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Bimodality in depth use by sharks reflects bimodality in
behaviour - a case study with Whale Sharks (*Rhincodon*
typus).

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Submission for the degree of Biosciences Research Masters

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1 **Abstract**

2 Movement (body translocation) is a fundamental aspect of life for many animals and tends to
3 have a clear purpose that enhances lifetime reproductive success. Obligate ram-ventilated
4 sharks must move continuously to respire, making their patterns of movement less defined by
5 clear behaviours. Among other functions, sharks must feed and behaviourally regulate their
6 body temperature, and their position in the water column can play a key role in both. Sharks
7 display bimodality in their use of depth, either 'surface swimming' or 'diving' (term used to
8 encompass all behaviour below the surface), and this study aims to examine how these modes
9 differ in functionality and costs for whale sharks (*Rhincodon typus*). Analysis of data from
10 animal-attached tags recording acceleration, heading, temperature and depth from 20 animals
11 indicated that the two modes were distinct in energetic costs and amount of time allocated to
12 them. Surface swimming was more tortuous and required significantly more energy than
13 diving, and diving accounted for a greater proportion of time (on average 65%) and feeding
14 events. The allocation of time to each mode varied between day and night, with personality
15 thought to play a role since individuals differed significantly. This study refutes the common
16 assumption that surface swimming is entirely a thermoregulatory behaviour since depth and
17 temperature were not correlated, yet bimodality was still shown. It also highlights a gap in our
18 understanding of whale shark behaviour, since they perform energy expensive, tortuous
19 movements even when not feeding – a behaviour that is not often discussed in the literature.
20 Although surface swimming and diving have broadly similar functions in whale sharks,
21 systematic differences in behaviour metrics imply that there are subtle behaviour differences
22 between the two modes. We also highlight the need for a novel focus on the behavioural
23 plasticity between individuals and different populations, considering the factors that contribute
24 to behavioural variations.

25

26 **Key words:**

27 Tortuosity, Energy efficiency, Feeding, Biologging, Vertical velocity

28

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1 Introduction

2 Obligate ram-ventilating sharks, for example great white shark (*Carcharodon carcharias*), bull
3 shark (*Carcharhinus leucas*) and thresher shark (*Alopiidae*) (Kelly *et al.* 2019), are distinct in
4 their patterns of movement (body translocation rather than just appendage movement)
5 because they cannot obtain enough oxygen without moving – a process that drives sufficient
6 water flow over the gills (Roberts 1975; Jacoby *et al.* 2015). A consequence of this, is that
7 ram-ventilating sharks never stop moving. This differs from many other animals which tend to
8 refrain from expending energy in movement unless a clear benefit is deemed likely (Halsey
9 2016). Benefits include optimisation of environments (e.g. exploiting the most productive sites,
10 or migrating to breeding grounds (Chapman *et al.* 2014; Riotte-Lambert & Matthiopoulos
11 2019)), foraging (John O'Brien, Evans & Browman 1989; Adachi *et al.* 2017) and evading
12 predation (Howland 1974; Richardson *et al.* 2018). As a result, the functions of animal
13 movements are often quite clear, e.g. deer moving as they graze (Gaudiano, Pucciarelli & Mori
14 2021) or wild dogs engaging in high-speed predatorial chases (Hubel *et al.* 2016). Discerning
15 the functions of ram-ventilated sharks behaviour is, however, much more challenging (Speed
16 *et al.* 2010).

17 Much literature has noted that many shark species are essentially bimodal in their use of
18 depth; either they swim near the surface (at around 2 m), or they move up and down the water
19 column (maintaining depth at times but with frequent descents/ascents; hereon referred to as
20 diving) (Graham, Roberts & Smart 2006; Shepard *et al.* 2006; Speed *et al.* 2010). Depth
21 change is enhanced by shark negative buoyancy because these animals can utilise passive
22 gliding to descend the water column, with active swimming only required for the ascent (Gleiss,
23 Norman & Wilson 2011; Meekan *et al.* 2015; Watanabe, Nakamura & Chiang 2021). There
24 are many theories as to the purpose of these disparate swimming modes, two of the most
25 discussed being foraging (Dewar, Domeier & Nasby-Lucas 2004; Andrzejczek *et al.* 2020)
26 and thermoregulation (Royer 2020; Watanabe, Nakamura & Chiang 2021).

27 Dives have been linked to foraging for many cited reasons, with evidence varying for different
28 species, for example; an increased body mass (indicative of foraging success) following dives
29 (northern elephant seals, *Mirounga angustirostris*) (Boeuf *et al.* 1988), or whale shark
30 (*Rhincodon typus*) stomach content analysis showing signature fatty acids for prey of meso-
31 and bathypelagic zones (Rohner *et al.* 2013). In general, marine animals of diverse taxa are
32 thought to increase foraging success by searching for prey during oscillatory dives up and
33 down the water column, which allows them to sample the water across a range of depth
34 (Asaga *et al.* 1994; Schreer, Kovacs & O'Hara Hines 2001; Sala *et al.* 2011; Gleiss *et al.* 2013;

1 Andrzejaczek *et al.* 2020). Recent work also indicates that a similar process might operate in
2 the horizontal dimension, with some species following horizontally tortuous paths – consistent
3 with area-restricted search behaviours (Adachi *et al.* 2017; Andrzejaczek *et al.* 2019).

4 Against this, surface swimming behaviour is considered by many to relate to thermoregulation.
5 Most sharks are ectothermic, having their body temperature dependent on the temperature of
6 the external environment (Nakamura, Matsumoto & Sato 2020), so their (chosen) position in
7 the water column, which typically shows well-defined temperature stratification, has a huge
8 impact on heat flux (Thums *et al.* 2013; Tyminski *et al.* 2015). Ram-ventilated sharks are
9 especially sensitive to temperature effects since the act of ram ventilating exposes internal
10 body parts to the ambient water temperature (Meekan *et al.* 2015). Accordingly, surface
11 swimming in high temperature surface waters is often suggested as a method of reheating the
12 body following dives to cooler depths (Hight & Lowe 2007; Speed *et al.* 2012; Thums *et al.*
13 2013; Arrowsmith *et al.* 2021) – equivalent to basking shown by many other animals, e.g.
14 reptiles (Van Damme, Bauwens & Verheyen 1987), insects (Carrière *et al.* 2008) and other
15 fish (i.e bigeye tuna, *Thunnus obesus*) (Hino *et al.* 2019). Alternatively, in tropical waters (e.g.
16 the Arabian Gulf – with temperatures of 35°C at the surface), sharks can overheat when
17 feeding in highly productive surface waters and must dive below the thermocline in order to
18 cool the body down (Robinson *et al.* 2017; Araujo *et al.* 2020).

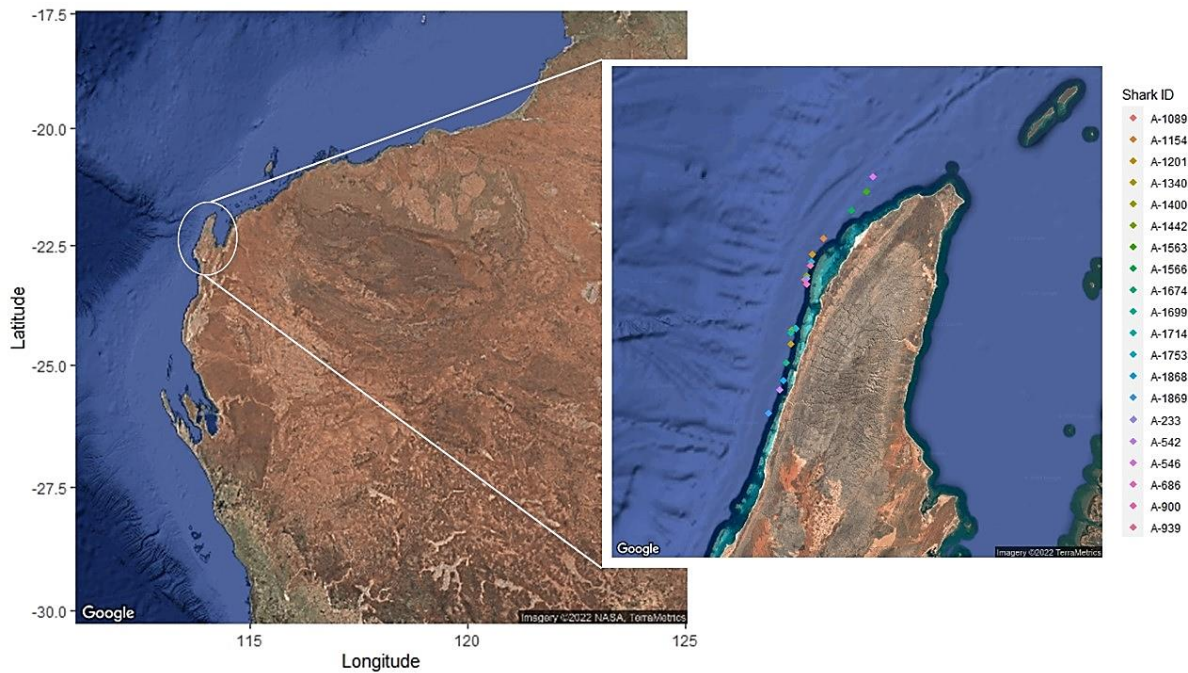
19 Whale sharks (*Rhincodon typus*) are an enigmatic species found in tropical, warm and
20 temperate waters globally (Sequeira *et al.* 2014). They are the largest extant elasmobranch
21 (Rowat & Brooks 2012) and are recognised as endangered in the IUCN red list due to their
22 rapid rate of population decline (> 50% in 75 years) (Pierce & Norman 2016). Their vagility
23 and long lifespans make studying them difficult, with much of what we know being based on
24 observations of them surfacing near coastlines (Martin 2007), but there remain large gaps in
25 our knowledge (Meekan *et al.* 2015). Over the past two decades, biologging technological
26 advancements have facilitated studies outside of observable environments (Williams *et al.*
27 2020). Accelerometers and time-depth recorders have highlighted the aforementioned
28 bimodal fashion of *R. typus*' diving behaviour; with regular periods of surface swimming,
29 interspersed with deep dives (up to 1900 m) and transitory periods through the epipelagic
30 zone (Graham, Roberts & Smart 2006; Stevens 2007; Gleiss, Norman & Wilson 2011;
31 Tyminski *et al.* 2015; Araujo *et al.* 2020). Whale sharks are known to be capable of making
32 extensive migrations (Guzman *et al.* 2018), with genetic studies suggesting Indo-Pacific
33 metapopulations (Rowat & Brooks 2012). The proportion of time spent at depth has been
34 shown to increase when away from coastal waters (Tyminski *et al.* 2015), with diurnal foraging
35 thought to occur in meso- and bathypelagic zones (in the Indian Ocean (Rohner *et al.* 2013)).

1 Whale sharks are at risk of boat strikes, not exclusively but increasingly, during these offshore
2 periods (Womersley *et al.* 2022). With the incidence of strikes thought to be rising (Lester *et*
3 *al.* 2020) and the risk of strikes being positively correlated with time spent at the surface
4 (Womersley *et al.* 2022), it is particularly relevant that we develop our understanding of whale
5 shark surface periods.

6 This study sought to ascertain why whale sharks (*Rhincodon typus*) engage in costly surface
7 swimming, developing our understanding of this enigmatic species through examination of
8 multisensory data derived from deployment of sophisticated tags on free-living individuals. A
9 major objective was, therefore, to examine how function impacted, or was impacted by, vertical
10 tortuosity, depth and temperature. In doing so, determining how surface swimming and diving
11 behaviour vary. This study will explore horizontal tortuosity, aiming to understand the purpose
12 of tortuous swimming paths and discern whether they are more common with surface
13 swimming or diving, and why. VeDBA will be used frequently as a gauge of energy
14 expenditure, and speed in some cases, highlighting important cost-differences between
15 swimming modes. A proxy for feeding events will also allow exploration of feeding patterns
16 and behaviours within the swimming modes – highlighting whether both modes are of equal
17 importance for feeding. Finally, variations of each metric between individuals will be used to
18 explore ontogenetic variation and potential causes.

19 **Methodology**

20 Field work took place at Ningaloo Reef (22°00'S, 113°50'E, Fig. 1), Western Australia, from
21 March to June 2019 - 2021. Ningaloo is a known aggregation site for whale sharks over austral
22 autumn and early winter, the zooplankton spawning attracting hundreds of individuals for
23 feeding off the reef (Wilson, Taylor & Pearce 2001a; Taylor 2007).



1

2 Figure 1. On the left, a map of Western Australia and the study site – Ningaloo Reef. On the
 3 right, a zoomed insert of the Ningaloo Reef; points denote the locations where each shark was
 4 tagged (coloured according to shark ID). Created using ggmap in R (Kahle & Wickham 2013).

5 Using ‘Daily Diary long board’ data-loggers (Wilson, Shepard & Liebsch 2008), the movements
 6 of 20 individuals were recorded over short- and long-term deployments (see Table 1). The
 7 terms short- and long-term are used from hereon as an indicator of procedure rather than
 8 deployment duration. Despite the terms reflecting duration, the distinction was based on
 9 whether the tag was attached and removed on one day (short-term) or attached then left for
 10 later retrieval (long-term; further detail in ‘tag attachment’ section). The short-term files were
 11 used primarily in the preliminary stages and unless stated otherwise, the analysis considered
 12 long-term files only.

