Table 2). Time spent below 100 m was significantly higher during day time ($t_{559.63} = -3.56$, $p < 0.001$), consistent with day–night patterns in median depth, but sharks spent more time below 150 m during the night ($t_{757.64} = -3.01$, $p = 0.002$). Sharks spent 14 % of their time in waters between 22 and 25°C , i.e. up to 5°C cooler than their median ambient temperature, but only 1 % of their time (~ 14 min d^{-1}) in water cooler than 18°C . Over 99 % of the shark's time was therefore spent in depths shallower than 150 m and warmer than 18°C .

3.5. Modelling of shark median depth against environmental variables

GLMMs were used to determine the influence of MLD, TOD, lunar phase (Moon), SST and shark TL on the sharks' semi-diel (i.e. day vs. night) median depth. Tag ID was included as a random factor, along with a second-order autoregressive term to account for autocorrelation in the time series data (Fig. S3). The 6 best models had similar AICc values, between 6335.2 and 6339.1 (Table 3, Table S6), with the model with the lowest AIC including MLD, TOD and TL as fixed predictors. Diagnostics plots did not reveal any issues with model residuals (Fig. S4). The most parsimonious model included just MLD and TOD as predictors, with a model AICc only slightly higher than the best-performing model. However, R^2_m (indicating variance explained by the fixed predictors) was improved from 0.27 for this base model to 0.32 by the addition of TL, and 0.34 for models including a TOD \times Moon interaction as well as TL (Table 3), indicating

