



# Water temperature is a key driver of horizontal and vertical movements of an ocean giant, the whale shark *Rhincodon typus*

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**ABSTRACT:** Integrated analysis of the vertical and horizontal movements of epipelagic fishes requires high-resolution data from tags that have been attached to animals for long periods. The recovery of a SPLASH tag deployed on a whale shark *Rhincodon typus* for 3 mo enabled access to archival data of horizontal and vertical movements of the shark that travelled 5380 km from Christmas Island to the Banda Sea. We examined water temperature and bathymetry to compare movements of the shark with key oceanographic features. Over 89 d, we identified 1931 dives and grouped these into 5 broad categories depending on dive shape. To investigate the potential for these dives to reflect behavioural thermoregulation, we used boosted regression trees to model the relationship between pre- and post-dive surface durations and dive characteristics. The movements of the shark were correlated with water temperatures, with the animal following frontal systems while remaining in a sea surface temperature (SST) range of 24–29°C. Across the continental shelf off north-western Australia, the shark mostly remained near the seafloor, likely avoiding very warm SSTs and strong currents at the surface. U- (foraging) and V- (searching) shaped dives accounted for ~78 % of dives. Foraging dives during the day descended to 200–500 m and were preceded and followed by extended periods at the surface, whereas at night, the shark rarely dived below 200 m, likely foraging near the thermocline. Our results show how water temperatures influence the movement of this whale shark, with ‘basking’ at the surface during the day likely to gather environmental heat for thermoregulation, aiding to maintain body temperatures.

**KEY WORDS:** Whale shark · Thermoregulation · Vertical movement · Diving behaviour · Migration · Movement

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## 1. INTRODUCTION

Sea surface temperature (SST) is one of the most important abiotic factor influencing the horizontal movements of epipelagic fishes (Tittensor et al. 2010, Andrzejaczek et al. 2018). Many species reside within narrow temperature bands to maintain opti-

mal metabolic functions (e.g. Sequeira et al. 2012). However, in the open ocean, food in the surface layer is limited (Hays 2003), and consequently, these fishes must descend to deeper waters (>200 m) during the day to access prey that forms the deep scattering layer (Queiroz et al. 2017, Andrzejaczek et al. 2018, Braun et al. 2019). These deep waters are much

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cooler than the surface layers that are warmed by the sun, presenting a physiological challenge for fishes that depend on external temperatures to maintain body heat. Ectothermic and some endothermic species use behavioural strategies, such as spending time at the surface where waters are warmer, for thermoregulation (Kitagawa et al. 2000, Dickson & Graham 2004, Nakamura et al. 2015, Hino et al. 2019). For ectotherms, the need to rewarm in surface waters and forage in deeper waters creates patterns of vertical movement that resemble the dives of air-breathing marine animals (seals, turtles, penguins and whales) (Queiroz et al. 2012, Meekan et al. 2015, Andrzejaczek et al. 2018, Nakamura et al. 2020).

The horizontal and vertical movements of epipelagic fishes must therefore integrate the demands of temperature regulation and food acquisition within a 3-dimensional environment. For example, the occupation of physical features such as warm current eddies may strongly influence vertical movements, with species such as blue sharks *Prionace glauca* using warm waters within eddies to access food deeper in the water column (Carey et al. 1990, Braun et al. 2019). Other epipelagic fishes, such as ocean sunfish *Mola mola*, have been found to spend time at the surface to raise their body temperatures after foraging excursions to deep waters (Nakamura et al. 2015). For this reason, an understanding of the ecology of epipelagic fishes requires the simultaneous collection of accurate and robust data on behaviour, positions within a 3-dimensional environment and the physical conditions that the species experiences at fine temporal and spatial scales.

Tracking tags linked by satellite telemetry routinely record data at resolutions sufficient for fine-scale analyses. However, limits to satellite bandwidths mean that in many cases, only summaries of data are transmitted and data archives can only be accessed when the tag is recovered and downloaded (Andrzejaczek et al. 2019). Tag recovery is relatively easy to organise for species that return predictably to locations to breed or feed (e.g. seals, seabirds etc.), but for epipelagic fishes, recovery must rely on the serendipitous return of detached tags that have washed up on shorelines or tag removal from the few animals that are occasionally recaptured (Whitney et al. 2018).

The whale shark *Rhincodon typus* is a deep-diving ectotherm (Nakamura et al. 2020), found in tropical and subtropical oceans (Stevens 2007), that spends most of its time in surface waters (<100 m) with sporadic descents to deeper waters (>500 m) occurring mostly during the day (Brunnschweiler et al. 2009,

Meekan et al. 2015, Tyminski et al. 2015). Known aggregations of this species occur from Ningaloo Reef, Western Australia (Meekan et al. 2006, Norman et al. 2016), to the Gulf of Mexico (Hoffmayer et al. 2021), and because this species shows widespread migrations, tag recovery tends to be a rare event. For this reason, most studies have focussed on horizontal patterns of movement, and analyses of vertical movements have largely been restricted to the summarised data sets reported by tags (Thums et al. 2013).

Here we took the rare opportunity provided by the recovery of a satellite tag deployed on a whale shark to analyse a track of over 5000 km from Christmas Island in the Indian Ocean to the Banda Sea in the Coral Triangle, during which time the animal made >1900 vertical oscillations between the surface and deeper waters. Importantly, the function of these movements, also referred to as dives, is revealed by their shape, with searching dives having V-shaped profiles, whereas foraging dives have a U-shaped profile (Queiroz et al. 2017). We examine links between movement patterns, ocean temperatures, frontal systems and bathymetry and search for evidence of behavioural thermoregulation in vertical patterns of movement.

## 2. MATERIALS AND METHODS

We used a 1 m tether and fin clasp to attach a satellite-linked radio transmitter SPLASH-217B tag (334.4L, 55.0W, 100.0H mm; Wildlife Computers) to the dorsal fin of a male whale shark, measuring 8 m in total length. The shark travelled 5380 km from Christmas Island, Australia (105° 37' E, 10° 29' S), on 17 January 2008 to the Banda Sea, Indonesia, until 14 April 2008 (when the tag detached from the animal and was recovered by a local fisher) (Fig. 1a). The tag recorded and stored depth, temperature and light levels at 60 s intervals for the entire duration of the deployment. Horizontal positions were received via the Argos satellite system when the shark was close enough to the surface for the antenna of the tag to break the surface of the water. Each available location was assigned an error class (3, 2, 1, 0, A, B, Z) depending on the range of accuracy (<250 m to >5 km). For our analysis, only positions with locations 3, 2 and 1 were used. Duplicated position estimates were removed, and we applied a state-space model to the track using the 'bsam' package (Jonsen et al. 2015) in R with the DCRWS model (single individual) to investigate the movement process.