13 Data loggers recorded all channels simultaneously; at 20 Hz for tri-axial acceleration, 6 Hz for
 14 tri-axial magnetic field intensity, and temperature and pressure at 2 Hz. Acceleration sensors
 15 logged measurements as acceleration with respect to gravity ($1 g = \sim 9.82 \text{ m/s}^2$) from each of
 16 the three orthogonally (anterior-posterior, medio-lateral, and dorsal-ventral) mounted sensor
 17 axes (measuring within the range of $\pm 16 g$). Orthogonal magnetometry measurements were
 18 logged in Gauss (G) (within the range of $\pm 0.88 \text{ G}$ at 0.73 mG/LSB resolution).

19

1 Table 1. Details on the whale sharks involved in the study – 16 long-term and 10 short-term.

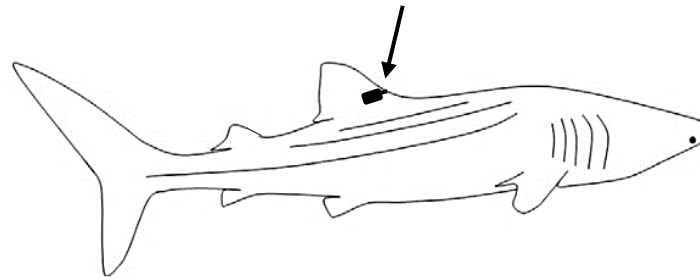
Shark ID	Size (m)	Sex	Short- or Long-term	Date deployed	Deployment duration
A-233	7.5	M	Long	13.05.21	~25 days
A-542	7.5	M	Short	27.04.21	4 hrs 9 mins 52 secs
A-546	7	M	Long	19.06.20	~11.5 days
A-686	6.5	M	Long	01.05.21	22 days 20 hrs 42 mins 3 secs
A-900	7	M	Both	24.04.21	4 hrs 4 mins 59 secs; 39 days 22 hrs 56 mins 0 secs
A-939	8	M	Long	14.05.21	21 days 21 hrs 22 mins 0 secs
A-1089	6.5	M	Short	02.05.21	2 hrs 27 mins 54 secs
A-1154	5.5	F	Long	11.05.21	1 days 19 hrs 22 mins 30 secs
A-1201	7	M	Short	25.04.21	4 hrs 13 mins 55 secs
A-1340	8	M	Long	26.04.21	14 days 22 hrs 16 mins 47 secs
A-1400	7	M	Both	12.05.21	4 hrs 35 mins 40 secs; 2 days 21 hrs 31 mins 0 secs
A-1442	7	M	Short	09.05.21	4 hrs 1 min 19 secs
A-1563	6	M	Short	06.05.21	4 hrs 22 mins 24 secs
A-1566	6.5	M	Long	06.06.20	Tag did not record for whole length of deployment
A-1674	6.5	M	Short	08.05.21	4 hrs 43 mins 18 secs
A-1699	7	M	Long	24.06.19	23 hrs 27 mins 0 secs
A-1714	8	M	Long	03.05.21	17 days 20 hrs 57 mins 21 secs
A-1753	6	M	Short	13.05.21	3 hrs 42 mins 0 secs
A-1868	8	M	Long	27.04.21	5 days 9 hrs 17 mins 40 secs
A-1869	5	M	Both	29.04.21	4 hrs 1 min 3 secs; 34 days 0 hrs 25 mins 42 secs

2

3 *Field protocol*

4 Initially whale sharks were approached in a rigid inflatable boat (RIB), their location having
 5 been identified from a spotter plane above the reef. If the whale shark showed no avoidance
 6 behaviours (e.g., diving or breaching) to the boat; three snorkelers then swam closer, with one
 7 using the tagging-gun (as described below). For individuals tagged for both deployment
 8 lengths, the long-term tag was deployed while the short-term tag was removed. The ethical
 9 permits for this field work can be found in appendix 1.

1 Consistent with the methods of Gleiss, Norman & Wilson (2011) and Gleiss *et al.* (2009); tags
2 and 3-stage VHF transmitters, paired within a positively buoyant housing, were clamped to
3 the whale shark's first dorsal fin (Fig. 2). The tag-package weighed ~ 90 g, which constituted
4 < 1% of the weight of the smallest individual. The tag-package was attached using a custom-
5 built tagging device, whereby a spring created tension enough to securely attach the clamp.
6 The clamp itself included two 1.5 cm long spikes which, when released from the trigger spring,
7 latched into the tough skin and cartilage of the shark's dorsal fin (Gleiss *et al.* 2009). A
8 galvanic-timed-release (GTR) connected the tag package to the clamp, so the tag-package
9 was released following corrosion of the GTR. Deployment duration depended on specific GTR
10 used (Whitmore *et al.* 2016). Upon release, the buoyant tag-package floated on the surface
11 until recovered and returned to the address listed upon it, whereby the SD card could be
12 retrieved and all the deployment data downloaded. For short-term deployments, the tag was
13 removed from the individual as the long-term tag was attached.



14
15 Figure 2. Tagging location on a whale shark (*Rhincodon typus*) on the first dorsal fin, as
16 adapted from Gleiss *et al.* (2009).

17 Data analysis

18 Data were visualised and treated using Daily Diary Multiple Trace (DDMT) software (Wildbyte
19 Technologies, <http://www.wildbytetechologies.com>). This programme displays the data in a
20 variety of ways and allows important metrics, such as shark heading and Vectorial Dynamic
21 Body Acceleration (VeDBA) (see below), to be calculated from the primary sensor data. The
22 programme also incorporates a Boolean approach ('behaviour builder') (Wilson *et al.* 2018a)
23 for isolating particular behaviours (termed 'bookmarks') so that, for example, surface
24 swimming could be separated from diving. The function within this part of the programme also
25 allows key data associated with surface swimming- and diving-events to be exported for
26 further analysis.

27 *Shark heading*

28 Heading was derived in DDMT (including calibrations), but briefly the method is as follows.
29

1 Legend for interpreting the symbols in statistical formulae 1, 2, 3 & 4; as given in Gunner *et al.* (2021):

2 θ = Pitch values

3 Φ = Roll values

4 $NGb_{x,y,z}$ = Normalised gravity-based component of acceleration across each axis (x, y, and z).

5 $NMbf_{x,y,z}$ = Tilt-corrected normalised magnetic vectors of the device in the x, y and z axes

6 $NMb_{x,y,z}$ = Normalised magnetic vector of device in the x, y and z axes

7 Ψ = Heading (yaw value)

8 Pitch and roll values (units in radians) are derived from the normalised static (gravity-based)
9 component of tri-axial acceleration (NGb_{xyz}) *via*;

$$10 \quad \theta = \text{atan2} \left(-NGb_x, \sqrt{(NGb_y \cdot NGb_y + NGb_z \cdot NGb_z)} \right) \quad (1)$$

$$11 \quad \Phi = \text{atan2}(NGb_y, NGb_z) \quad (2)$$

12 The normalised tri-axial magnetic vectors of the device (NMb_{xyz}) (pre-corrected for soft and
13 hard iron distortions (Renaudin, Afzal & Lachapelle 2010) and expressed in the animal's body-
14 carried North-East-Down (NED) frame (*cf.* (Gunner *et al.* 2021), for method)) are de-rotated
15 to the Earth frame (tilt-corrected) *via*;

16

$$17 \quad \begin{bmatrix} NMbf_x \\ NMbf_y \\ NMbf_z \end{bmatrix} = \begin{bmatrix} \cos(\theta) & \sin(\theta) \cdot \sin(\Phi) & \sin(\theta) \cdot \cos(\Phi) \\ 0 & \cos(\Phi) & -\sin(\Phi) \\ -\sin(\theta) & \cos(\theta) \cdot \sin(\Phi) & \cos(\theta) \cdot \cos(\Phi) \end{bmatrix} \cdot \begin{bmatrix} NMb_x \\ NMb_y \\ NMb_z \end{bmatrix} \quad (3)$$

18 The static component of acceleration is approximated by employing a centre-aligned running
19 mean over 2 s (Shepard *et al.* 2008). Yaw (ψ) (hereafter named heading – defined by the
20 compass convention), can then be computed from the $NMbf_x$ and $NMbf_y$ *via*;

$$21 \quad \psi = \text{atan2}(-NMbf_y, NMbf_x) \cdot \frac{180}{\pi} \quad (4)$$

22 , which outputs values in the scale -180° to $+180^\circ$ and changed here to the scale 0° to 360°
23 (both reflecting magnetic North) using logical expressions.

24

25 Heading dispersion is a key aspect of this study, but requires more specialised working than
26 standard linear distributions, due to magnetic heading values around 360° giving spurious
27 variation figures (Benediktová *et al.* 2020). The package ‘circular’ in R (Agostinelli & Lund
28 2022) defines the standard deviation of circular data (Mardia 1972; Fisher 1995;
29 Jammalamadaka & Sengupta 2001) *via*;

1 Legend for interpreting the symbols in statistical formula 5:

2 \ln = natural log

3 r = the mean resultant length divided by the number of observations

4 sd.circular: $\sqrt{(-2 \times \ln(r))}$ (5)

5 *Vectorial dynamic body acceleration (VeDBA)*

6 The vectorial sum of dynamic body acceleration (VeDBA) (Qasem *et al.* 2012) has been
7 validated as a powerful proxy for activity extent and travelling speed, since generally the faster
8 an animal moves, the more mechanical work is performed (*via* muscular contraction) and the
9 greater the corresponding magnitude of the accelerometry readings from the attached tag
10 (Wilson *et al.* 2020). Rate of oxygen consumption ($\dot{V}O_2$) has also been tested against VeDBA
11 across many taxa, validating the use of this metric (Halsey *et al.* 2008; Gleiss, Wilson &
12 Shepard 2011; Wright *et al.* 2014). VeDBA is calculated *via*;

13 Legend for interpreting the symbols in statistical formula 6:

14 $A_{x,y,z}$ = raw components of acceleration across the x, y and z axes (units in g)

15 $G_{x,y,z}$ = smoothed components of acceleration across the x, y and z axes (units in g)

16
$$\text{VeDBA} = \sqrt{(A_x - G_x)^2 + (A_y - G_y)^2 + (A_z - G_z)^2},$$
 (6)

17 *Pressure, depth and vertical velocity*

18 Pressure, stored in bar, was used to indicate depth (in metres) by dividing the pressure in bar
19 by 10.3 (because seawater has an approximate density of 1.03 g/mL). Pressure values were
20 smoothed over 10 s (200 events) to ensure that minor pressure changes from tail beats or
21 waves did not influence the dive patterns.

22 Vertical velocity is the rate of change of smoothed pressure (bar/s), calculated over a 1 s range
23 (20 events) in this study. The use of smoothed pressure in this calculation reduces the
24 resolution of data but, as above, removes the potential errors caused by minor pressure
25 changes.

26 When surface swimming, it is potential for the sharks' caudal fin to breach the water surface
27 (observed by Sleeman *et al.* (2010)) exposing the tag to evaporative cooling. This process
28 was also recorded in the tagging of wandering albatross (*Diomedea exulans*) (Wilson,
29 Weimerskirch & Lys 1995) and to prevent spurious values from distorting interpretations of
30 temperature in the surface waters, the top 0.5 m of water was discounted in Fig. 7.

31

1 *Boolean terms for separating surface swimming from diving*

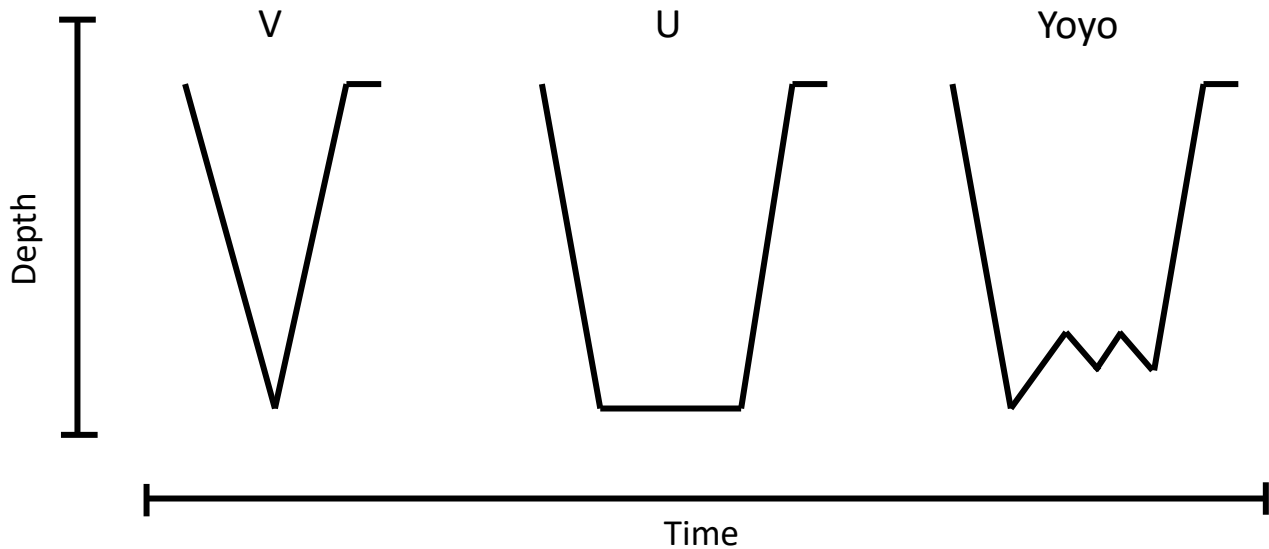
2 The primary distinction between diving and surface swimming is dependent on the pressure.
3 Preliminary observation of the data showed the sharks spent extended time travelling
4 horizontally, with the depth of the sensor on the dorsal fin, between 3 and 5 m depth so a
5 maximum depth of 5 m was used as the threshold for surface swimming. The relevance of this
6 threshold depends on shark size and wave height, with the volume of water above a shark
7 capable of massive change through just these two factors. Five metres is therefore a cautious
8 measure, aiming to reduce errors associated with a lower. Any movement that occurred at a
9 greater pressure was assumed to be part of diving behaviour. Surface periods and dives were
10 'bookmarked' using this rule. 'Bookmarks' highlight user-defined sections of data which can
11 be saved and categorised accordingly. The bookmarking of the shark's behaviour as either
12 surface swimming or diving, allowed for easy comparison once exported.