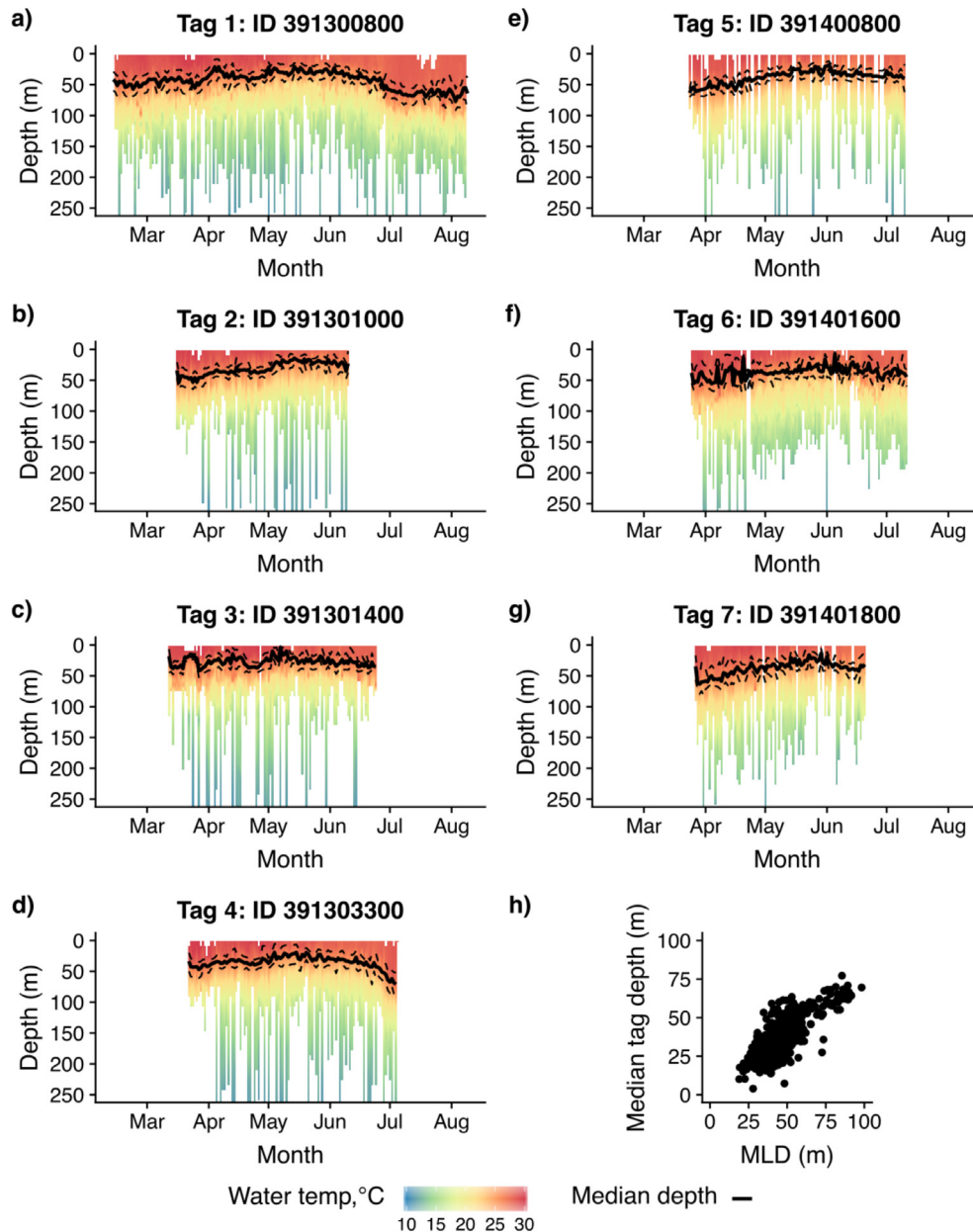


Fig. 2. (a–g) Bathythermographs based on daily depth and temperature records for 7 silvertip sharks tagged in (a–d) 2013 and (e–g) 2014. Depth range has been truncated to show greater detail. Solid line: median daily depth for each shark; dashed lines: upper and lower quartiles of daily depth distribution. Colour indicates ambient water temperature recorded by tags. (h) Overall relationship between median daily depth and mixed layer depth (MLD), pooled for all sharks (Pearson's correlation = 0.77)

that the addition of both TL and the lunar variable explained additional variation in the data. SST appeared to make only a small contribution to improving model R^2_m for the associated increase in AICc. Marginal and conditional R^2 values were similar for all models (Table S6), indicating that the random effect of Tag ID made a relatively small contribution to the explained variance. Effect sizes for the fixed predictors were consistent across models. Predicted depth increased by ~3 m for every 10 m

increase in MLD and, on average, by ~10 m during daylight (Table 3). The influence of SST as an environmental factor was smaller (0.7–0.8 m increase in depth per 1°C SST), and standardised effect sizes for MLD and SST (0.29 vs. 0.04; Table 3) showed that MLD exerts a much larger influence on shark depth than variations in SST. For the models including the interaction between TOD and lunar phase, shark depth was ~5.5 m deeper on nights with a full moon relative to nights of the new moon (Table 3). Larger