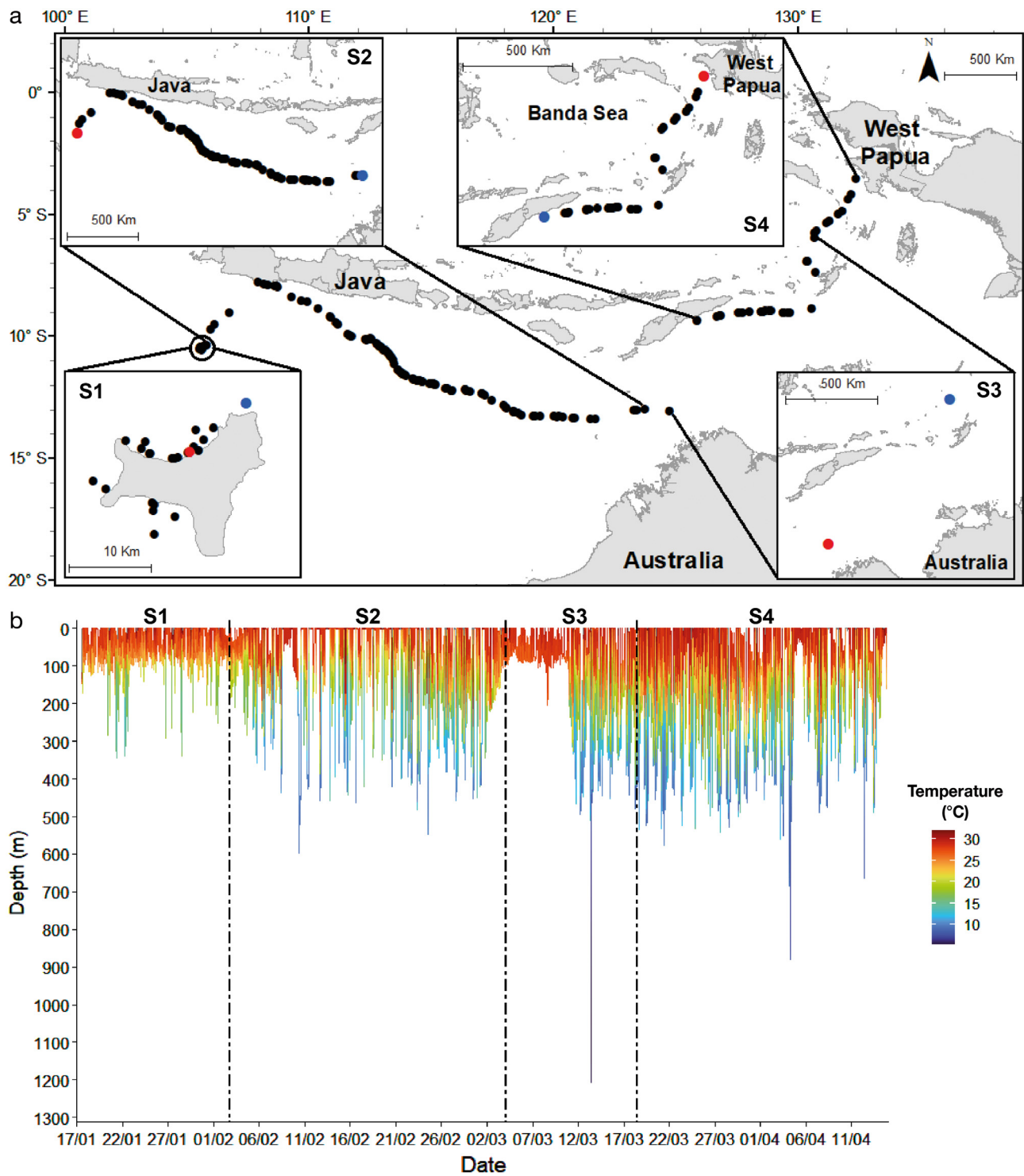


Fig. 1. (a) Study site. Black dots show the recorded positions of the whale shark from Christmas Island to the Banda Sea, where the tag detached off the coast of West Timor. Inset maps show the track split into sections (S1–S4), with red (blue) dots showing the first (last) location within each section. S1: Christmas Island; S2: migration between Christmas Island and the continental shelf of Australia; S3: migration between the continental shelf of Australia and south-west West Papua with no horizontal positions recorded on the tag (only dive movement recorded); and S4: return migration between the western side of West Papua and eastern Timor-Leste where the tag stopped transmitting. Lines from the inset maps indicate the start and endpoints of each section. (b) Time–depth series of the entire track coloured by water temperature. Vertical black dotted lines correspond to the sections (S1–S4) in panel (a). Dates given as dd/mm

During the track, there were periods of up to 14 d when no horizontal positions were transmitted by the tag to a satellite. State-space models fit poor quality tracks when there are large gaps in location data records (Bailey et al. 2008, Block et al. 2011), and this occurred for our track (Fig. S1 in Supplement 1 at [www.int-res.com/articles/suppl/m679p101\\_supp/](http://www.int-res.com/articles/suppl/m679p101_supp/)). Therefore, we instead used a combination of the maximum depths from the dive profiles, the water temperature recorded by the tag, the maximum bathymetry depths and the average daily travel speeds to recreate the track the shark may have occupied during those 14 d. The dive profiles and water temperature data were obtained from the tag archives. Bathymetry data were obtained from the 2015 General Bathymetric Charts of the Oceans (GEBCO 2015), at a resolution of 30 arc-second interval grids and analysed in ArcGIS (ESRI 2011). The daily average speeds ( $0.07\text{--}1.6\text{ m s}^{-1} = 6.05\text{--}138.24\text{ km d}^{-1}$ ) (Eckert et al. 2002, Motta et al. 2010, Rohner et al. 2018) were used to determine a speed buffer radius applied to the 2 known positions at the start and end of the 14 d gap, on 4 and 18 March, respectively. The location data were analysed in R v.4.0.1 (R Core Team 2020) and RStudio Desktop v.1.3.959 (RStudio Team 2020).

We analysed the time–depth profiles obtained from the tag using the package ‘diveMove’ (Luque 2019) in R. We defined ‘dives’ as descents that began at and then returned to 10 m depths following Thums et al. (2013). Small movements around the 10 m threshold for a dive (1–2 m deeper) were removed from the dataset of dives and included in the surface interval data (Thums et al. 2013). Using the ‘diveStats’ function, descent time, ascent time, bottom time, total dive time, descent distance, ascent distance, bottom distance (to determine ‘wiggle’), maximum depth, pre- and post-dive surface duration and vertical velocities (see Luque 2019 for further details) were extracted and used to analyse the dives. Dives were then visually classified into 4 broad categories: (1) V-shapes, defined as having little (<1 min) to no bottom time; (2) U-shapes, usually ‘square’ in shape with distinctive descent, bottom and ascent phases; (3) bounce dives (B), consisting of short and shallow undulations with no surface time between dives; and (4) W-shapes, characterised by having 2–4 undulations in the middle of the dive, with similar descent and ascent phases to V-dives (Fig. 2). V- and U-shaped dives were further categorised into 6 dive shapes. V-dives were characterised into: (1) single V-dives (>30 min at the surface between dives, either