13 *Boolean terms for separating dive phases*

14 Shark dives are typically separated into descent, bottom and ascent phases (Howey *et al.*
15 2016; Andrzejaczek *et al.* 2018) and this study wanted to assess variations between them
16 according to context. Each phase was identified through their vertical velocity (rate of pressure
17 change calculated over 1 s). Descent was considered to have occurred when the vertical
18 velocity > 0.005 bar, ascent < -0.005 bar; and bottom was recognised as any time vertical
19 velocity was between the two. Observational trial and error, using short-term files, enabled the
20 determination of these thresholds. Any phases with a duration < 600 events (30 s) were
21 removed, to ensure only minor shifts were not misclassified as dives. The full protocol for
22 DDMT use and data exporting can be found in appendix 2.

23 To facilitate automatic dive type identification, visual observations of dive type were recorded
24 for the short-term data files. Using the following rules all dives were recorded as V-, U- or
25 yoyo-dives (Asaga *et al.* 1994; Carter *et al.* 2016) (Fig. 3):

- 26 - V-dives ascend straight after descending,
- 27 - U-dives descend and spend a period (> 15 s) at the bottom before ascending,
- 28 - Yoyo-dives involve several (> 2) ascents and descents of the water column at depths
29 > 5 m, before returning to surface level.



1 Figure 3. Schematic dive profiles of the three dive types (V-, U- and Yoyo-dive) performed by
 2 the whale sharks, used as a guide when making visual observations.

3 Within the bookmarked dives, the ascent, descent and bottom phases were allocated and
 4 exported for assessing their proportions within each dive. Each phase was listed as a 'marked
 5 event', user-defined sections of data that can be nested within bookmarks, in this case dives.
 6 Combining the bookmarks into a single file, in R (open-source statistical programming
 7 software, <http://www.R-project.org>), and creating frequency distribution plots, allowed an
 8 accurate assessment of vertical velocity threshold values for each dive type and phase.

9 Exploration of data found that the proportion of the dive spent in bottom phase (vertical velocity
 10 < 0.005 & > 0.005 bar/s) to be the most accurate determinant of dive type (a method also used
 11 in Schreer, Kovacs & O'Hara Hines (2001)) with V-dives allocating $< 30\%$ their time in the
 12 bottom phase, Yoyo-dives allocating $> 50\%$ of their time, and U-dives encompassing the time
 13 in between. Such rules seem counterintuitive based on the above definitions, but the dives
 14 contain far more 'bottom phase' than would be expected based on the use of vertical velocity
 15 as the determinant. For example, a shark performing a V-dive may be descending at a vertical
 16 velocity of 0.01 bar/s, but as they invert their body to begin their ascent their vertical velocity
 17 must pass through 0 before reaching the value they actually travel at. Observation showed
 18 that this shift could take several minutes – hence having a greater proportion of bottom phase
 19 than apparent from the dive profile alone.

20 The performance of these rules could then be compared against the observed dive types, as
 21 a baseline, with the above rule achieving a 70% match between observed and calculated dive
 22 types.

23

1 *Boolean terms for determining feeding events*

2 Whale shark feeding often comprises of circling movements to optimally exploit a prey
3 aggregation (Nelson & Eckert 2007; Stevens 2007; Meekan *et al.* 2015). The energetic
4 expense of such tortuosity requires the prey aggregation to be dense enough for the rewards
5 to outweigh the costs (Wilson *et al.* 2013), and increase their efficiency of feeding through ram
6 filtration. These spirals have a distinct trace signature and can be identified, using the Boolean
7 'behaviour builder' within DDMT, as whenever the shark's magnetic heading passes in a full
8 circle; i.e. If difference in heading (across 5 s) is consistently > 40 degrees for a selected
9 period of 3 minutes. Observations from the short-term data showed 3 minutes to be the
10 minimum time required to complete a full circle, when turning at an angle > 40 degrees.
11 Bookmarks for these feeding events were then integrated with the rest of the data to provide
12 an overview of the sharks' feeding patterns in relation to dive phases and types. This approach
13 is hyper conservative, as feeding can occur outside of these circling motions; nevertheless,
14 this methodology still offers an insight into this type of feeding.

15 Statistical analysis

16 R studio (version 4.1.2) was used to generate figures and perform all analysis of the data. The
17 results of all statistical tests were considered to be significant with P-values < 0.05.

18 *Linear mixed effects models*

19 Linear mixed effects models (LMM), of the package lme4 (Bates *et al.* 2015), were performed
20 to determine the relationship between VeDBA and heading dispersion with depth,
21 temperature, time of day and the incidence of feeding. Interactions between depth and
22 temperature were recognised within the models, and shark ID was included as the random
23 effect (see appendices 3a and b for model selection tables). A random slope model was also
24 constructed to test whether interactions between Shark ID, depth and day/night had a
25 significant impact on slope coefficients for the VeDBA or heading dispersion. To ensure model
26 assumptions were met, where necessary, Box-Cox power transformations (using the 'car'
27 package (Fox & Weisberg 2019)) were carried out on the response variable via the formula;
28 $x' = (x^p - 1) / p$, where p represents the power maximising normality likelihood.

29 The significance of each model was then tested using the model simplification method with
30 likelihood ratio tests, backward selection; assessing the effect of removing particular
31 parameters of interest on the fit of the model (Lewis, Butler & Gilbert 2011).

32

1 *Generalised linear mixed effects models*

2 Generalised linear mixed effects models (GLMM), of the package lme4 (Bates *et al.* 2015),,
3 were fitted to test the responses of the number of feeding events (family = "poisson", link =
4 "log") against dive duration, depth and whether it was day or night, with Shark ID as the
5 random effect. Additional GLMM using 'AD Model Builder', "glmmADMB" package (Fournier
6 *et al.* 2012), were fitted to test the responses of the percentage of time spent at the surface
7 (family = "beta", link = "logit") against time of day (triated both day/night, and hour separately),
8 dive duration, temperature and depth (again recognised as interacting with temperature), with
9 Shark ID as the random effect. A random slope model was constructed to test whether
10 interactions between Shark ID and day/night, had a significant impact on slope coefficients for
11 time spent at the surface. As with LMM, likelihood ratio tests were performed to assess
12 significance of model parameters, see appendices 3c and d for model selection tables.

13 *Compound Poisson linear mixed model*

14 A compound Poisson-gamma distribution model, cplm package (Zhang 2013), was fit to test
15 the response for feed count (standardised and raw) to duration, day/night, swimming mode,
16 depth interacting with temperature, and Shark ID as the random effect (appendix 3e).
17 Standardising feed counts left a right skewed response variable with an inflated number of
18 zeros, hence making this test the best choice. This test does not produce a p-value
19 automatically, so instead p was calculated *via*,

20
$$p\text{-value} = 2 \times pnorm(t - value) \tag{7}$$

21 *Spearman's Rank Correlation Test*

22 A Spearman's rank test was performed to test for correlation between depth (m) and
23 temperature (°C). The non-parametric test favoured, despite both variables being normally
24 distributed, following visual inspection highlighting the non-linearity between the variables. The
25 null hypothesis assumed no correlation between the variables.

26 *Wallraff test*

27 Wallraff tests were used to compare the angular dispersion of heading values around a circular
28 mean, between dive phases (descent, ascent, bottom phase, and surface swimming), and
29 between swim periods with and without feeding events. The null hypothesis was that
30 dispersion was equal across all groups.

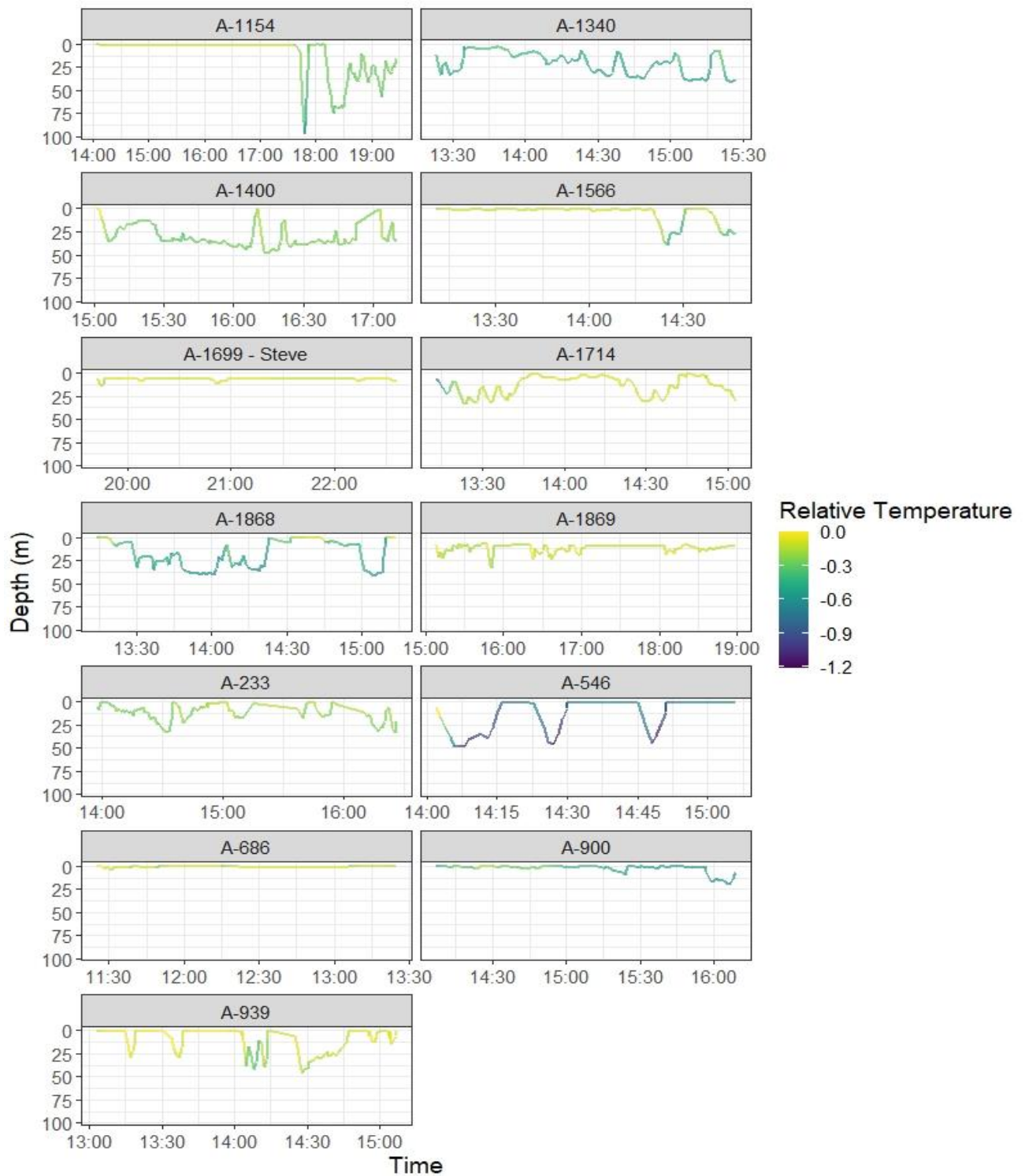
31 The package ggplot2 (Wickham 2016), within R, facilitated the visualisation of this data.