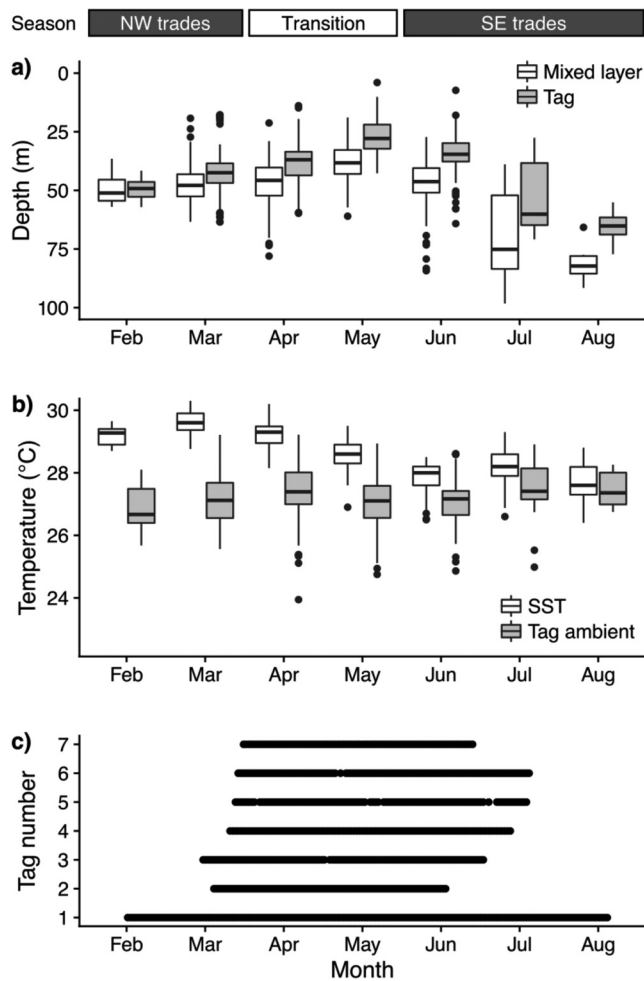


Fig. 3. Boxplots by month of (a) daily mixed layer depth and daily median tag depth (grey fill) and (b) daily mean sea surface temperature (SST) and daily median tag ambient temperature (grey fill), pooled across tags ($n = 7$) and years. Heavy horizontal line: monthly median; box indicates interquartile range; whiskers: 95% range; dots: outliers. (c) Distribution of data records over time for each tag, with time series aligned by calendar month. Seasons correspond to trade wind regimes

individuals were predicted to occupy deeper depths, with predicted median depth increasing ~ 1.5 m for each 10 cm increase in total length.

3.6. Diving behaviour

The tag recovered with the full archival time series data set (Tag 1, ID 391300800; Table 1) contained records of 61 dives below 200 m, averaging one every 3 d. Dives were typically short in duration, averaging 5.3 ± 0.7 min, with a steady descent to 'target' depth and a rapid ascent from depth (Fig. S5a,b). On return-

ing from dives below 200 m, the vertical ascent rate decreased sharply between 200 and 100 m depth (Fig. S5a,b). Mean vertical ascent rates before and after this transition point in the ascent were 0.59 ± 0.05 and 0.12 ± 0.01 m s^{-1} , respectively, a mean reduction of 80% (Welch's t -test: $t_{71.5} = 19.892$, $p < 0.001$). The change in ascent rate occurred at an average depth of 121.3 ± 7.2 m (IQR: 103.5–138.0 m). The correlations between the depth of the transition point in the ascent rate and the estimated depth of the upper boundary of the OMZ and the 2.5 ml l^{-1} DO isopleth on individual dives were 0.35 ($t_{60} = 2.887$, $p = 0.005$) and 0.32 ($t_{60} = 2.625$, $p = 0.01$), respectively, both stronger than the correlations between transition point depth and other environmental or dive parameters such as temperature or maximum dive depth, although the differences are small (Table S7). Comparison of mean transition point depth and the average estimated DO and observed temperature profiles of the dives also suggested that the point at which the ascent rate slowed was more strongly associated with increasing oxygen levels at the upper boundary of the OMZ than with abrupt changes in temperature (Figs. 5 & S5c,d). The shark's vertical ascent rate slowed as estimated DO concentration increased at >0.03 ml l^{-1} m^{-1} of ascent, i.e. when the shark had reached increasingly oxygen-rich depths (Fig. S6).

4. DISCUSSION

Using data from 7 PATs, we modelled the vertical movements of silvertip sharks around the Chagos Archipelago. While the sample size was small, the tagged sharks exhibited consistent and predictable vertical space use with respect to environmental drivers, suggesting that our tag data results may be more widely generalisable. Water column thermal structure appeared to be a key driver of overall depth use, with the sharks following seasonal variations in the thermal contours of the mixed layer and occupying a relatively narrow temperature band (25–28°C) similar to that reported elsewhere (Bond et al. 2015) for the species. Depth use varied predictably at shorter time scales, deeper during daylight and on nights of the full moon, and increased with the size of the tagged individuals, consistent with observations of diel vertical migration and ontogenetic variation in depth range in other ectothermic predators (Vianna et al. 2013, Afonso & Hazin 2015). There was also some evidence, albeit limited to a single tag, that the sharks' diving behaviour is influenced by DO levels in the water column.