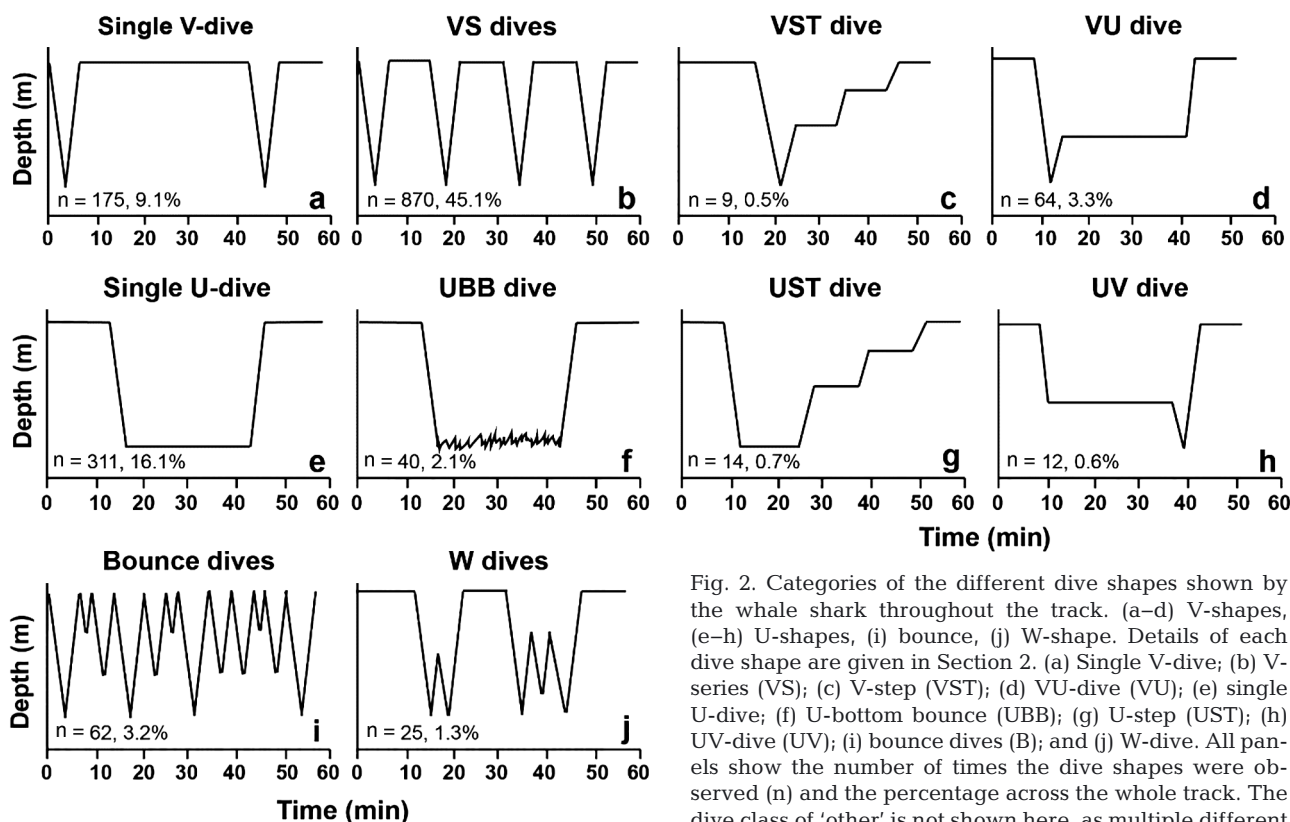


Fig. 2. Categories of the different dive shapes shown by the whale shark throughout the track. (a–d) V-shapes, (e–h) U-shapes, (i) bounce, (j) W-shape. Details of each dive shape are given in Section 2. (a) Single V-dive; (b) V-series (VS); (c) V-step (VST); (d) VU-dive (VU); (e) single U-dive; (f) U-bottom bounce (UBB); (g) U-step (UST); (h) UV-dive (UV); (i) bounce dives (B); and (j) W-dive. All panels show the number of times the dive shapes were observed (n) and the percentage across the whole track. The dive class of ‘other’ is not shown here, as multiple different shapes were seen (n = 349, 18 %)

prior to, or after a dive); (2) V-series (VS, <30 min surface intervals between dives); (3) V-step (VST, a V-shaped dive followed by 'stepping' to reach the surface); and (4) VU-dives (VU, combination of a V-shaped dive followed by a U-shaped dive before proceeding to the surface). U-shaped dives were further characterised into (5) single U-dives (square in shape with similar descent and ascent phases); (6) U-bottom bounce dives (U-shaped dives with fast 'bounce' dives during the bottom time of the dive, usually associated with feeding events); (7) U-step (UST, U-shape dive followed by 'stepping' to reach the surface); and (8) UV-dives (UV, combination of a U-shaped dive followed by a V-shaped dive before proceeding to the surface) (Fig. 2) (Wilson et al. 1996, Pütz & Cherel 2005, Thums et al. 2008, Gleiss et al. 2011, Queiroz et al. 2017, Andrzejczek et al. 2019). Dives that did not have any of the 4 broad shapes defined were mostly comprised of a mix of multiple V- and U-shaped dives at depth and were characterised as 'other' (O).

The spatial location of the dives was also categorised as occurring on the continental shelf (water depths <200 m) and open ocean (water depths >200 m). To determine which dives constituted open ocean, a maximum bathymetry radius of 200 m was set and a 1 km buffer was applied to all known locations. All locations outside the 200 m maximum bathymetry range or further than 1 km from the coastline were classed as open ocean dives. Time-at-depth and time-at-temperature were compared during day and night using histograms from the package 'RchivalTag' (Bauer 2018). Using functions within the 'RchivalTag' package, light levels, time and geolocations recorded by the tag were used to calculate the estimated times of dawn, day, dusk and night intervals. We then identified times of descent, bottom and ascent, dive duration and maximum depth, pre- and post-dive surface duration, and minimum and maximum temperatures experienced by the shark during each dive.

To investigate the relationship between time spent at the surface before and after a dive, and the characteristics of each dive (i.e. dive duration, maximum depth, etc.) we used the R package 'dismo' (Elith et al. 2008) to develop 2 sets of boosted regression tree (BRT) models. BRTs are statistical learning techniques that use a combination of regression trees and boosting to fit numerous individual trees in a forward, stage-wise method (Elith et al. 2008). We used pre-dive surface duration and post-dive surface duration (variables extracted during the dive analysis process) as response variables for each of the BRT models. We

ran 2 models to identify if different variables were influencing the time spent at the surface before and after a dive to identify if behavioural thermoregulation was occurring during this track. We added the maximum depth, dive time, maximum temperature, minimum temperature, dive shape, time of day and percentage of time above and below the thermocline, determined as occurring at 100 m (Locarnini et al. 2018), as explanatory variables. For this analysis, we also developed a thermal index (TI) that reflected the total temperatures that were experienced by the shark during each dive. This TI was calculated as the sum of all temperatures (T) recorded by the tag multiplied by the sampling interval in seconds and then divided by the dive duration (N) in seconds ( $TI = (\sum T \times 60) / N$ ). All continuous variables were standardised using the 'scale' function in R.

Following Elith et al. (2008), we estimated the best values for the BRT learning rate (the shrinkage parameter, *lr*), tree complexity (controls if interactions are fitted; *tc*) and bag fraction (proportion of data selected at each step), by creating a training and test dataset from partitioning the original data by 90 and 10% respectively. BRT models of 10 000 trees were then fitted over a range of values for *lr* (0.01, 0.05, 0.001, 0.005 and 0.0005) and *tc* (1–10) to establish the optimal parameters. The BRT model parameters for the pre-dive surface duration and post-dive surface duration were *lr* = 0.005, *tc* = 5 and bag fraction = 0.5 to have the number of trees (*nt*) at least 1000.