32

1 **Results**

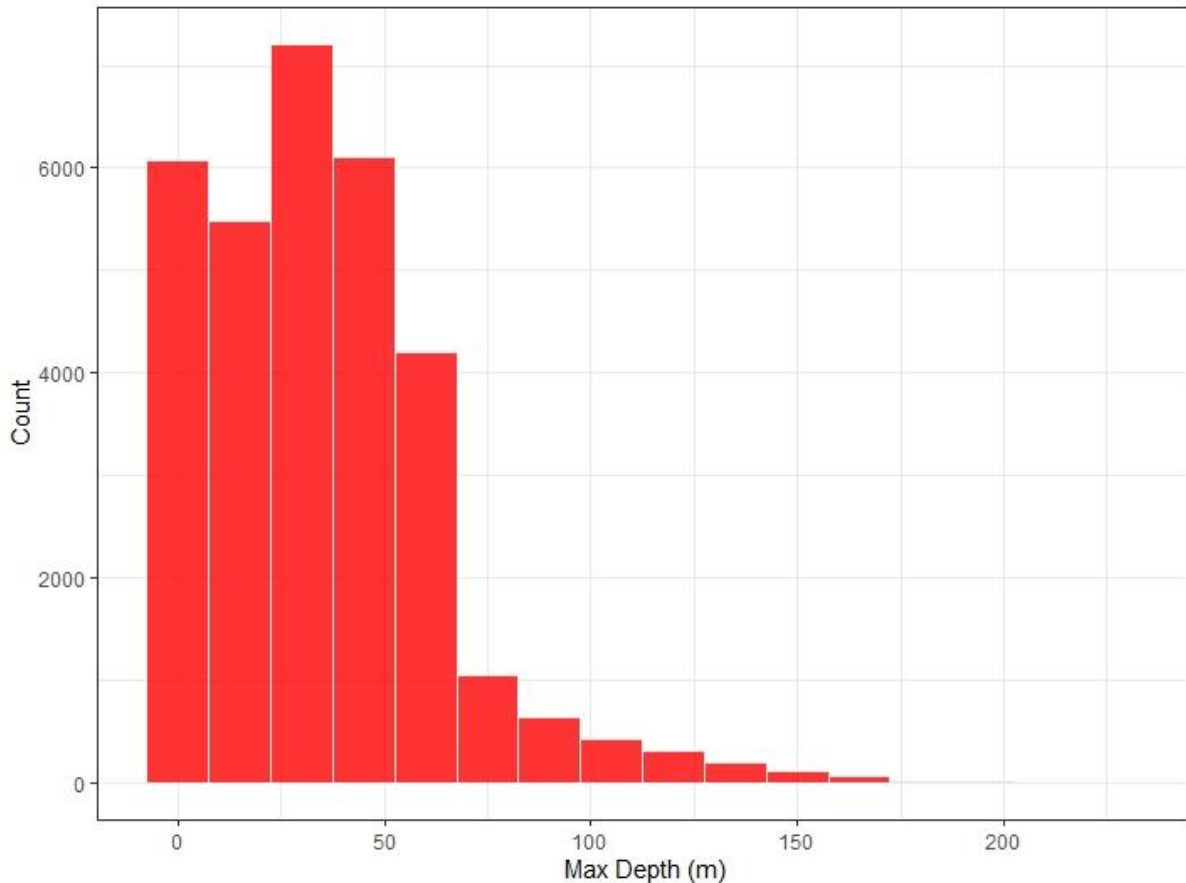
2 Of the 20 whale sharks tagged; 19 were males, with a mean (± 1 SD) body length of 6.9 m \pm
3 0.8, and the one female was 5.5 m. Short-term data was gathered from 10 individuals, with a
4 mean (± 1 SD) deployment time of 4 hours and 2 minutes (± 37 minutes), and long-term from
5 13 individuals, with deployment durations ranging between just less than 2 days, and 25 days
6 (see Table 1 for full deployment details).

7 The sharks showed bimodality of depth use, with surface swimming in the top 5 m indicating
8 a very clear, and generally unchanging preference for that depth at that time (Fig. 4). By
9 contrast, 'diving' showed virtually continuous change in depth. These averaged 30 m but
10 reached a maximum depth of 221 m (Fig. 5). Max depth had no significant relationship with
11 vertical velocity, but as depth increased so did duration ($p < 0.01$). The maximum duration was
12 a dive of 12 hours and 52 minutes (a yoyo type dive), and the mean (± 1 SD) duration for
13 surface swimming was 7 minutes (± 12 minutes) and 18 minutes (± 40 minutes) for diving.



1

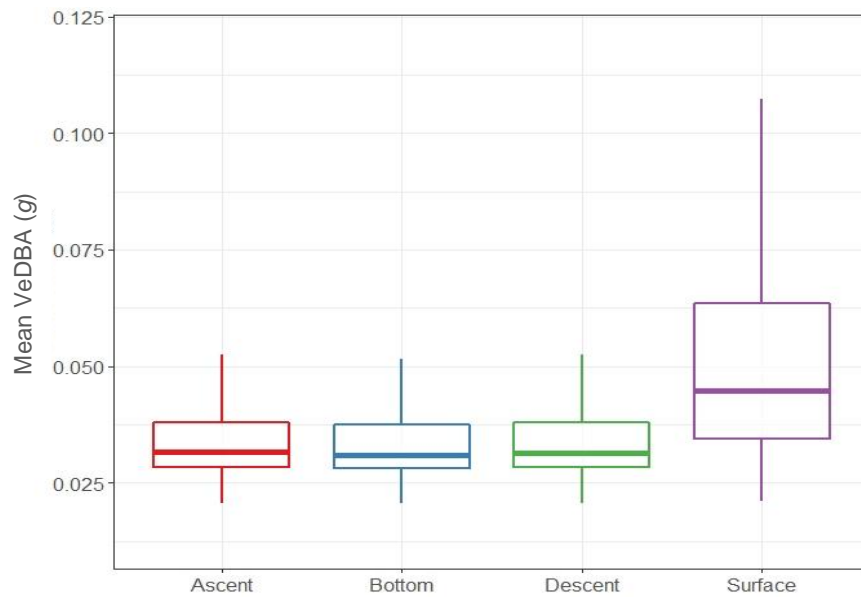
2 Figure 4. Sample dive profiles for each individual shark, showing the surface swimming and
 3 dives recorded over several hours. The colour gradient is representative of relative
 4 temperature ($^{\circ}\text{C}$). Relative temperature was calculated by taking the maximum temperature,
 5 to which the shark was exposed, away from the temperature at each given point – based on
 6 the assumption that surface waters have the greatest temperature.



1

2 Figure 5. The frequency distribution of maximum depth reached when diving, pooled from all
 3 whale sharks. Each bin represents 15 m.

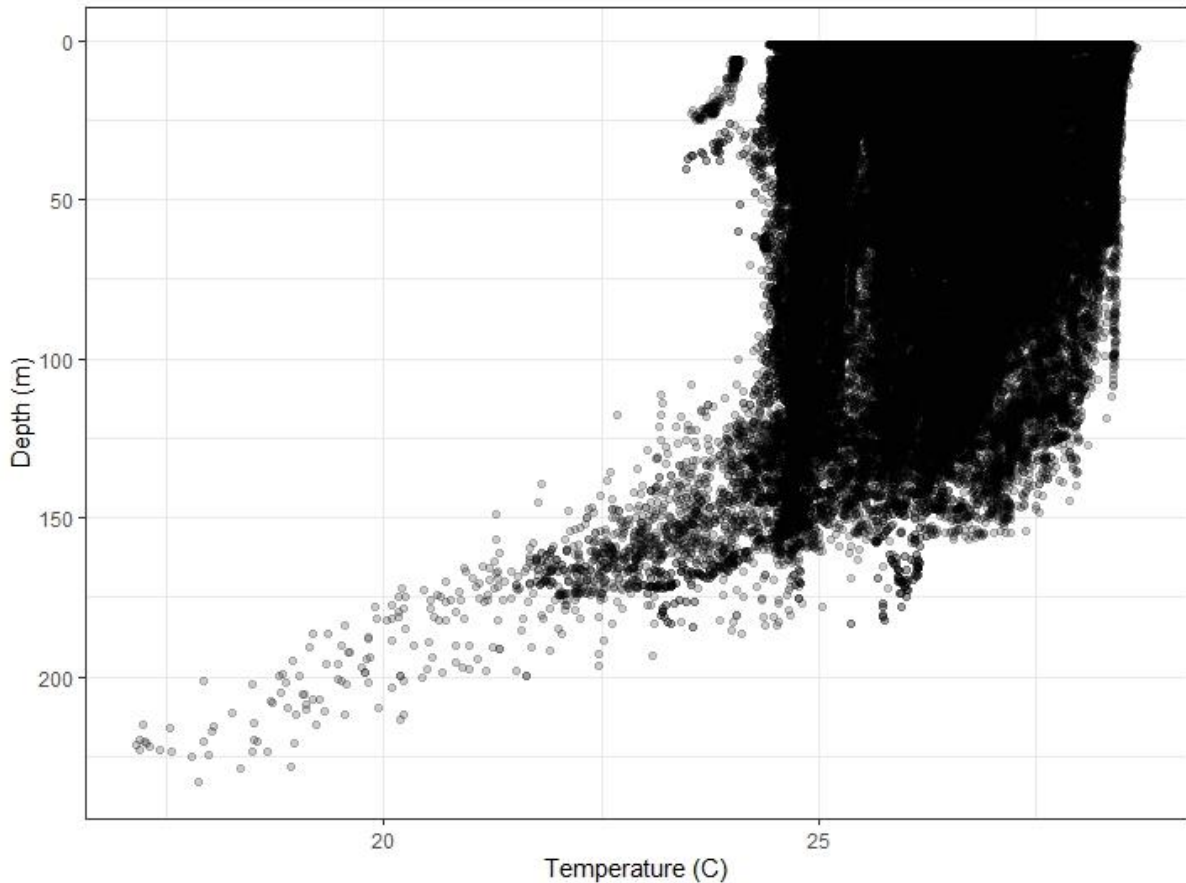
4 The mean VeDBA (± 1 SD) for surface swimming was significantly higher, at $0.054\text{ g} (\pm 0.022)$,
 5 than that of diving, at $0.037\text{ g} (\pm 0.015)$ (Fig. 6). VeDBA decreased linearly with increasing
 6 depth (LMM: $\chi^2 = -8.19$, $p < 0.001$), temperature (LMM: $\chi^2 = -10.48$, $p < 0.001$), and during the
 7 night (LMM: $\chi^2 = -7.4$, $p < 0.001$), while the presence of feeding events had no significant
 8 impact. AIC values led to incorporation of both random slopes and random intercepts for the
 9 best goodness of fit. Surface swimming also had a much greater spread (1.8 g) compared to
 10 diving (0.16 g).



1

2 Figure 6. Box-whisker plot showing VeDBA (g) metrics for surface swimming and diving (split
 3 into dive phases: descent, ascent and bottom phase) pooled from all individuals. Horizontal
 4 bars show medians, box height denotes interquartile range, and whiskers indicate range.

5 The mean water temperature (± 1 SD) recorded by the tags across all sharks was 26.5°C (\pm
 6 0.88), with lower and upper limits of 17.1°C and 28.7°C , respectively. Figure 4 shows the
 7 variation of relative temperature with depth for each shark, although a Spearman's rank test
 8 showed there to be no significant correlation between depth and temperature (correlation
 9 coefficient = -0.116 , $p\text{-value} < 0.05$; Fig. 7) with data pooled across individuals.



1

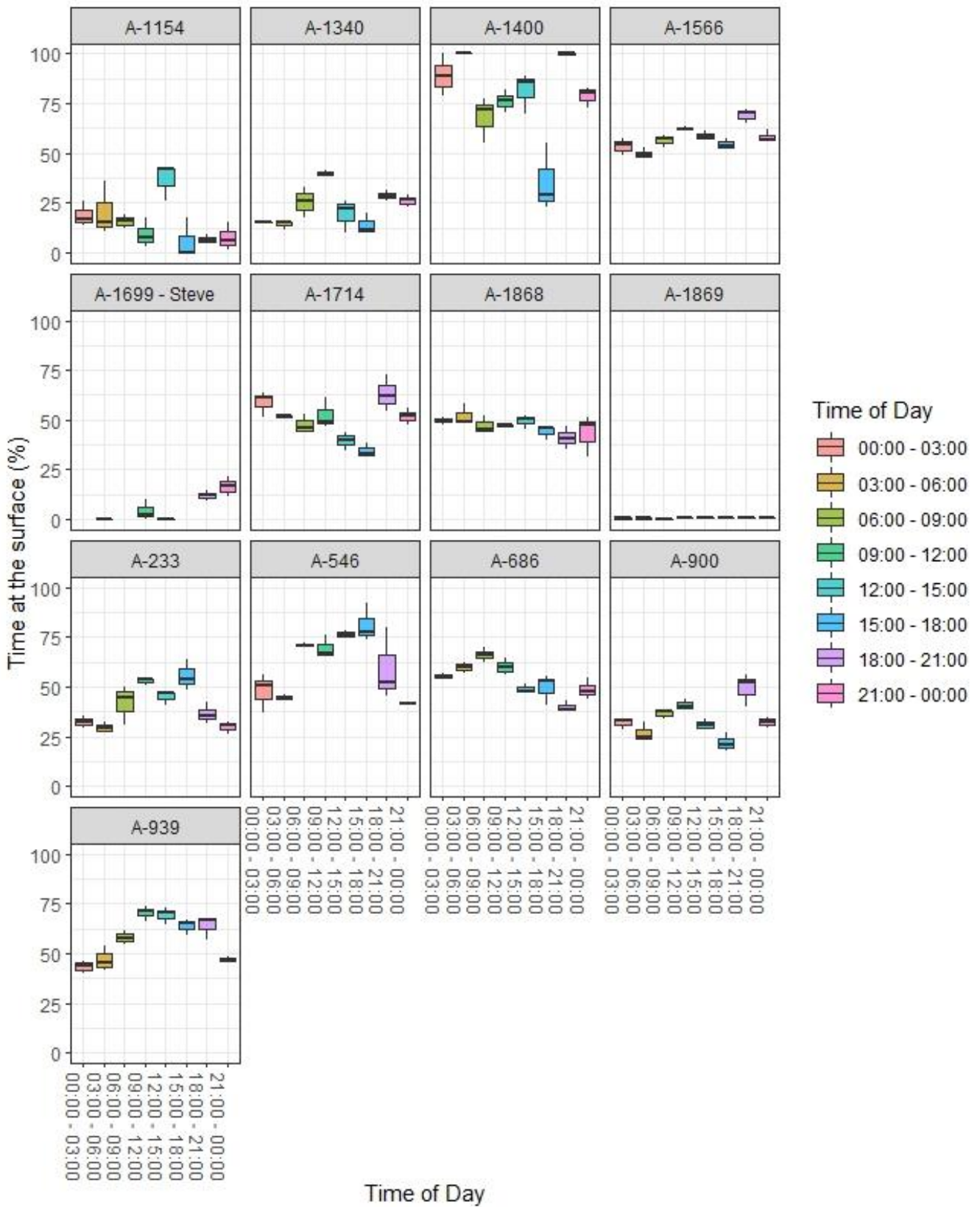
2 Figure 7. Temperature (C) against depth (m) for every minute of data recorded by tags
 3 attached to all whale sharks. Data less than 1 m depth removed due to anomalous evaporative
 4 cooling of tag when dorsal fin breached the water surface.