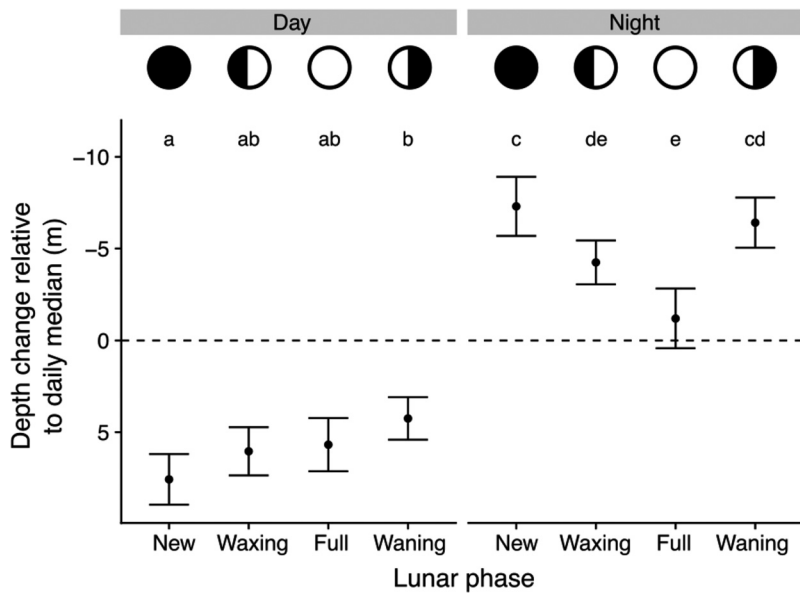


Fig. 4. Change in the median depth occupied by 5 silvertip sharks with time of day (day or night) and lunar phase, adjusted for seasonal variation. Error bars: 95% CI of mean values for all sharks. Changes in median depths are standardised relative to each shark’s 30 d rolling median depth. Lowercase letters above plots: results of Tukey’s HSD test after ANOVA of depth change against time of day, lunar phase and their interaction. Factor combinations labelled with the same letter are not significantly different ($\alpha = 0.05$)

4.1. Temperature and light as predictors of vertical space use in silvertip sharks

Variation in silvertip sharks’ daily median depth was strongly linked to the changing depth of the mixed layer over the study period, but, despite the daily median depth of the 7 sharks varying by over 50 m, tags recorded a consistent median ambient temperature of around 27°C. The depth changes exhibited by the animals are hypothesised to be directly related to variations in the temperature gradient

within the mixed layer, which altered the depth at which their ‘Goldilocks zone’ was located (i.e. the depth that the water temperature was ‘just right’). Median daily water temperature recorded by tags on silvertip sharks around the Chagos Archipelago was similar to the 26.3°C average recorded by Bond et al. (2015) for an individual in Fiji, suggesting consistency in silvertip sharks’ thermal preference across locations. While Espinoza et al. (2015a) did not directly measure ambient water temperature for silvertips sharks tagged on the Great Barrier Reef (GBR), they proposed behavioural thermoregulation (a ‘hunt warm, rest cool’ strategy) as an explanation for diel variation in depth use, and consequently the detection patterns observed in their passive telemetry study. Thermoregulation is proposed as a key driver in the vertical movements of several ectothermic shark species, including blue sharks (Carey & Gibson 1987, Campana et al. 2011, Watanabe et al. 2021), whale

(Thums et al. 2013), blacktip reef (Speed et al. 2012) and leopard sharks *Triakis semifasciata* (Hight & Lowe 2007), and it also appears to be a driver of vertical space use in other ectothermic taxa around the Chagos Archipelago. Curnick et al. (2020) found that silky sharks tagged around the Chagos Archipelago spent the majority of their time in the top 100 m, in water from 24 to 30°C. Andrzejaczek et al. (2020) obtained similar results from PAT deployments on reef manta rays *Manta alfredi* in the same location, finding that reef mantas spent most time within the

Table 2. Proportion of time spent by tagged silvertip sharks below given depth and temperature thresholds. Mean proportion of time ($\pm 95\%$ CI) spent below a threshold reported overall, and separately for daytime (06:00–18:00 h) and night-time (18:00–06:00 h) periods. *t*-test results for difference between day and night proportions are shown in last columns