We obtained water column data including SST at 12 h intervals from the Regional Ocean Modelling System (ROMS), in combination with ozROMS, a modelling system for the continental shelf region of Australia, using a 3-dimensional numerical model with a high spatial resolution (Haidvogel et al. 2008, Wijeratne et al. 2018), and analysed in MATLAB v.9.3.0.713579 (R2017b) (MATLAB 2010). We collated water temperature, surface elevation, *u*-velocity (positive towards east) and *v*-velocity (positive towards north) for the entire region used by the whale shark.

### 3. RESULTS

Latitude and longitude positions of the whale shark were obtained on 55 of the 89 days of deployment over a track covering 5380 km (Fig. 1a), as derived from the ARGOS satellites. We retrieved 127 064 data points of time, depth, temperature and light levels from the tag archival data. During the first 2 wk



after deployment, the shark remained at Christmas Island (Fig. 1a, labelled section 1 [S1]), before moving out into the open ocean towards the coastline of Java (Fig. 1a, labelled S2). The shark then headed south-east towards the continental shelf region of Australia before migrating into the Banda Sea, towards the coastline of the western side of West Papua. In the final part of the track, the shark headed south to West Timor where the tag detached (Fig. 1a, labelled S3 and S4). Diving behaviours were recorded throughout the track, with the shark showing multiple dives through pelagic zones (Fig. 1b), averaging depths of 99.3 m. The maximum depth of a

dive was 1209 m, which occurred in the open ocean off the northern shelf of Australia.

Using a combination of ROMS and ozROMS water temperature data, we found that the shark was exposed to SSTs between 22 and 32°C but spent ~60 % of its time in temperatures of 24–29°C (Fig. 3; Animation S1 in Supplement 2). During the first 2 wk after tag deployment, the shark remained at Christmas Island (Fig. 3a) in water temperatures exceeding 30°C. On 4 February (Fig. 3b), the shark moved into the open ocean at a time that coincided with the arrival of a cold water mass. During the next month, the shark travelled more than 2000 km (Fig. 3c–e),

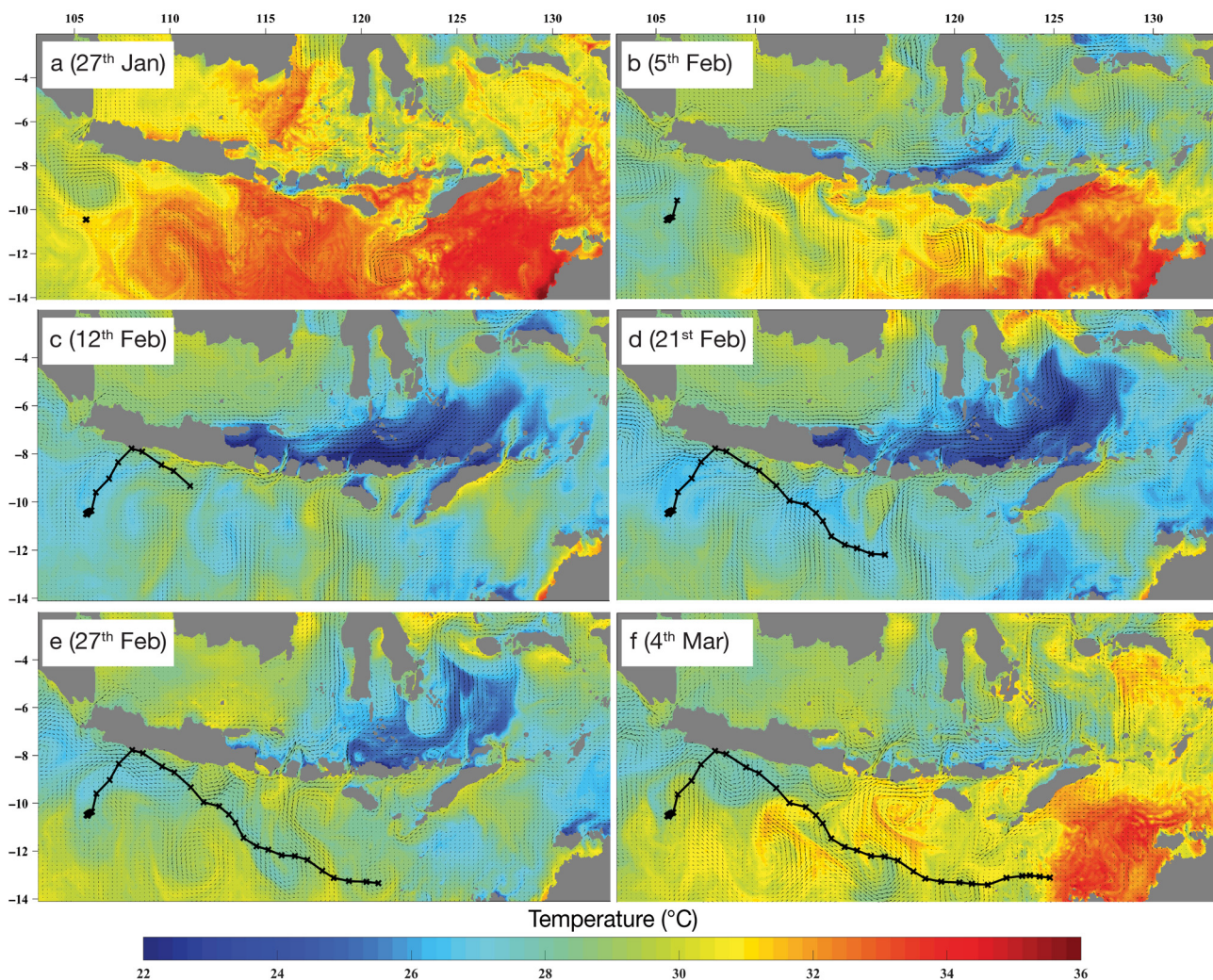


Fig. 3. Recorded latitude (°) and longitude (°) positions (black crosses) with changes in sea surface temperature (SST). (a) On 27 January, the whale shark was located at Christmas Island; (b) 5 February; (c) 12 February; (d) 21 February; and (e) 27 February, where the shark travelled more than 2000 km to the continental shelf of Australia. (f) 4 March was the last position of the shark until 18 March. All SST readings were taken on a 12 h daily cycle, with temperatures ranging from 22 to 36°C. See Animation S1 in Supplement 2 for a video animation showing changes in SST of the region overlaid with the whale shark track from Christmas Island (tagging location) to the Banda Sea. The track is shown by the black line, black arrows of varying sizes indicate surface velocity currents (strength and direction of the water movement, exact values not shown)

remaining in the SST range of 24–29°C and following cooler water masses separated by frontal systems. On 4 March (Fig. 3f), the shark arrived at the edge of the shelf off the continent of Australia where SST exceeded 30°C. From this point, no contact was received from the tag for the next 14 d, until the tag transmitted again showing a return trip from the western side of West Papua to the eastern side of Timor-Leste, where transmission ceased.