5 On average (± 1 SD), the sharks spent 41.46% (± 22.84) of their time at the surface, and there
 6 was significant difference between day and night-time allocation (41.46% in the day and
 7 38.49% at night; see Table 2) using the model incorporating random slopes in addition to
 8 intercepts (GLMM: $\chi^2 = -2.03$, $p < 0.05$; Fig. 8). The random effects of shark ID significantly
 9 affected time spent at the surface. The proportion of time at surface was greatest for hours
 10 07:00 to 15:00 (e.g. at 11.00, GLMM: $\chi^2 = 3.8$, $p < 0.001$), then peaked again at 18.00 (GLMM:
 11 $\chi^2 = 2.3$, $p < 0.05$).

12

- 1 Table 2. The proportion of time spent swimming at the surface by each shark, in total and split
- 2 into day and night. Daytime was classified as 06.00 – 19.00 and night-time as 19.01 – 05.59,
- 3 based on dawn and dusk times at Ningaloo over April - June.

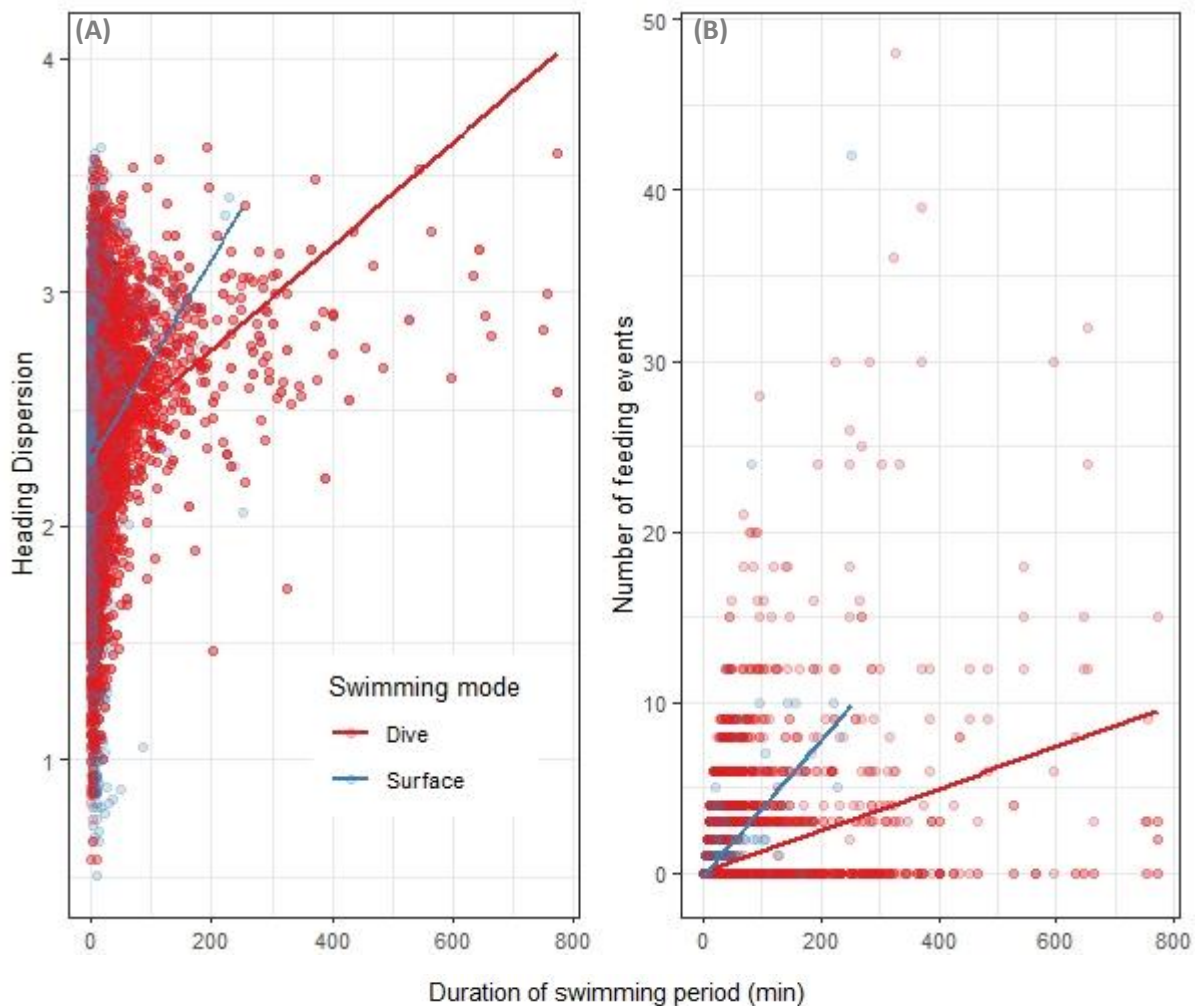
Shark ID	Total assessment time (dd.hh.mm.ss)	Total time surface swimming (%)	Daytime surface swimming (%)	Night-time surface swimming (%)
A-233	08.06.58.46	38.82	46.92	30.72
A-546	04.14.23.10	58.63	72.27	45.00
A-686	08.18.01.07	53.69	53.67	53.70
A-900	07.08.51.24	33.44	35.76	31.12
A-939	07.18.04.16	56.34	65.69	46.99
A-1154	00.13.37.51	14.13	13.68	14.57
A-1340	05.12.21.53	22.42	25.32	19.53
A-1400	00.22.59.56	78.82	66.49	91.16
A-1566	06.00.02.51	57.37	59.71	55.03
A-1699	00.02.54.36	7.80	5.07	10.53
A-1714	06.17.17.25	50.78	47.28	54.27
A-1868	02.00.48.05	46.88	46.48	47.28
A-1869	04.08.25.12	0.62	0.70	0.54
Total:		39.98%	41.46%	38.49%



2 Figure 8. Box-whisker plots for the percentage of time (%) spent at the surface throughout the
 3 day for the individual sharks. Horizontal bars show median values, box height denotes
 4 interquartile range, and whiskers indicate minimum and maximum values.

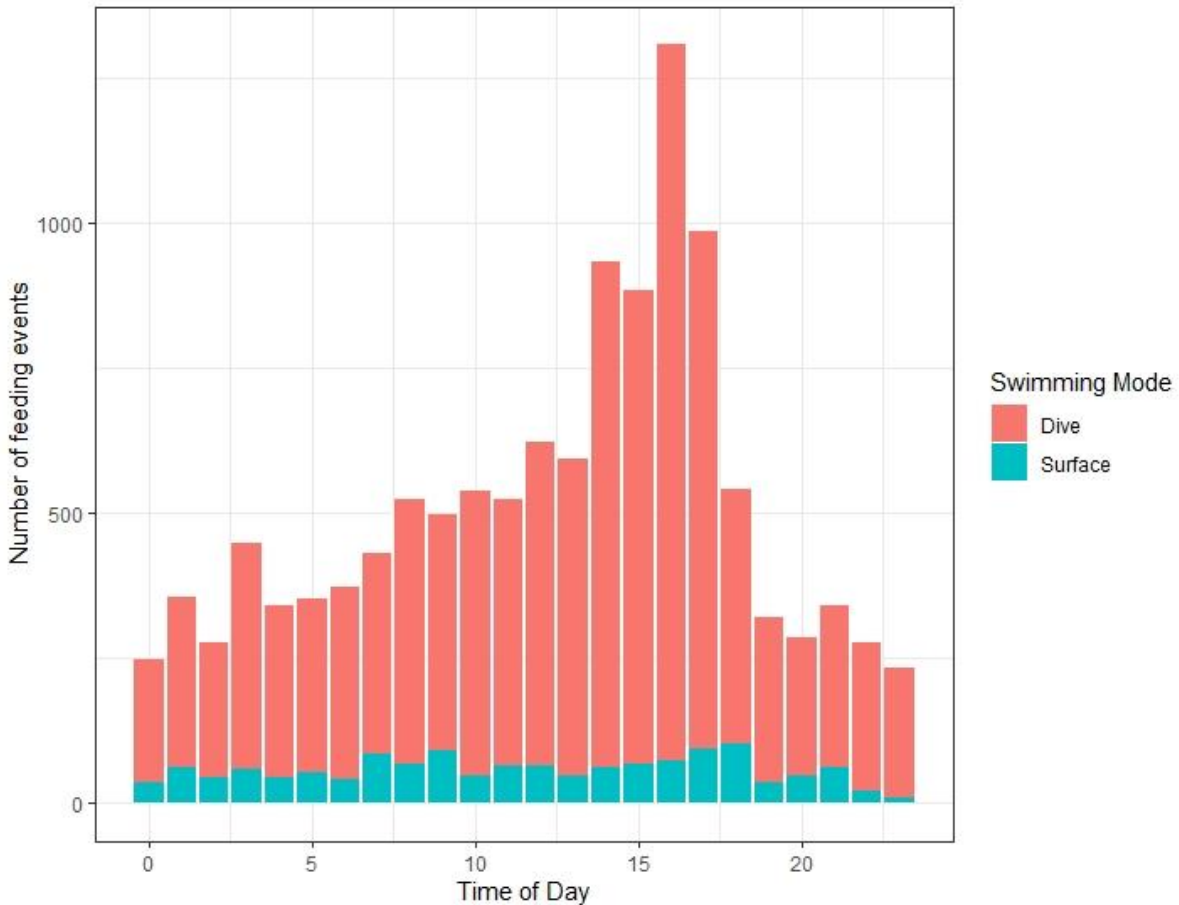
1 Shark heading dispersion (for definition see methods) was validated as a good proxy for
2 tortuosity *via* a linear model on the short-term files, confirming a significant positive correlation
3 ($R^2 = 0.9$, $p < 0.001$) when standardised by the swim period duration (see appendix 4).

4 The durations of swimming periods were used to standardise the dispersion of heading and
5 the number of feeding events (as defined in the methods). Duration (s) significantly affected
6 heading dispersion (LMM: $\chi^2 = 36.087$, $p < 0.01$) and number of feeding events (GLMM: $\chi^2 =$
7 5210 , $p < 0.001$). The longer the shark swam, the less straight the track and the more likely
8 they were to have fed (Fig. 9). Standardising these metrics allowed time-corrected
9 representative comparisons to be made. From here on, unless specified otherwise, heading
10 dispersion is standardised by the duration of swimming period. Swimming mode had a
11 significant impact on both raw and standardised heading dispersion, with surface swimming
12 being more tortuous than diving.



13
14 Figure 9. (A) The dispersion (standard deviation) of magnetic heading against the duration of
15 swimming period in minutes, with the linear regression lines for both swimming modes. (B)
16 The number of feeding events within a distinct swim period, against the duration of that period
17 in minutes, also with the linear regression lines for both swimming modes.