Threshold	Proportion of time spent below threshold depth or temperature ($\pm 95\%$ CI)			<i>t</i>	df	p
	Overall %	Daytime %	Night-time %			
Depth						
75 m	5.1 \pm 0.5	9.1 \pm 0.9	4.1 \pm 0.6	-6.64	567.77	<0.001
100 m	1.5 \pm 0.1	1.8 \pm 0.3	1.1 \pm 0.1	-3.56	559.63	<0.001
150 m	0.3 \pm 0.1	0.3 \pm 0.1	0.4 \pm 0.1	3.01	757.64	0.002
Temperature						
25°C	20.4 \pm 0.8	33.0 \pm 1.7	14.5 \pm 0.9	18.89	838.02	0.001
22°C	6.4 \pm 0.5	11.3 \pm 1.0	4.1 \pm 0.4	13.35	745.46	0.001
18°C	1.1 \pm 0.1	1.2 \pm 0.2	0.9 \pm 0.1	2.52	635.78	0.012

Table 3. Fixed effects of highest ranked generalised linear mixed models modelling the semi-diel (day–night) depth of 5 silvertip sharks. Candidate fixed effects were mixed layer depth (MLD: m), sea surface temperature (SST: °C), time of day (TOD), lunar phase (moon: new, waxing, full, waning) and shark total length (TL: cm). The predictors' estimated coefficients (and standardised beta values shown in brackets for continuous predictors) for each of the 6 candidate models are shown below the models' Akaike information criterion corrected for sample size (AICc) score and marginal R^2 (R^2_m ; an estimate of the variance explained by the fixed effects in a mixed-effects model; Schielzeth & Nakagawa 2013). Predictors and/or interactions with t -test p -values less than 0.05 are indicated in **bold**

Model: Depth ~	MLD + TOD + TL	MLD + TOD	MLD + TOD + SST	MLD + TOD × Moon + TL	MLD + TOD × Moon + SST	MLD + TOD × Moon + SST + TL
AICc	6335.2	6335.5	6336.4	6337.9	6339	6339.1
R^2_m	0.32	0.27	0.28	0.34	0.29	0.34
Fixed effects						
(Intercept)	2.39	26.47	3.15	4.22	3.96	-16.16
MLD	0.33 (0.29)	0.33 (0.29)	0.33 (0.30)	0.33 (0.29)	0.33 (0.29)	0.33 (0.29)
SST	-	-	0.81 (0.04)	-	0.85 (0.04)	0.73 (0.03)
Night	-9.97	-9.98	-9.99	-12.54	-12.57	-12.55
MoonWaxing	-	-	-	-2.01	-1.95	-1.97
MoonFull	-	-	-	-3.36	-3.31	-3.33
MoonWaning	-	-	-	-2.51	-2.55	-2.56
TL	0.15 (0.16)	-	-	0.15 (0.16)	-	0.15 (0.16)
Night:MoonWaxing	-	-	-	2.09	2.11	2.10
Night:MoonFull	-	-	-	5.48	5.50	5.49
Night:MoonWaning	-	-	-	2.40	2.40	2.40

mixed layer between 25 and 50 m, with a median temperature of 27.3°C.

While water column thermal structure predicted the sharks' average depth, shorter-term variations in depth were predicted by time of day in combination with lunar phases, suggesting that silvertip sharks engage in light-based diel vertical migration, as seen in pelagic species such as blue (Campana et al. 2011) and bigeye thresher sharks *Alopias superciliosus* (Weng & Block 2004, Coelho et al. 2015). Espinoza et al. (2015a) hypothesised that silvertip sharks on the GBR 'rested' in deep channels between reefs during the day before hunting in the shallows around on reefs at night, and Bond et al. (2015) reported that a silvertip shark tagged with a satellite tag had a significantly deeper mean depth during daytime than at night. Depth histograms reported in that study suggest a median daytime depth of ~70 m, vs. ~30 m at night (Bond et al. 2015). Baited camera surveys of reef-associated sharks in the Chagos Archipelago also found that silvertip sharks were more abundant at depths of 70–80 m than on shallow reef