To interpolate a probable track for the 14 d period (4–18 March) with no horizontal data, we applied an average rate of movement from the earlier track ( $71.54 \text{ km d}^{-1}$ ;  $0.83 \text{ ms}^{-1}$ ) to the last known position on 4 March (Fig. 4). Based on the rate of movement and dive depths, successive calculated points suggested that from 4 to 11 March, the shark was likely to be over the continental shelf of Australia (Fig. 4). During this time, the shark spent <5% within the top 10 m of the water column and >72% of time between 50 and 100 m depths over a shelf where water depths reached a maximum of 119 m.

A total of 1931 individual dives occurred during the track, with 1002 taking place in the open ocean in waters deeper than 200 m (Fig. 1b, sections S2 and S4) and 929 occurring on continental shelves (Fig. 1b, sections S1 and S3). In total, the shark spent ~83% of its time within the epipelagic zone (0–200 m) (Fig. 5a; time-at-depth plots for the individual sections are given in Fig. S2) and when not restricted by bathymetry (i.e. in the open ocean), the shark still spent 76% of time within 200 m of the surface, with deep dives (>500 m) only occurring 18 times (10% of all dives). U- and V-shaped dives were most common (~77% of the total number of dives), with multiple V-shape undulations, characterised here as V-series (<30 min surface time between dives; Fig. 2), accounting for the highest proportion (46%) of dives. We also observed that ~23% of V-shaped dives were followed by U-shaped dives, and using a Pearson correlation test, we found a significant positive correlation between the maximum depth of the V-dive and the maximum depth of the subsequent U-shaped dive

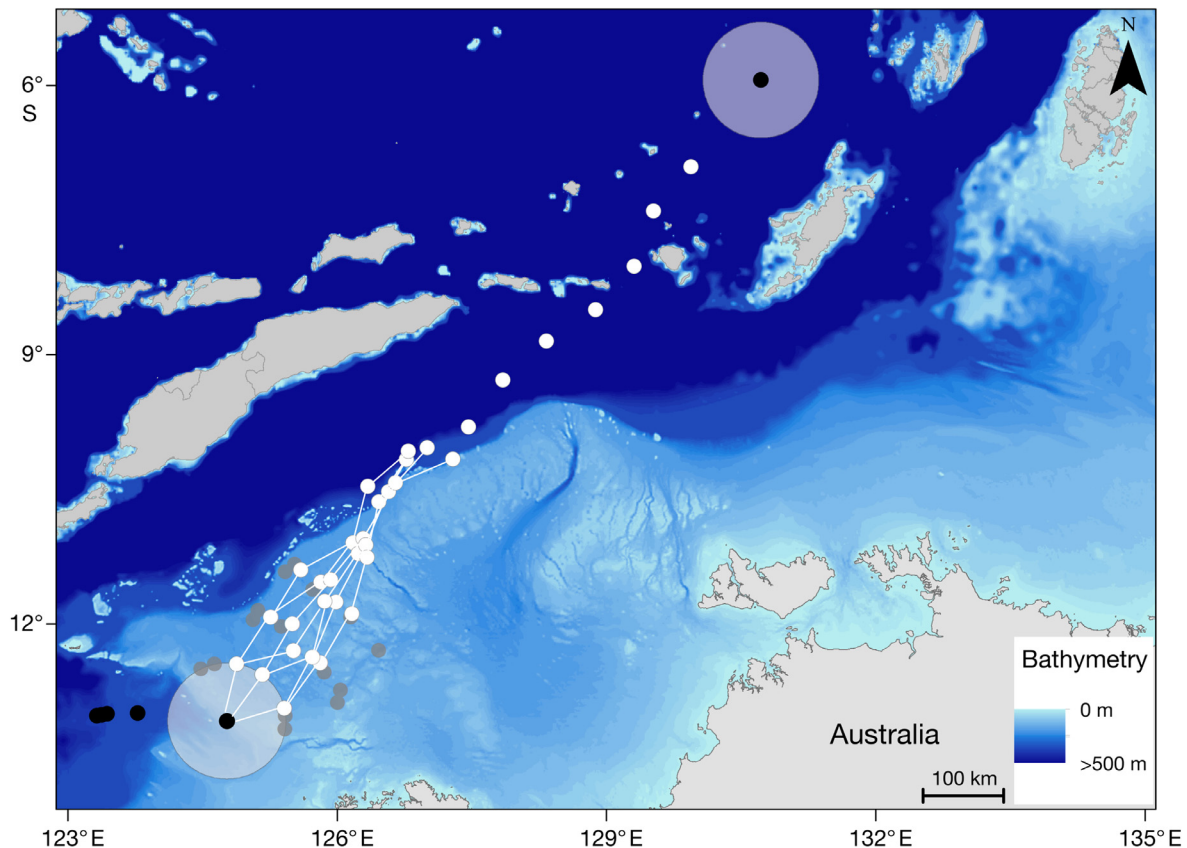


Fig. 4. Full reconstructed whale shark track from 4 to 18 March, when no positions were transmitted by the tag. Faded circles represent the  $71.54 \text{ km d}^{-1}$  ( $0.83 \text{ m s}^{-1}$ ) speed buffer radius. Black dots are known positions, grey dots are possible locations based on time, maximum depth and maximum bathymetry, and white dots indicate the most likely track the shark could have taken during this period. Bathymetry was set at 0–500 m to show high definition over the continental shelf region of Australia