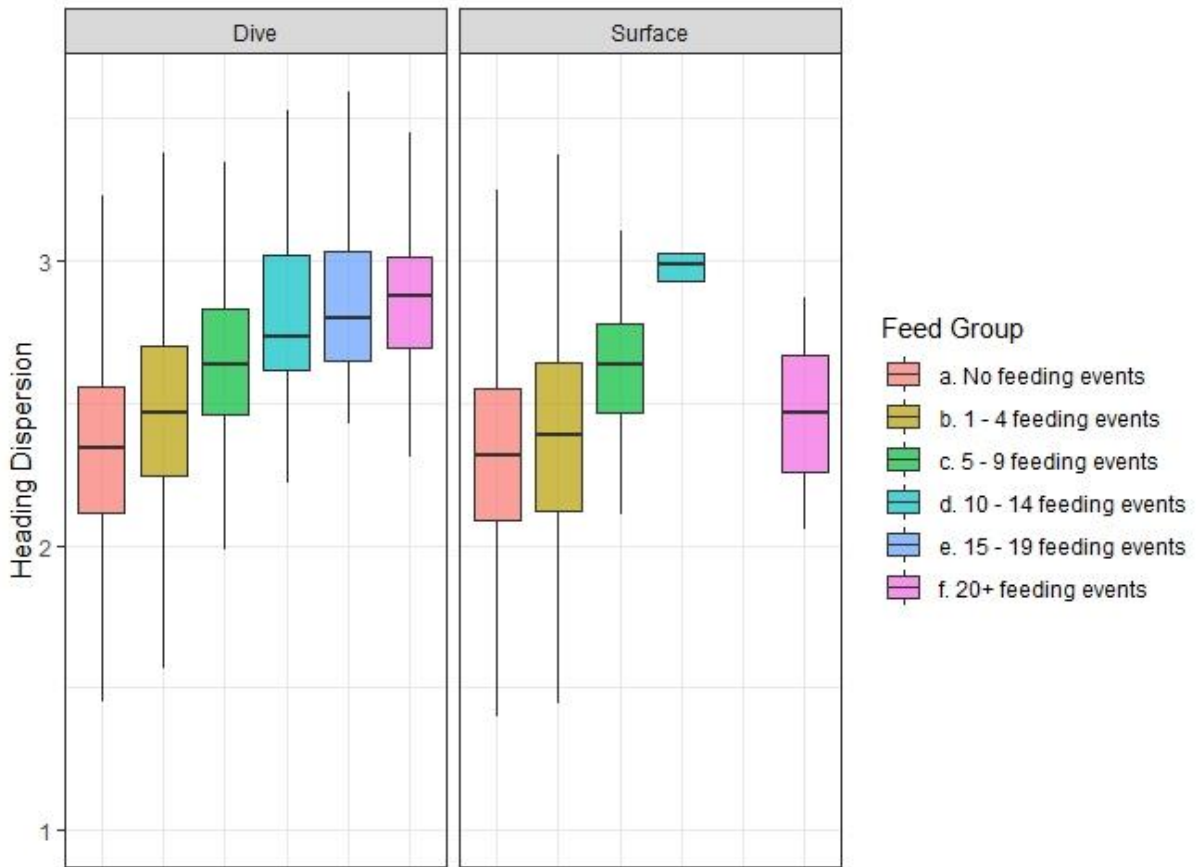
1 Increased duration of both surface swimming and diving was; positively correlated with the
2 number of feeding events (Fig. 9). However, the incidence of feeding was significantly higher
3 for diving than surface swimming: on average, 11% of feeding events took place when surface
4 swimming, and 89% when diving, this difference was significant for raw and standardised
5 feeds (CPLM: $t = -5.85$, $p < 0.001$). The number of feeding events (both raw and standardised)
6 significantly differed between day and night (CPLM: $t = -13.57$, $p < 0.001$), daytime was more
7 important for feeding (Fig. 10).



8

9 Figure 10. The number of raw feeding events as a function of time of day - data pooled from
10 all sharks.

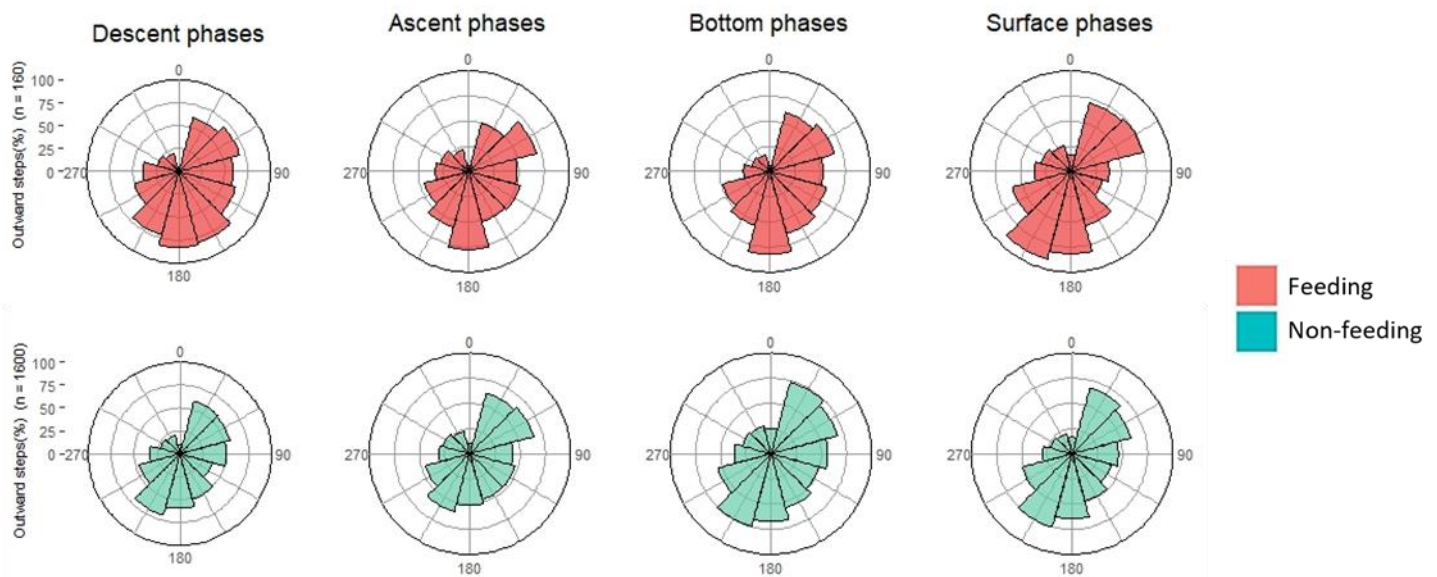
11 Tracks became more tortuous (greater heading dispersion) as the number of feeding events
12 per swim period increased (LMM: $\chi^2 = -15.24$, $p < 0.001$; see appendix 5 for frequency
13 distribution).



1

2 Figure 11. The dispersion of heading, based on the number of feeding events per swim period.
 3 On the left, diving and on the right, surface swimming.

4 Heading dispersion was significantly greater during surface swimming (LMM: $\chi^2 = 17.44$, $p <$
 5 0.001), and remained consistent between the 3 phases of a dive (descent, bottom phase and
 6 ascent) (Fig. 12). AIC values supported the incorporation of both random slopes and random
 7 intercepts into the model for best improved goodness of fit – shark ID impacted this
 8 relationship. There was no significant difference in circular mean heading (actual direction
 9 swam in, not dispersion) between swimming modes ($\chi^2 = 0.673$, $p = 0.89$), nor was there
 10 between feeding and non-feeding dives ($\chi^2 = 0.821$, $p = 0.37$; Fig. 12).



2 Figure 12. The frequency distribution for magnetic heading of each dive phase, for feeding
 3 and non-feeding dives. These rose plots have a circular axis of 360°, with the bars showing
 4 the frequency with which sharks swam in that direction. On top are the swim periods containing
 5 at least one feeding event, the outward steps each represent 25% with n =160. Underneath
 6 shows the non-feeding swim periods, each outward step represents 25%, with n = 1600.

7 Unfortunately, determining dive phases using a template created from dives within the short-
 8 term deployments was unsuccessful when applied to the long-term data. R results relating to
 9 this can be found in appendix 6 but are not discussed in this study.

10 Discussion

11 *Temperature effects*

12 Previous studies have found that surface durations increased when individuals were exposed
 13 to lower water temperatures, except when the minimum temperature is around 25°C, then no
 14 pattern was present (Thums *et al.* 2013). In this study, increased surface time corresponded
 15 to lower mean temperatures (although there was no relationship with maximum depth
 16 reached), supporting the idea that water temperature is a key factor in determining surface
 17 periods durations. While it is the accepted norm for temperature to decrease down the water
 18 column (Tyminski *et al.* 2015), this was not apparent in my data (Figs. 4 & 7), as the waters
 19 are poorly stratified in Ningaloo (Xu *et al.* 2015). Inspection of Figure 7 shows there was a
 20 heterogeneity of temperature within the top 100 m of water, with this effect decreasing with
 21 greater depth, temperature seemed to decrease more consistently, despite not being
 22 scientifically significant.

1 The proportion of time whale sharks spend at the surface varies between studies. We found
2 35% in this study, compared to ~31% in studies off Mexico (Motta *et al.* 2010; Tyminski *et al.*
3 2015), 25% at Ningaloo (Gleiss *et al.* 2013), and, in Oslob (Cebu, Philippines) whale sharks
4 were recorded spending on average 11% of their time at the surface, but 58% when
5 'provisioned' (Araujo *et al.* 2020). Provisioning is the providing of food for species, in order to
6 benefit tourism by making sightings more predictable (Maljković & Côté 2011). This does not
7 currently occur at Ningaloo reef (Sanzogni, Meekan & Meeuwig 2015). The results of this
8 study differ to those of Gleiss *et al.* (2013), also at Ningaloo, where whale sharks spent
9 significantly less time at the surface compared to other sites globally. This discrepancy is likely
10 due to differing definitions of surface water – Gleiss *et al.* (2013) considered the top 2 m to be
11 surface, but this study defined it as occurring in the top 5 m (cf. Fig. 4).

12 *Metabolic considerations*

13 Surface swimming can be disadvantageous to sharks for several reasons, but primarily due
14 to the increased temperature usually associated with surface waters (Araujo *et al.* 2020).
15 Specifically, metabolic rates (oxygen consumption) increase with increasing temperature
16 (Schmidt-Nielsen 1997) – making prolonged periods in warmer surface waters energetically
17 costly. Our results also support the idea that surface swimming had a significantly increased
18 cost associated, *via* the proxy of VeDBA for power (Fig. 6). A 4°C increase in water
19 temperature resulted in reduced growth rates in juvenile epaulette sharks (*Hemiscyllium*
20 *ocellatum*), along with a lesser ability to behaviourally thermoregulate (Gervais *et al.* 2018).
21 The thermal sensitivity (Q_{10}) of the species impacts this relationship, and while the temperature
22 sensitivity of whale sharks is not known explicitly, it is assumed to be similar to other
23 ectothermic elasmobranchs. Thermal sensitivity is a quantification of the effects temperature
24 has on cellular structures (Angilletta 2009), with Q_{10} being the temperature coefficient that
25 denotes how dependent a muscle is on temperature, based on rates of contraction (Mundim
26 *et al.* 2020). Leopard sharks (*Triakis semifasciata*) were found to have a thermal sensitivity
27 (Q_{10}) of ~2.5, consistent with other elasmobranchs and teleosts (Cameron 1989; Miklos,
28 Katzman & Cech 2003), a figure that indicates appreciable thermal sensitivity and it seems
29 germane to assume that whale sharks are similar.

30 Against this, the large size of whale sharks provides them a level of thermal inertia, slow
31 thermal conductivity (Nakamura, Matsumoto & Sato 2020), and their thin band of localised red
32 muscle near their dorsal surface, acts to retain heat within central white muscle (Meekan *et*
33 *al.* 2015). These adaptations offer a means to limit extensive impacts of temperature on the
34 body – and may explain their large operating temperature range (26°C) (Graham, Roberts &
35 Smart 2006; Dove & Pierce 2021). As mentioned above, it has been suggested that surface

1 swimming is a necessary behaviour to reheat following cooling at depths to unsustainable
2 levels (Thums *et al.* 2013). While this is a substantiated theory in many cases,
3 thermoregulatory behaviours require highly contrasting thermal environments within close
4 proximity of each other (Nakamura, Matsumoto & Sato 2020). It is therefore not relevant at
5 Ningaloo where the first 125 m has the same temperature range (Fig. 7).

6 Moving into deeper, cooler waters aids digestion and improves nutrient absorption following
7 feeding (Tyminski *et al.* 2015). Since metabolic rate scales with temperature, in cooler waters,
8 metabolism, and therefore digestion, is slower – enabling more nutrients to be absorbed from
9 food before being excreted (Neer, Rose & Cortés 2007). This process is known as post-
10 feeding thermotaxis and is an energy-conserving behaviour displayed by several
11 elasmobranchs, including Atlantic stingray (*Dasyatis sabina*) (Di Santo & Bennett 2011) and
12 small-spotted catshark (*Scyliorhinus canicula*) (Sims *et al.* 2006). It therefore seems that dives
13 that immediately follow periods of feeding at the surface might conceivably assume this
14 function, although the temperature change with depth over the first 100 m is minimal (Fig. 7),
15 and the large size of whale sharks gives them a thermal inertia (Nakamura, Matsumoto & Sato
16 2020) that would seemingly require long periods at these depths for the effect to be meaningful
17 (Thums *et al.* 2013).

18 *Comparison of depth use across studies*

19 The sharks in this study stayed almost solely in the epipelagic zone (< 200 m; Fig. 5), mean
20 dive depth for whale sharks are cited within the literature as generally ranging between 30 m
21 and 60 m (Graham, Roberts & Smart 2006; Gleiss, Norman & Wilson 2011; Ramírez-Macías
22 *et al.* 2017). This is consistent with our sharks averaging 30 m. The sharks' chosen position
23 in the water column is assumed to be a trade-off between several biotic factors including
24 metabolic rate and prey availability (Staniland, Boyd & Reid 2007). Blue sharks (*Prionace*
25 *glauca*), for example, travel at an average depth of ~400 m, where they have a 40% lower
26 metabolic rate than in surface waters (Lawson *et al.* 2019), despite foraging apparently being
27 optimal at ~200m (Le Croizier *et al.* 2022).