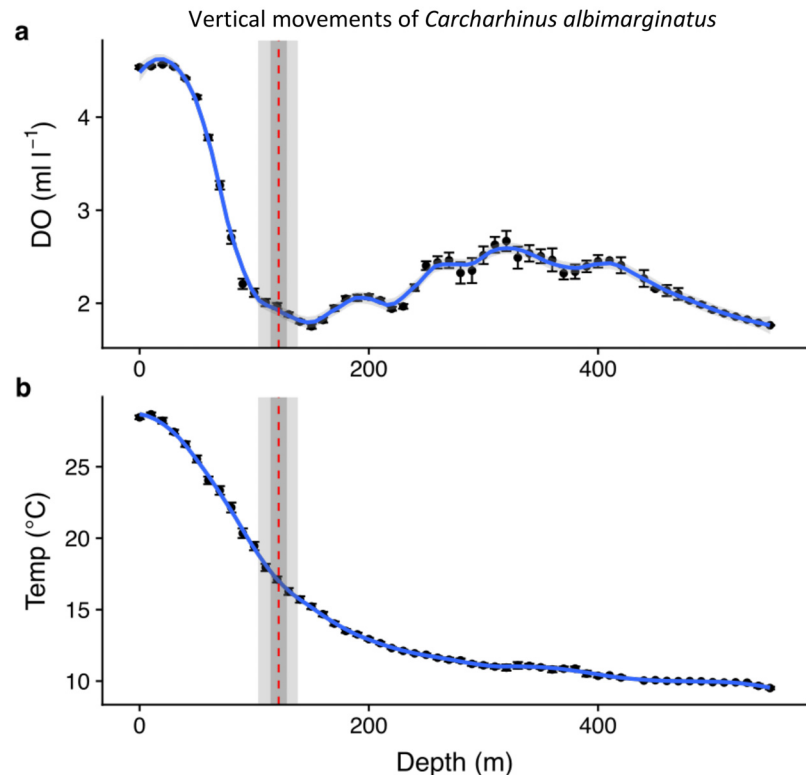


Fig. 5. Average (a) dissolved oxygen (DO) and (b) temperature profiles for the deep dives (i.e. where max. depth was >200 m) recorded for a single silvertip shark (Tag 1, ID 391300800). Dashed vertical red line: mean depth of the ascent rate transition point in ascents from these dives. Dark and light shaded bands: CI and interquartile range of transition point depth, respectively. Error bars: 95% confidence intervals of average temperature and DO

sites during daytime (Tickler et al. 2017). Vertical movements synchronised with diel and lunar cycles have also been observed on reefs in Palau for grey reef sharks, a close congener (Vianna et al. 2013). While thermoregulation might also be a driver of short-term vertical movements by silvertip sharks, as hypothesised by Espinoza et al. (2015a), the fact that their vertical space use also varies with changes in moon phase (i.e. light levels) at night suggests light as a primary driver of vertical movements, potentially mediated by the light-driven vertical migration of prey species. Diet and stable isotope-based studies suggest that silvertip shark diets contain a high percentage of pelagic prey resources (Cortés 1999, Curnick et al. 2019). In the Chagos Archipelago, where the outer reefs of atolls abut deep pelagic waters (1000–3000 m), light-driven diel vertical migration may bring mesopelagic prey into the surface waters adjacent to the reefs at night, drawing predators like silvertip sharks into these waters to forage. Curnick et al. (2020) and Andrzejczek et al. (2020) found that silky sharks and reef mantas both exhibited diel vertical migration near reefs in the Chagos Archipelago, with the latter study hypothesising that reef mantas exploited vertically migrating mesopelagic zooplankton in offshore surface waters at night. Together, these results suggest that temperature and light levels may be fundamental drivers of vertical space use of large ectothermic predators around reefs, driving similar patterns in space use across disparate taxa.

4.2. Diving behaviour

Silvertip sharks tracked in this study spent 98% of their time in the top 100 m of the water column, but dives to almost 800 m were recorded, approaching the maximum depth reported for this species (Compagno 1984). Data from a single tag showed that dives below 200 m were short (~5 min) and relatively infrequent. Purposes for these dives might include predator avoidance, thermoregulation and foraging (Howey et al. 2016, Andrzejczek et al. 2020, Royer et al. 2023). Predator avoidance cannot be discounted, given the presence in the MPA of larger predatory shark species like shortfin mako *Isurus oxyrinchus* (Forrest 2019) and hammerhead sharks (Sphyrnidae; Tickler et al. 2017) that prey on smaller sharks; however, silvertip sharks might be expected to take refuge on the reefs rather than dive to extreme depths. Thermoregulation, seeking cooler water temperatures, also seems as unlikely motivation for deep diving, as the water temperature drops