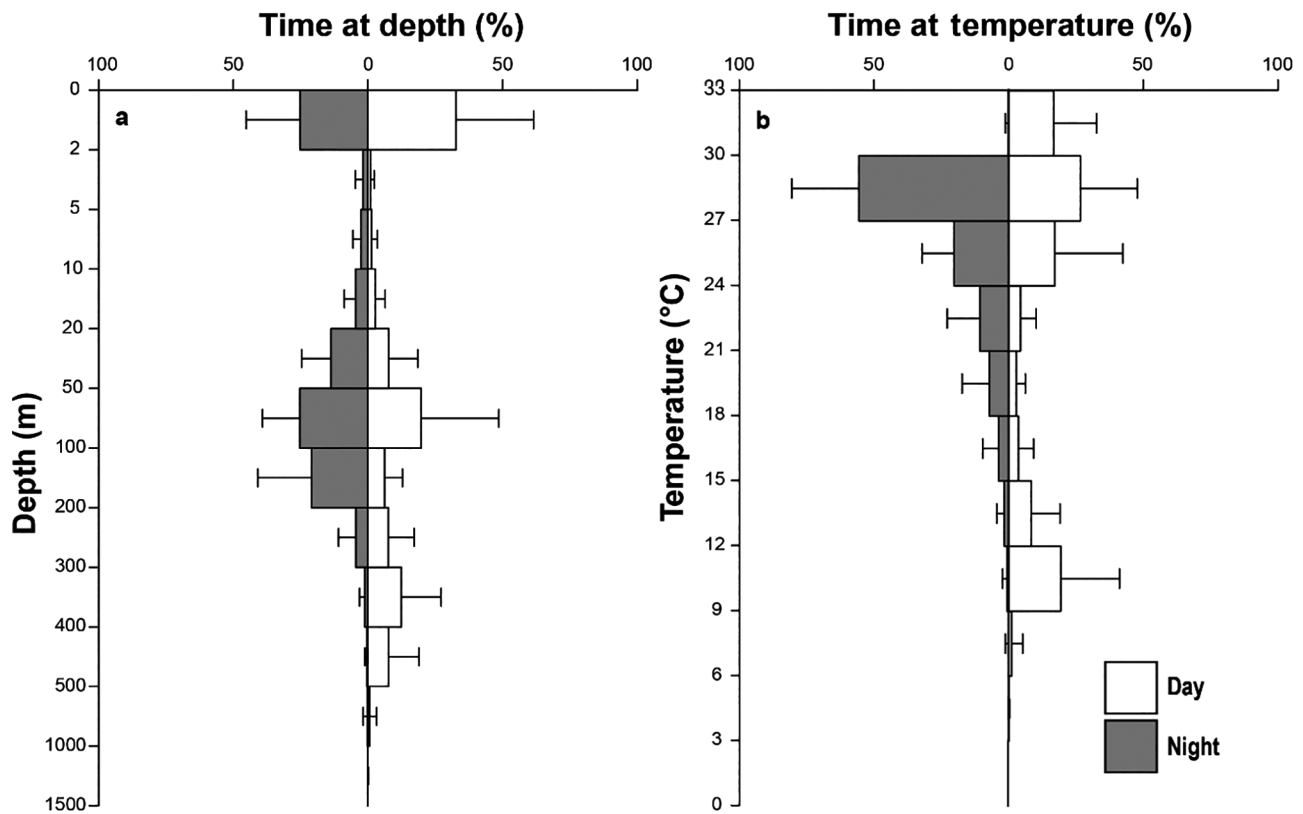


Fig. 5. (a) Time-at-depth (%); and (b) time-at-temperature (%) for the entire track (N = 89 d) of the tagged whale shark. White bars represent daytime, and grey bars represent night periods. Error bars show SD

( $r = 0.47$ ,  $df = 239$ ,  $p < 0.001$ ). During points of migration, dives followed similar patterns of movement to the mesopelagic organisms that make up the deep scattering layer, consistent with the theory of foraging at depth (Hays 2003, Wilson et al. 2006, Rohner et al. 2013). Deeper dives to ~500 m occurred predominately during the day and dives to  $\leq 200$  m occurred >63% of the time at night (Fig. 5a). Prolonged (>1 h) surface times were also observed during transiting events, with the shark spending time in shallow water before diving to depths >400 m (Fig. 6a,b). Approximately 17% of total dives were classified as 'other', and their duration was usually longer than 3 h. Total mean vertical velocities of all dive types varied from  $0.22$  to  $2.71 \text{ m s}^{-1}$ , with the fastest mean descents recorded for U-dives ( $1.29 \text{ m s}^{-1}$ ), and the fastest mean ascent velocities for V-dives ( $0.68 \text{ m s}^{-1}$ ). Maximum mean vertical velocities of dives occurred when the shark was in the open ocean, whereas in shelf waters (<200 m deep), velocities of dives did not exceed  $1.8 \text{ m s}^{-1}$ . Time-at-temperature profiles (Fig. 5b) showed that the shark experienced water temperatures ranging from  $5.25$  to  $32^\circ\text{C}$ . In total, the

shark spent ~61% of time within the temperature range of  $24$ – $30^\circ\text{C}$  for both day and night periods, and ~23% in waters < $20^\circ\text{C}$  (time-at-temperature plots for the individual sections are given in Fig. S2).

The first BRT model showed the variables with the highest relative contributions on pre-dive surface duration were: dive type (19.5%), followed by maximum depth (16.4%), dive time (14.4%) and thermal index (12.9%) (Fig. 7a). Interactions were found between 6 of the 9 explanatory variables, with the strongest interaction being between dive type and the minimum temperature (12.14%) (Table 1), followed by dive type and maximum depth (9.44%). In the second BRT model, total dive time was the most important predictor of post-dive surface duration (24.1%) (Fig. 7b), followed by thermal index (20.6%), with all other variables accounting for <13% relative importance. Interactions occurred between 5 of the 9 explanatory variables within the second set of BRT models, with dive time and the thermal index having the largest interaction size (28.11%). The remainder had interaction sizes of <5% (Table 2).