28 *Diel patterns of depth use*

29 The proportion of surface time varied significantly between day and night-time for the sharks
30 in this study, when shark ID was modelled as interacting (Table 2). It has been suggested that
31 'personality' and behavioural plasticity may facilitate the significant differences in the allocation
32 of time between individuals (Fig. 8) (Tyminski *et al.* 2015) (expanded on below). Previous
33 studies have also found that time of day, and the abundance of prey in surface waters, affected
34 the proportion of time that sharks in general spend at the surface (Tyminski *et al.* 2015). For
35 example, variation in minimum prey abundance had a greater impact on surface durations

1 than median or maximum abundance, with lower levels forcing basking sharks (*Cetorhinus*
2 *maximus*) to forage at depth (Sims *et al.* 2003). This pattern may also hold for whale sharks
3 since both species feed on plankton known to exhibit diel vertical migration (DVM) (Stevens
4 2007; Araujo *et al.* 2020) and both ram-ventilate, so must continue to swim. The same study
5 also found the proportion of time spent near the surface to decrease throughout the day, likely
6 following plankton DVM (Sims *et al.* 2003). However, if the primary driver of whale shark
7 surface time allocation was zooplankton prey availability, then it would be assumed that all
8 individuals follow the same cues and timing of DVM. This was not the case for the sharks in
9 this study (Fig. 8). Differences in the date of tag deployment could be one reason for individual
10 variation, since some zooplankton species display seasonality in their patterns of DVM (Liu *et*
11 *al.* 2022) but even the individuals deployed within the same month show differences in their
12 surface time allocation (cf. Table 1 for deployment dates).

13 Overall though, zooplankton DVM leads to a significant increase in prey availability at the
14 surface at dusk, coinciding with an increased presence of feeding behaviours by whale sharks
15 at the surface (West 2013). The sharks in this study displayed an increased proportion of
16 surface time and feeding just before dusk (15.00 – 18.00; Fig. 10), in time with this predictable
17 prey availability (Gleiss *et al.* 2013).

18 *Impacts of tagging on behaviour*

19 It must be acknowledged that the process of tagging may have impacted the whale sharks'
20 behaviour for a period immediately after. Device attachment to the dorsal fin, as in this study,
21 has been shown to instigate shallow dives, breaching or rapid acceleration, among other
22 effects, in cetaceans (Walker *et al.* 2011). Besides behavioural implications, tagging may also
23 have had physiological implications on the individuals. Heart rate variation and decreased
24 respiration have been recorded (Eskesen *et al.* 2009), along with a change in temperature
25 distribution around attachment site (McCafferty, Currie & Sparling 2007); all of which could
26 divert swimming behaviours away from normality. While these studies have not been done on
27 whale sharks directly, the above-stated patterns of other marine animal studies encourage
28 questions of the reliability of this study's short-term data as representative of 'normal life'. It
29 was for this reason that, unless direct comparison between short- and long-term data was
30 referred to, long-term data was used for all analysis.

31 *Alternative theories for surface swimming*

32 Surface swimming has been theorised, throughout the literature, as having various functions
33 for sharks. As mentioned in the introduction, thermoregulation is a regularly suggested
34 function of surface swimming, with sharks needing to reheat following dives to cooler
35 temperatures (Carey, Scharold & Kalmijn 1990; Thums *et al.* 2013). Besides this however,

1 surface swimming has been suggested as a navigational method, with individuals receiving
2 visual cues from celestial bodies (Gruber, Nelson & Morrissey 1988; Klimley 1993), and by
3 reference to the earth's main dipole (Klimley *et al.* 2002). The dipole is a magnetic field that
4 interacts with minerals within the earth, causing distortions associated with ocean topography
5 (Elsasser 1946), and it is most uniform at the surface so can be used for maintaining
6 directionality (Klimley *et al.* 2002).

7 Ram-obligate sharks must conduct all essential activities while on the move (Roberts 1975;
8 Jacoby *et al.* 2015), presumably assuming an optimum position in the water column for each
9 activity (e.g. feeding, migrating, etc). Sleeping is another theorised function of surface
10 swimming (Kelly *et al.* 2019), as it could be hypothesised that surface waters would have a
11 reduced risk of bumping into the reef or anything on the ocean floor. Basking sharks
12 (*Cetorhinus maximus*) have been observed idly swimming at the surface, sometimes ventral
13 side up – an activity deemed as sleeping since they remained undisturbed when touched
14 (Weber 1961). It has, however, been hypothesised that ram-ventilating sharks can remain
15 motionless when sleeping provided they are facing into currents, therefore having oxygenated
16 water passing by them without the need for movement (Kelly *et al.* 2019). This theory has
17 been evidenced, by obligate ram-ventilating sharks being observed resting on the seabed,
18 when strong currents were present (Clark 1973), but this requires further study.

19 Whale sharks are known to aggregate in shallow sites (compared to non-aggregation sites),
20 close to deep water, with a steep sloping seabed – characteristics that lead to increased
21 primary productivity and upwelling events (Copping *et al.* 2018). These sites therefore have
22 high zooplankton concentrations, a constant correlator with whale shark aggregations
23 (Heyman *et al.* 2001; Nelson & Eckert 2007), and enable individuals to perform deep foraging
24 dives while remaining near the productive surface waters. They tend to swim in close proximity
25 to the coastline (Norman *et al.* 2017), a widely known pattern as some have been tracked
26 moving up to Ningaloo from Shark Bay (Norman, Reynolds & Morgan 2016). The Ningaloo
27 environment offers an optimal habitat consistently, many sharks are found at Ningaloo all year
28 round, despite their 'season' being March – August (Wilson, Taylor & Pearce 2001b; Norman,
29 Reynolds & Morgan 2016). It is assumed that maintaining this proximity to the coast ensures
30 foraging ease, exploiting the productivity of the reef (Taylor & Pearce 1999). The similarities
31 in heading distribution (Fig. 12) between dive phases and feeding/non-feeding, reflect this
32 coastline tracking.

33 *Track tortuosity*

34 Whale sharks are primarily planktivorous, feeding by ram filtration and suction feeding,
35 methods that enable them to efficiently exploit prey aggregations (Stevens 2007; Meekan *et*

1 *al.* 2015). They are reported to do this by swimming in circles (Nelson & Eckert 2007; Stevens
2 2007; Meekan *et al.* 2015), see methods. This circling behaviour explains why heading
3 dispersion increased with the number of feeding events (circles producing the greatest
4 dispersion of any path trajectory) (Fig. 11). Importantly, since prey aggregations will be
5 encountered, perhaps probabilistically, over time (Wilson *et al.* 2018b), the number of feeding
6 events should increase over time, which it does (Fig. 9). But heading dispersion also increased
7 over time, even when no prey was encountered, presumably because the longer the monitored
8 period, the more likely the shark will have changed direction. 89% of feeding events occurred
9 when diving (Fig. 9), and this difference remained significant when feed count was time-
10 corrected. While present in both modes, feeding can be assumed a primary function of diving.

11 Despite being a key indicator, circular swimming is not the only way whale sharks feed and,
12 as recognised previously, this approach is highly conservative. Linear feeding occurs at and
13 below the surface, with the shark sucking the water (ram feeding) or passively filtering the
14 water while swimming (Nelson & Eckert 2007; Whitehead *et al.* 2021). This type of feeding is
15 not recognised through the proxy used in this study and would require additional means to
16 confirm feeding (e.g. camera tag or constant observation). It is therefore highly possible that
17 time spent swimming at the surface, not performing circular feeding behaviour, could be
18 feeding in this linear fashion.

19 Since high levels of tortuosity are associated with feeding behaviours, it would be expected
20 that when not feeding; the dispersion of heading would be smaller, with sharks travelling more
21 energy-efficiently in a straighter line. The mean circular heading was unchanged by swimming
22 mode, dive phase (Fig. 12), or the presence of feeding; implying individuals favoured the same
23 direction regardless. VeDBA was greater when surface swimming (Fig. 6), but not influenced
24 by the presence of feeding. This implies that sharks have a purpose for high-energy, tortuous
25 movements, other than when just foraging. High tortuosity, when not feeding, is often
26 recognised as area-restricted prey searching (ARS) (Curio 2012; Knell & Codling 2012) -
27 documented in many shark species (Pereira 2017; Andrzejaczek *et al.* 2018; Ryan *et al.* 2022).
28 The frequency distribution of magnetic heading in Figure 12 highlights a broad dispersion
29 across each phase and mode - implying that prey searching across them all. This is consistent
30 with ARS in all three dimensions – the whale sharks do not know at what depth the prey is,
31 hence vertical and horizontal tortuosity (Andrzejaczek *et al.* 2019).

32 As well as being a proxy for energy expenditure, VeDBA can also be deemed a proxy for
33 speed (Wright *et al.* 2014). The results (Fig. 6) therefore suggest that sharks move faster at
34 the surface, a phenomenon also recognised in other shark species (Watanabe *et al.* 2019;
35 Wilson *et al.* 2022), but the reason for this is unknown and requires further investigation.

1 *Ontogenetic variation*

2 Ontogenetic variation and individuality is an increasingly popular area of study (Shaw 2020),
3 with, for example, substantial inter-individual, and inter-age differences being found in the diet
4 of white sharks (*Carcharodon carcharias*) (Kim *et al.* 2012) and individualised dispersion
5 dynamics in basking sharks (*Cetorhinus maximus*) (Doherty *et al.* 2017; Johnston *et al.* 2022).
6 Body size was shown to correlate with boldness in port jackson sharks (*Heterodontus*
7 *portusjacksoni*), indirectly driven by gape-limitations (Lundvall *et al.* 1999; Byrnes & Brown
8 2016). The 3 m range in body size of sharks in this study may therefore also play a role in
9 dictating patterns (or lack of them). Personality studies of fish are generally biased towards
10 smaller species, for practical ease (Dingemanse *et al.* 2009; Castanheira *et al.* 2013), but the
11 development of methodologies for larger species would offer further opportunities to
12 understand how megafaunal individual differences can shape ecosystems and subsequently
13 impact management.

14 It is worth noting that the horizontal positions of each whale shark within the reef were
15 unknown, and hence could be a contributing factor in the individual variation in allocation of
16 surface time (Table 2 and Fig. 8). Ningaloo reef is a vast area, occupying nearly 300 km of
17 coastline (Kobryn *et al.* 2013), and the distribution of prey within it is unlikely to be uniform
18 (Holzman *et al.* 2005). Differences in the whale sharks' horizontal positioning around the reef
19 may therefore be an additional reason for the variation in time spent at the surface (Fig. 8).

20 *Relevance of surface swimming for boat strikes and conservation*

21 It is estimated that almost a third of whale sharks have scarring attributed to boat strikes
22 (Speed *et al.* 2008), with collisions happening in both coastal home ranges and offshore
23 (Rohner *et al.* 2020). Collisions are thought to be less frequent at Ningaloo, compared to other
24 sites such as Seychelles and Mozambique (Speed *et al.* 2008). The caudal fin is regularly
25 damaged, as it is the closest body part to passing boats, but no direct relationship was found
26 between scarring and survival rates (Speed *et al.* 2008). Nonetheless, offshore mortalities
27 likely go unnoticed in this coastal observation-based approach, and it is suspected that high
28 levels of unreported strikes could be driving population declines (Womersley *et al.* 2022).
29 Understanding the proportion of time that whale sharks spend surface swimming, especially
30 during their long-distance geographical migrations, may help more effective protective
31 management strategies to be put in place. Provisioning, as mentioned above, is a double-
32 edged sword in that it encourages ecotourism and increases reliability of sharks aggregating
33 in the same sights regularly, but it risks altering natural behaviours and developing a
34 dependence on anthropogenically-provisioned food (Brena *et al.* 2015; Legaspi *et al.* 2020).
35 A habituation of whale sharks to boats, that is likely when they are a source of food, also

1 increases their risk of boat strikes, since they would be less cautious around them (Schleimer
2 *et al.* 2015; Penketh *et al.* 2021).

3 *Limitations of the study*

4 The large amount of data (200 data points were collected per tag per second) in this study,
5 meant that at several points in the methodology data had to be excluded (e.g. removing any
6 swim periods shorter than 3 minutes long), simply to make the data handling more
7 manageable. It could be argued that, in decreasing the data resolution, key elements could
8 have been lost. Against this, whale sharks are large and do things slowly (Martin 2007), so for
9 the purpose of this study (focusing on functionality) only the longer swim periods were of
10 interest. This study also lacks equal representation of both male and female whale sharks,
11 since 19 of the 20 sampled were male – meaning the results are ignorant to any potential sex
12 biases in behaviours and assume what was displayed by these sharks is representative for all
13 others. This sample sex bias is, however, consistent with other studies, with female whale
14 sharks being even more enigmatic than their male counterparts – other studies have had 85%
15 (Norman & Stevens 2007), 74% and 89% (Rohner *et al.* 2015) male dominance. Comparing
16 the results of this study with others of its kind brings up issues due to differing definition of the
17 depth classified as ‘surface water’. The threshold of 5 m in this study was based on
18 examination of the data (Fig. 4) but is considerably more inclusive than the 2 m depth threshold
19 used in several other papers (Gleiss *et al.* 2013; Thums *et al.* 2013; Araujo *et al.* 2020), a
20 difference that should not be overlooked. Finally, determining feeding events based on when
21 the individual completes a 360° turn is not 100% accurate, since the shark may turn but not
22 successfully feed, or they may feed without making the full circle. Despite this, this proxy
23 indicator of feeding offers greater insight into shark behaviours, without the need for video
24 footage or stomach content analysis, for example.