below 20°C at relatively shallow depths of ~100 m, beneath the mixed layer (Hosegood et al. 2019). Foraging may, therefore, be the most parsimonious explanation. Periodic deep dives are hypothesised to provide opportunities for pelagic sharks, including oceanic white tip (Howey et al. 2016), blue (Braun et al. 2019, Watanabe et al. 2021) and scalloped hammerhead sharks *Sphyrna lewini* (Royer et al. 2023), to encounter slow-moving mesopelagic prey. Silvertip sharks, which are known to exploit pelagic prey (Curnick et al. 2019), may employ similar strategies. Previous studies have suggested that reef shark foraging behaviour horizontally connects pelagic and reef ecosystems (McCauley et al. 2012, Williams et al. 2018). By foraging at depth, silvertip sharks may also be contributing to coupling deep pelagic and shallow reef ecosystems around the Chagos Archipelago.

DO concentration is thought to influence the vertical space use and diving behaviour of several marine predators, including billfish and tunas (Prince & Goodyear 2006, Prince et al. 2010, Carlisle et al. 2016, Pohlot & Ehrhardt 2018) and mako sharks (Vetter et al. 2008, Abascal et al. 2011), and analysis of the individual dive trajectories of one shark found possible evidence of an influence of DO availability on the vertical space use of silvertip sharks. Mesopelagic dives, identified in the high-resolution depth and temperature data from a physically recovered tag, were characterised by a rapid and constant rate of descent, a period of assumed searching and potential foraging followed by a return to surface waters in 2 distinct ascent rate phases. These transition point dives were characterised by a 50–80% reduction in vertical ascent rate, occurring at a fairly consistent depth. Howey et al. (2016) observed a similar pattern in dives by oceanic whitetip sharks in the Bahamas and hypothesised that this behaviour might coincide with the sharks moving out of the OMZ after mesopelagic dives, though they lacked *in situ* oxygen measurements to explore further. In the current study, we inferred local DO levels by interpolating across depth–time records from climatological data sets to estimate vertical DO profiles at the assumed dive locations. Since the exact dive locations themselves were uncertain, given the imprecision of light-based geolocation, our calculated DO values were an estimate of likely average conditions in the area of a dive, rather than DO measurements at the exact place and time. While preliminary, our results indicate that transition point depths were more strongly correlated with the estimated upper bound of the local OMZ (i.e. DO levels consistently below 2.5 ml l⁻¹)

than with changes in water temperature, which showed no distinct features at the depth of the ascent rate change. Under this oxygen-limitation hypothesis, the rapid portion of the silvertip shark's ascent from dives within the OMZ is designed to minimise continued exposure to low DO levels, while the sudden deceleration reduces energy expenditure once better-oxygenated waters are reached. A recent study on billfish found that individuals exhibited rapid swimming speeds immediately after capture and release by sports-fishers, a behaviour hypothesised to increase ventilation and reduce high lactate levels accumulated during capture (Logan et al. 2022). Thus, rapid ascents by silvertip sharks after time spent in low-oxygen waters might also serve to increase ventilation.

4.3. Vertical space use, management and conservation

Species' horizontal space use is often considered when evaluating their exposure to fisheries (Queiroz et al. 2019, Jacoby et al. 2020) and the efficacy of MPAs (Dwyer et al. 2020). However, vertical space use also has important management implications, and predictable vertical movements by silvertip sharks may increase their vulnerability to fishing but also be used to tailor enforcement activities to periods of greatest risk. The core depth range of the silvertip sharks in the MPA overlaps with the relatively shallow (30–100 m depth) longlines set by regional fishing fleets (Aneesh et al. 2016, Hewapathirana & Gunawardane 2017), some of whom are known to illegally fish around the Chagos Archipelago (Martin et al. 2013, Tickler et al. 2019). Jacoby et al. (2020) found that wider movements of the silvertip sharks around the Chagos Archipelago increased their exposure to illegal fishing activity; predictable vertical space use may increase their vulnerability by allowing fishers to target them based on simple environmental cues. Vianna et al. (2013) hypothesised a similar problem for grey reef sharks in Palau, which showed predictable depth changes correlated with diel and lunar cycles, and Andrzejczek et al. (2020) noted that reef manta rays occupied a predictable depth range which might increase their vulnerability to fishing gears. The deployment period of our study was focussed on the March to July period, thus missing the peak fishing season for pelagic tuna fisheries in the region and seasonal offshore productivity peaks. Longer tag release times would help to fill the gap in our understanding of shark movements and fisheries exposure.