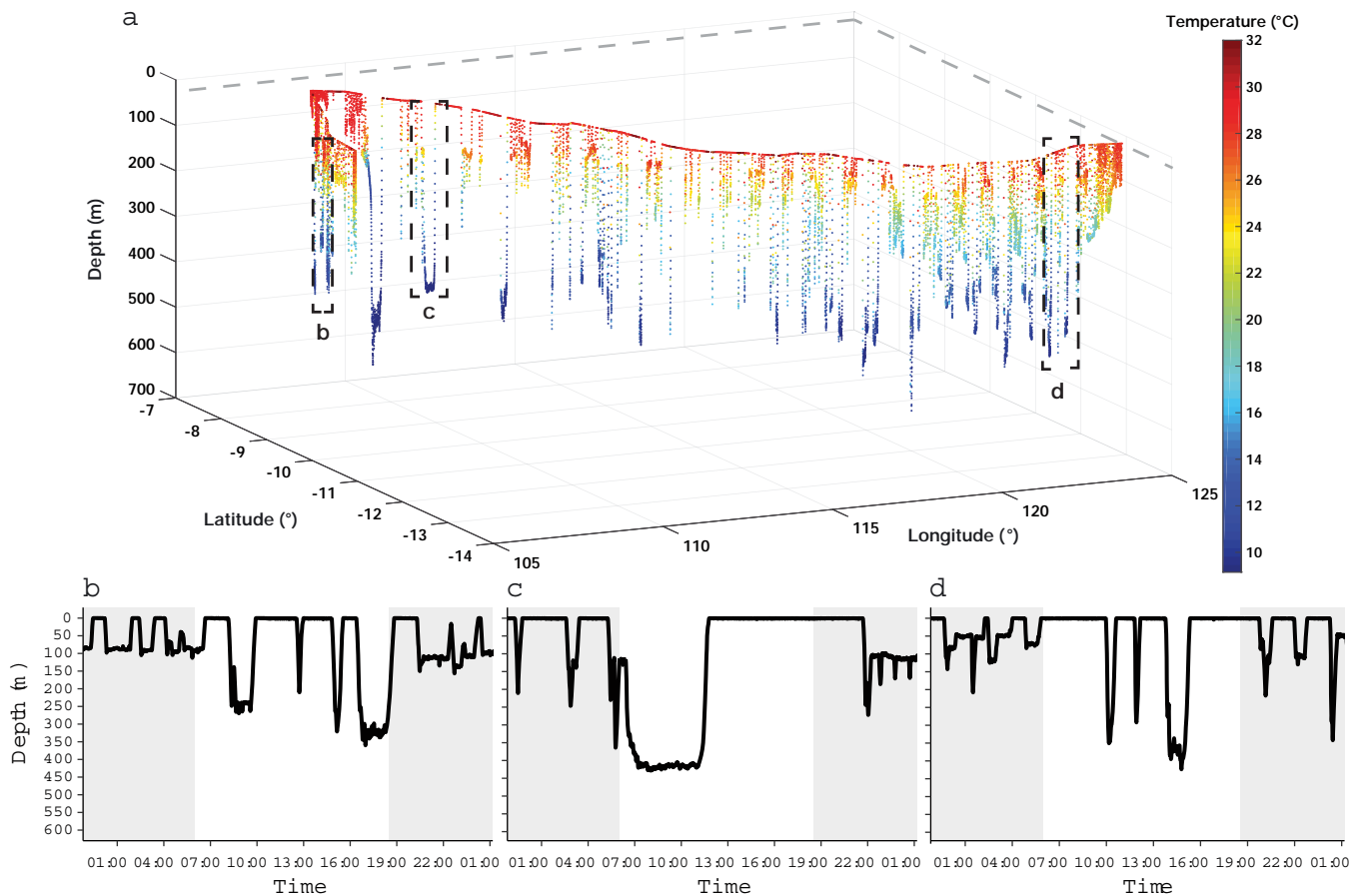


Fig. 6. (a) Time-at-depth profile with temperature recorded by the tag from Christmas Island to the continental shelf of Australia. The dashed grey line shows the 10 m depth mark. Movements between 0 and 10 m depth were classified as surface times. Dashed black boxes marked b, c and d correspond to plots b–d below, which show examples of V-dives, U-dives and basking events in 3 different periods during the migration from Christmas Island to the continental shelf region of Australia: (b) 5 February, (c) 11 February and (d) 20 February

#### 4. DISCUSSION

Our study indicated that both horizontal and vertical movements of the whale shark were strongly influenced by water temperature. We found evidence supporting the hypothesis of behavioural thermoregulation, with the duration of pre- and post-dive surface intervals related to the type of dive (foraging or searching). This implied that water temperature was a critical determinant of foraging patterns and thermoregulatory (basking) behaviour, at least during the day. Additionally, across a track length of 5380 km, the shark tended to occupy surface waters in a relatively narrow temperature range of 24–29°C and embarked on large-scale, open-ocean movements that took advantage of the arrival of water masses of this temperature range for foraging opportunities and/or to avoid warmer SSTs.

SSTs along the track ranged from 24 to 34°C; however, when at the surface (<10 m water depth), the shark spent approximately 60% of its time within a temperature range of 24–29°C, which appears to be a behavioural feature of this species (Sequeira et al. 2012). After remaining in the vicinity of Christmas Island for almost 3 wk, the departure of the shark into the open ocean coincided with the arrival of a cooler water mass from the east associated with the South Java Current (Wijeratne et al. 2018). Similarly, while transiting between Java and the continental shelf of Australia, the shark moved close to frontal zones of the preferred temperature range. It is likely that these zones not only offered water temperatures that optimise metabolic efficiency for large ectotherms, but also the possibility of relatively high concentrations of food in an otherwise oligotrophic ocean. Numerous studies have shown that boundary layers between water masses of different temperatures

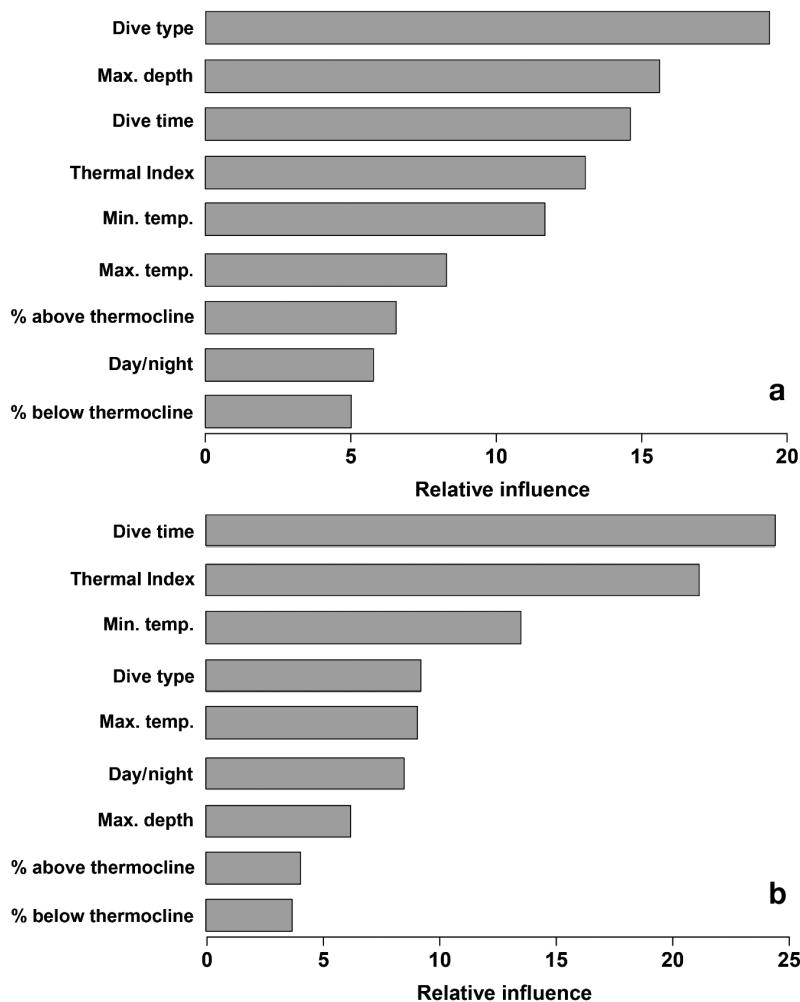


Fig. 7. (a) Relative influence (%) of the pre-dive surface duration boosted regression tree (BRT) model. The top 4 variables are dive type (19.5), maximum depth (16.4), dive time (14.4) and thermal index (12.9). (b) Relative influence (%) of the post-dive surface duration BRT model. The top 4 variables are dive time (24.1), thermal index (20.6), minimum temperature (12.5) and dive type (11.2)

act to concentrate planktonic organisms that form potential prey (Queiroz et al. 2012, Scales et al. 2014, González Carman et al. 2019). Furthermore, other filter-feeding sharks, such as basking sharks, focus

on frontal zones to optimise feeding efficiency (Sims & Quayle 1998). The numerous U-shaped dives of the whale shark that occurred during this transit strongly suggest that it foraged at depth, and the occupancy of frontal zones may have optimised this process (Queiroz et al. 2017).