25 **Conclusions**

26 Whale sharks show a distinct variation in their depth use, either swimming at the surface or
27 executing regularly undulating dives down the water column. Feeding can be assumed a key
28 function of diving, and diving accounts for a greater proportion of whale shark time with,
29 however, marked inter-individual variation. Surface swimming is more tortuous than diving and
30 has much greater VeDBA values, implying surface swimming is faster and more energy
31 expensive. Such systematic differences between surface swimming and diving indicate that
32 there are functional behavioural differences between the two modes although it is still not
33 possible to ascertain exactly what these might be. However, despite being widely accepted as
34 a reason for surface swimming versus diving, surface swimming as a thermoregulatory
35 behaviour is rejected for the sharks at Ningaloo.

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9

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Appendices

Appendix 1.

This research was conducted under Western Australian Department of Biodiversity Conservation and Attractions Licence No. FO25000033-9, FO25000033-16, CE006122 and CE006335, and Animal Ethics Approvals from The University of Queensland (Permit No. SBS/085/18/WA/INTERNATIONAL), Murdoch University (Permit No. RW3327/21) and Swansea University (Approval No. SU-Ethics-Student-280122/4953).

Appendix 2.

Protocol for data analysis in DDMT. Phase 1 creates marked events for the phases (descent, ascent and bottom) within traces. Phase 2 creates bookmarks for dive periods and phase 3 exports these dive bookmarks, with the identified phases. Finally, phase 4 exports bookmarks for the surface periods.

Phase 1:

1. Load in file
2. Load TDO
3. Check mag is on the sphere (confirms TDO accuracy)
4. Smooth appropriate parameters
 - a. Pressure – 200
 - b. VeDBA – 40
 - c. Pitch, roll and heading – 160
 - d. Acceleration for compass – 200
5. Import behaviour builder expression list 1
6. Extend marked events by 20 events each way
7. "Run all expressions"
8. Auto create bookmarks
9. Delete bookmarks < 600 events
10. Delete marked events
11. Auto create bookmarks
12. Delete smaller than 600 events
13. Clear marked events
14. Mark events for bookmarks
15. Export Global Marked Events for phases

Phase 2:

16. Clear bookmarks and marked events
17. Import behaviour builder expression list 2
18. Extend marked events by 300 events each way
19. Run expression
20. Auto create bookmarks
21. Delete smaller than 600 events
22. Clear marked events
23. Save .bmk file for dives

Phase 3:

24. Load phase 1 marked events
25. Load dives bookmarks
26. Name file and set working directory
27. Under sample data by 1 Hz
28. Select what to save options
29. Initialise multisession and save
30. End multisession

Phase 4:

31. Delete bookmarks
32. Delete marked events 2 & 3
33. Auto create bookmarks for marked events 1
34. Rename category to SURFACE
35. Delete marked events
36. Rename file "..._SURFACE"
37. Initialise multisession and save
38. End multisession

Appendices 3: Model selection tables

Appendix 3a. Model selection table for a linear mixed model with mean VeDBA as the response variable, models tested in R studio. Explanatory variables are depth, mean temperature (C), category (surface swimming or diving), day_night (binomial variable, 06:00-19:00 classified as daytime and 19:01-05:59 classified as night) and shark ID is distinct for each individual..

Model	Response	Explanatory	Model type	Random	AIC	Additional comments
1 (null)	VeDBA mean	1	lmer	(1+Shark ID)	-203465.3	Poor residuals
2 (transformed null)	VeDBA mean (box-cox transformed)	1	lmer	(1+Shark ID)	470789.3	
3	VeDBA mean (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Category + Feed_present	lmer	(1+Shark ID)	455396.2	
4	VeDBA mean (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Feed_present	lmer	(1+Shark ID)	464581.3	
5	VeDBA mean (box-cox transformed)	Depth + Day_Night + Feed_present	lmer	(1+Shark ID)	464771.8	
6	VeDBA mean (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Category + Feed_present	lmer	(1+Depth Shark ID)	455072.9	
7	VeDBA mean (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Category + Feed_present	lmer	(1+Day_Night Shark ID)	454632.3	
8	VeDBA mean (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Category*Feed_present	lmer	(1+Depth Shark ID) + (1+Day_Night Shark ID)	454203.1	Best model

Appendix 3b. Model selection table for a linear mixed model with mean heading dispersion (standard deviation of heading) as the response variable, models tested in R studio. Explanatory variables are depth, mean temperature (C), category (surface swimming or diving), day_night (binomial variable, 06:00-19:00 classified as daytime and 19:01-05:59 classified as night) and shark ID is distinct for each individual..

Model	Response	Explanatory	Model type	Random	AIC	Additional comments
1 (null)	Standard Deviation	1	lmer	(1+Shark ID)	30940.3	Poor residuals
2 (transformed null)	Standard Deviation (box-cox transformed)	1	lmer	(1+Shark ID)	56686.1	
3	Standard Deviation (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Category + Duration.s. + Feed_present	lmer	(1+Shark ID)	54565.3	
4	Standard Deviation (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Duration.s. + Feed_present	lmer	(1+Shark ID)	54753.6	
5	Standard Deviation (box-cox transformed)	Depth + Day_Night + Category + Duration.s. + Feed_present	lmer	(1+Shark ID)	54827.7	
6	Standard Deviation (box-cox transformed)	Depth + Depth*Temp.mean + Day_Night + Category + Feed_present	lmer	(1+Depth Shark ID)	54337.8	Best model

Appendix 3c. Model selection table for a generalised linear mixed model with number of feeding events as the response variable, models tested in R studio. Explanatory variables are duration of swim period (in seconds), depth, day_night (binomial variable, 06:00-19:00 classified as daytime and 19:01-05:59 classified as night) and shark ID is distinct for each individual.

Model	Response	Explanatory	Model type	Error Family	Random	AIC	Additional comments
1 (null)	Feed counts	1	glmer	Poisson (log link)	(1 Shark_ID)	70381.4	

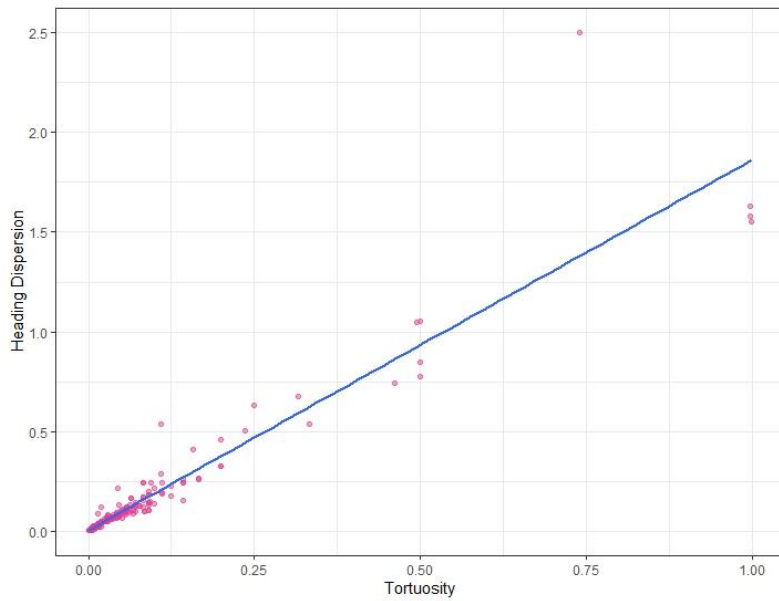
2	Feed counts	Duration.s.+ Depth + Day_night	glmer	Poisson (log link)	(1 Shark_ID)	63521.5	Best model
3	Feed counts	Duration.s.	glmer	Poisson (log link)	(1 Shark_ID)	65172.8	

Appendix 3d. Model selection table for a generalised linear mixed model with mean time at the surface (binomial) as the response variable, models tested in R studio. Explanatory variables are duration of swim period (in seconds), depth, temperature (C), day_night (binomial variable, 06:00-19:00 classified as daytime and 19:01-05:59 classified as night) and shark ID is distinct for each individual..

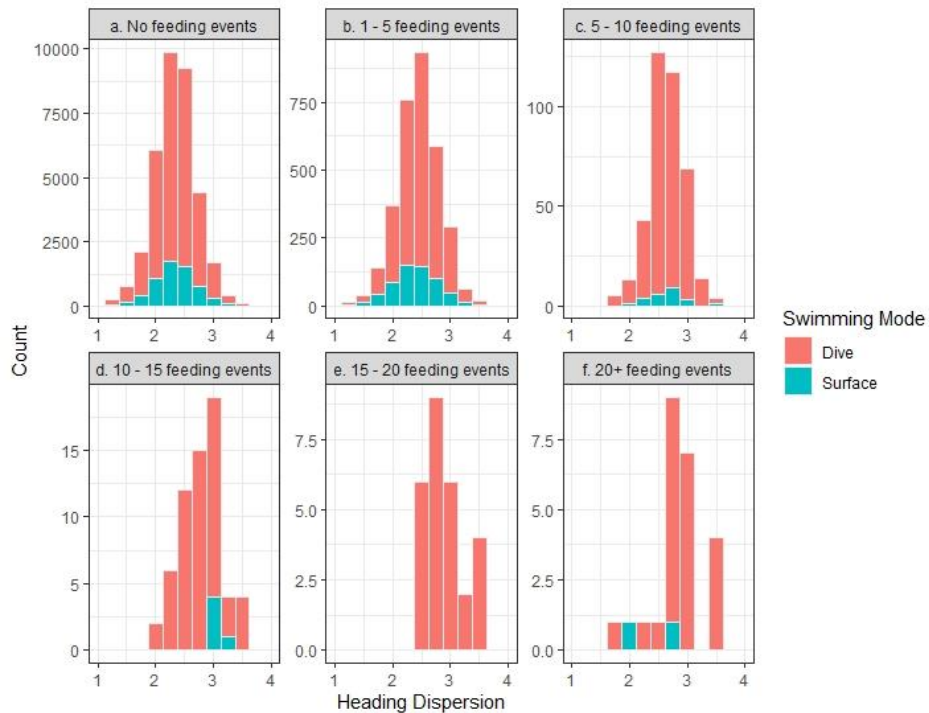
Model	Response	Explanatory	Model type	Error Family	Random	AIC	Additional comments
1 (null)	Surface binomial	1	glmmadmb	Beta	(1 Shark_ID)	-469.8	
2	Surface binomial	Day_Night + Duration.s. + Depth + Depth*Temp.C	glmmadmb	Beta	(1 Shark_ID)	-602.3	Best model
3	Surface binomial	Day_Night + Duration.s. + Depth + Temp.C	glmmadmb	Beta	(1 Shark_ID)	-603.9	
4	Surface binomial	Day_Night + Duration.s. + Depth + Depth*Temp.C	glmmadmb	Beta	(1+ Day_Night Shark_ID)	-649.1	Most significant
5	Surface binomial	Hour + Duration.s. + Depth + Depth*Temp.C	glmmadmb	Beta	(1 Shark_ID)	-583.1	Shows effect of hour in detail but less significant than m2

Appendix 3e. Model selection table for a compound poisson linear mixed model with (standardised) feed count as the response variable, models tested in R studio. Explanatory variables are duration (of swim period in seconds), mean temperature (C), category (surface swimming or diving), and shark ID is distinct for each individual..

Model	Response	Explanatory	Model type	Random	AIC	Additional comments
1 (null)	Standardised feed count	1	cpplmm	(1 Shark_ID)	-2754	
2	Standardised feed count	Duration.s. + Day_Night + Category + Depth*Temp.mean	cpplmm	(1 Shark_ID)	-1447	
3	Standardised feed count	Duration.s. + Day_Night + Category	cpplmm	(1 Shark_ID)	-138.1	Best model
4	Standardised feed count	Duration.s. + Day_Night + Category + Depth	cpplmm	(1 Shark_ID)	-1363	
	Standardised feed count	Duration.s. + Day_Night + Category + Temp.mean	cpplmm	(1 Shark_ID)	-505.6	



Appendix 4. The dispersion (standard deviation) of magnetic heading against the tortuosity, with a linear regression line ($R^2 = 0.9$) – using the short-term tag deployments. Both metrics were made relative to the data by standardising (dividing) them by the duration of the swim period they were calculated over.



Appendix 5. The frequency distribution for dispersion of heading, based on the number of feeding events per swim period and mode.

Appendix 6. The results of dive type identification for the short- and long-term data, that led to discussions of dive type being disregarded. The code used for determining dive type was based on the short-term data with a 70% success rate but was not successful for the long-term deployments. Yoyo dives were being recognised as a sequence of many V-dives, since their characteristics were in line, hence the misrepresentation.

Dive Type	Short-term proportions (%)	Long-term proportions (%)
V-dive	73	> 99
U-dive	2	0
Yoyo-dive	25	< 1