A preference for relatively cool waters and an apparent intolerance of low-DO conditions may have longer-term implications for silvertip sharks, particularly in remote locations like the Chagos Archipelago with limited connectivity to other reef systems. Climate change is leading to warming oceans (Cheung et al. 2016), changes in MLD (e.g. Jang et al. 2011, Mohan et al. 2021), shoaling and expanding OMZs (Gilly et al. 2013) and an overall reduction in DO in the ocean (Breitburg et al. 2018). Declining oxygen availability as oceans warm is expected to lead to a poleward shift in species' ranges (Cheung et al. 2009, Sunday et al. 2011, Robinson et al. 2015). The Chagos Archipelago is relatively isolated, however, and surrounded by water 4 km deep, making (southerly) poleward migration by its inhabitants difficult, if not impossible. Behavioural thermoregulation, i.e. moving to deeper, cooler water (Dulvy et al. 2008), may allow short-term adaptation to warming surface waters for species such as silvertip sharks. However, continued surface warming, estimated at 0.11°C per decade globally and 0.15°C per decade in the Indian Ocean (Roxy et al. 2020), may interact synergistically with changing oxygen availability to constrain their available vertical habitat. Shoaling of OMZs (Stramma et al. 2012, Gilly et al. 2013) and MLD (Jang et al. 2011, Mohan et al. 2021) may push species like silvertip sharks towards the surface as warming surface waters compress their thermal niche from above. In addition to the physiological strain, this may also increase the vulnerability of the silvertip sharks to fishing by making their vertical space use more constrained and predictable. Climate change is forecast to have important impacts on fish stocks (e.g. Cheung et al. 2016), and our study suggests that important non-target species such as reef sharks may also be affected in terms of both physiological fitness and increasing restrictions to their useable habitat. Reducing direct anthropological pressures on reef sharks and their habitats, e.g. through well-enforced MPAs, may help maintain biodiversity and enhance species' resilience to environmental change (Dulvy 2006, Edgar et al. 2014, Davies et al. 2017), but tackling the root causes of the warming will be necessary to avert longer-term impacts.

5. CONCLUSIONS

Human fishing impacts on reef sharks is an ongoing concern, and the relatively restricted and predictable vertical niche of species such as silvertip sharks may accentuate their vulnerability, even in

nominally protected areas (Bradley et al. 2019, Tickler et al. 2019, Collins et al. 2021). Moving closer to the surface at night may increase their exposure to illegal fishing when detection and enforcement are most difficult. Enforcement reports by the authorities managing the MPA include accounts of vessels being encountered at dawn with their fishing gear already deployed (e.g. IOTC Secretariat 2015), suggesting that night-time fishing is already the norm for those fishing illegally in the MPA. Combining vertical spatial ecology with data on horizontal space use allows managers of both fisheries and protected areas to predict the times and locations of greatest vulnerability to fishing for particular species, to better prioritise enforcement efforts and to potentially regulate fishing activity to avoid bycatch of species of concern, as has been attempted with gillnet depths to avoid cetacean bycatch (Kiszka et al. 2018).

In addition to helping predict the spatial overlap of species such as silvertip sharks with fishing activities, archival tags, including designs fitted with additional environmental sensors (Coffey & Holland 2015), may allow us to model the responses of sharks and other taxa as the ocean warms and temperature and oxygen availability change both horizontally and vertically (Cheung et al. 2009, Gilly et al. 2013). Refining our understanding of the physiological constraints of taxa, and their vulnerability and likely responses to ocean warming and deoxygenation, will be vital to managing the future ocean. While acoustic telemetry is typically considered a more cost-effective option for the study of reef-associated shark species (Whoriskey & Hindell 2016, but see Bond et al. 2015, Bradley et al. 2019, Andrzejaczek et al. 2020), our study provides further evidence that satellite archival tags can reveal valuable insights into their spatial ecology, expanding our knowledge of the vertical dimension of shark ecology (Andrzejaczek et al. 2022).

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