SSTs exceeded the upper limits of the preferred range for this species (24–29°C; Sequeira et al. 2012) when the whale shark arrived at the continental shelf of Australia. At this point, the shark altered its behaviour, and based on records from the tag and bathymetry of the region over the shelf, it remained close to the seabed in depths around 100 m. This transit at depth for a species that spends most of its time at the sea surface is likely to be a response to warm waters and avoidance of further heating by the sun at the surface, particularly when the sun was at an apogee during the day. Alternatively, or in addition, the shark may have also encountered strong surface currents that were energetically expensive to overcome. This region of the eastern Indian Ocean is influenced by the South Equatorial Current and the Indonesian Throughflow, which transports warm surface waters from the Pacific to the Indian Ocean via the Indonesian Archipelago (Feng et al. 2018, Wijeratne et al. 2018), resulting in deep thermoclines and higher SSTs (Schneider 1998). Additionally, the northwest shelf of Australia experiences one of

the largest tidal ranges globally (Haigh et al. 2014). Movements close to the seabed could have taken advantage of the benthic boundary layer where bed friction reduced current velocities. It is notable, however,

Table 1. Interaction size between the top 4 explanatory variables in the pre-dive surface duration boosted regression tree model

Variable 1	Variable 2	Interaction size (%)
Dive type	Minimum temperature	12.14
Dive type	Maximum depth	9.44
Dive time	Thermal index	6.23
Day/night	Dive type	3.19

Table 2. Interaction size between the top 4 explanatory variables in the post-dive surface duration boosted regression tree model

Variable 1	Variable 2	Interaction size (%)
Dive time	Thermal index	28.11
Day/night	Thermal index	4.82
Max. depth	Thermal index	4.32
Min. temp.	Maximum depth	1.97

that the shark still maintained some vertical movements between the seabed and the surface. This confirmed that the tag was still attached to the shark when no horizontal positions were transmitted. However, it is difficult to explain if the animal was strongly optimising energy costs and avoiding higher temperatures at the surface. It may be possible that these movements were necessary to take advantage of foraging opportunities at the surface (Araujo et al. 2020).

Water temperature was a key driver of patterns of vertical movement of this whale shark in the open ocean. We found evidence that the shark basked at the surface both before and after feeding dives (U-shaped dive profiles) that descended to similar depths thought to be where the deep scattering layer occurs (200–500 m depths) during the day, supporting the theory of foraging in this layer, as suggested for multiple other fishes (Josse et al. 1998, Hays 2003, Sims et al. 2005, Nakamura et al. 2015, Andrzejaczek et al. 2018). Surface basking prior to dives would enable whale sharks to harvest environmental heat and store this in large, poorly vascularised muscle blocks that surround the central nervous system (Meekan et al. 2015). This is necessary since feeding in the deep scattering layer requires the use of the gills in water temperatures up to 20°C cooler than the surface. Returns to the surface after feeding dives were typically accompanied by prolonged basking in surface waters, likely to allow the animal to recover from heat loss during feeding at depth. However, we did find that surface basking was not commonly associated with search dives (V-shaped dives).

Interestingly, the shark displayed predictable sequences of V-shaped dives followed by basking either prior to or after a U-shaped dive (Fig. 6a). This suggests that after locating potential food during the search dive, the whale shark prepared for a longer foraging dive by basking. Having fed at depth, the animal then again basked at the surface to recover body temperatures. Consistent with this hypothesis, the first BRT model of pre-dive surface intervals found that the type of dive (searching or foraging) and maximum depth were the strongest predictors of the duration spent at the surface before the dive, whereas the dive time and the thermal index were the strongest predictors of the time spent at the surface following a dive. This suggests that this whale shark might anticipate feeding events and the depth at which they will occur and can adjust their body temperatures accordingly before diving. Once the dive was completed, the duration of the post-dive interval was largely determined by the amount of time spent at depth and the water temperatures

encountered throughout the dive. As gigantotherms (Meekan et al. 2015, Nakamura et al. 2020), it seems plausible that both thermoregulatory behaviour and dive characteristics such as duration should be proportional to body size (volume), given that smaller sharks should lose body heat more quickly than larger individuals. This hypothesis could be tested by recording the vertical movement patterns of sharks across a wide range of body sizes. Vertical velocities during descent and ascent phases were also consistent with strategies to conserve body temperatures. The fastest mean ascent velocities occurred during V-shaped search dives, whereas the fastest mean descent velocities occurred during U-shaped dives. The ascent phase of a search dive would provide relatively little new information about the location of food, so to minimise heat loss during this time, it would be advantageous to ascend as swiftly as possible. Similarly, if a search dive had already provided information about the vertical location of food, descents during a feeding dive should be rapid to the appropriate depth to maximise the time available for foraging. To test this hypothesis, studies examining the prey distribution and vertical movements of whale sharks using accelerometer and animal-borne cameras are necessary (Papastamatiou et al. 2018).

At night, the shark spent the majority of time in waters from 50 to 200 m deep. In comparison to the day, very little time was spent in waters <10 m deep and few dives occurred beyond 200 m depths. Most foraging dives at night focussed on the thermocline at around 100 m. This pattern of behaviour was consistent with the rise of the deep scattering layer to the thermocline in the early evening and suggests that foraging of the shark followed the diel vertical migration of planktonic communities in the open ocean, a pattern common to many epipelagic fishes (Abecassis et al. 2015, Tyminski et al. 2015, Dewar et al. 2018, Andrzejaczek et al. 2019). Our evidence is in agreement with the hypothesis that whale sharks feed in the deep scattering layer during the day (Wilson et al. 2006, Rohner et al. 2013, Tyminski et al. 2015). This suggests that whale sharks may act as an important link in energy flows and nutrient cycling between surface waters and the deeper ocean, as is the case for whales (Roman & McCarthy 2010). By feeding at depth during the day and returning to the surface to rewarm, whale sharks can potentially create an upward pump of nutrients for planktonic species making up the deep scattering layer.

In our study, only 18 (<10%) of the 1931 dives by the shark descended to depths greater than 500 m, with 1 dive going beyond 1000 m. The purpose of

such extremely deep dives is unknown, but may offer foraging opportunities (Thorrold et al. 2014, Braun et al. 2021), navigational cues associated with the geomagnetic fields in the seabed or chemical composition of the water column (Klimley et al. 2002), or be associated with predator avoidance strategies (Baird et al. 2008). The profile of these very deep dives for the whale shark we tracked was not consistent with foraging, given that the dives were V- rather than U-shaped. We found that these dives had a relatively short bottom time at the maximum depth of the dive (~3 min), unlike foraging dives, which averaged  $54 \pm 04$  min in duration. The deepest dive of the shark attained a maximum depth of 1204 m, and it was notable that this dive coincided with the shark leaving warm shelf waters where it had resided for several days while travelling against prevailing surface currents. It may be possible that this deep dive served to reduce body temperatures while maintaining forward travel, particularly if the descent involved gliding rather than swimming (Gleiss et al. 2011, Meekan et al. 2015). In any event, low levels of oxygen at these greater depths are likely to limit bottom time. Further studies that combine measures of internal temperatures with position and depth data will be required to disentangle these hypotheses.

## 5. CONCLUSIONS

The data archived within the recovered tag revealed the complex interactions between water temperatures and foraging of a whale shark on both horizontal and vertical axes. Most horizontal movements occurred in water masses within a narrow band of temperatures, and during open ocean migration, dives across the diel cycle mirrored the vertical movements of the nekton that comprise the deep scattering layer. The shark seemed to anticipate foraging in deep waters during the day by basking at the surface prior to descent for times that were correlated to the depth and temperature where foraging occurred. Surface intervals after foraging at depth were proportional to the water temperatures encountered by the shark and the duration of the dive, suggesting that the animal was basking to recover from heat loss. The deployment of accelerometer tags, coupled with animal-borne cameras and body temperature sensors are vital to appropriately measure the effects of water temperature and foraging on the movements of whale sharks. This information needs to be considered in future studies to assess how and why these ocean giants migrate.

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