



Swansea University
Prifysgol Abertawe

Judicious Power Use in Whale Sharks (*Rhincodon typus*);
Under What Conditions Do They Employ Power Above
Minimum?

Amy Fisher

Swansea University

Submitted to Swansea University in fulfilment of the requirements for the
Degree of MRes Biosciences


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This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended

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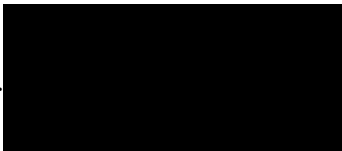
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5. Definitions and Abbreviations

AIC	Akaike information criterion
DBA	Dynamic Body Acceleration
DD	Daily Diary
DDMT	Daily Diary Multiple Trace
edf	Effective Degree of Freedom
GAMM	Generalised Additive Mixed Model
GPS	Global Positioning System
h	Hours
IUCN	International Union for Conservation of Nature
min	minutes
ODBA	Overall Dynamic Body Acceleration
P_{min}	Minimum Power
PPA_{min}	Putative Power Above Minimum
SD	Standard Deviation
UNESCO	United Nations Educational, Scientific and Cultural Organization
VeDBA	Vector of Dynamic Body Acceleration

6. Abstract

There is a strong selection pressure for animals to move in a way that maximises efficiency, often incurring minimal costs. By using the Vector of Dynamic Body Acceleration (VeDBA), as a measure of power in relation to vertical velocity, the “Minimum Power” (P_{\min}) can be calculated by a functional relationship for any speed of an animal in a fluid medium.

“Putative Power above Minimum” (PPA_{\min}), is a metric which quantifies how much the power to move exceeds P_{\min} , indicated by subtracting P_{\min} from VeDBA. The dynamics of energy expenditure and efficiency of swimming animals are critically dependent on the drag and velocity as major modulators of PPA_{\min} . For 15 whale sharks (*Rhincodon typus*) tagged with acceleration/depth tags, periods when substantial PPA_{\min} occurred were identified in relation to periods of dive descent, ascent and level swimming, examined with the corresponding body geometry, depth, time of day and swim track tortuosity (a proxy for feeding). Within the whale shark data, incidences of PPA_{\min} during ascents (mean = $0.0161\text{ g} \pm 0.0094\text{ SD}$) and predominantly when swimming horizontal ($0.016\text{ g} \pm 0.021\text{ SD}$) are suggested to be due to an increase in the drag coefficient by the animal opening its mouth to feed. This effect is magnified by increased surface drag (within 2 m of the water surface). As power usage increases with the cube of swim speed, other high PPA_{\min} values likely correspond to speed increases, principally observed during rapid descents ($0.012\text{ g} \pm 0.011\text{ SD}$). Crucially, PPA_{\min} is suggested to be a due to human interactions. Instances of PPA_{\min} may negatively impact the energy budget of the endangered whale sharks, which is of particular concern for this species working on an energetic “knife-edge”.

7. Lay Summary

Animals are under strong pressure to move in ways that are as efficient as possible, helping them conserve energy and reduce effort. This becomes more complicated for dense marine animals, like sharks, that work in a three-dimensional environment, because of the increased energy needed to overcome gravity to prevent sinking. It is possible to derive a metric used to describe the minimum power needed to move at any speed, calculated from the relationship between a shark's body acceleration and speed up or down the water column, both of which can be recorded from animal-attached tags. However, certain environmental conditions are expected to cause animals to expend more energy than the minimum for movement. These higher than minimum power moments can occur because sharks can increase their drag (by opening their mouth) or by swimming faster than necessary. Such periods can be highlighted by examining how much body acceleration for a given vertical speed exceeds the minimum, called Putative Power above Minimum.

Using data from fifteen whale sharks tagged at Ningaloo Reef, Western Australia, incidences when the animals exceeded minimum power and by how much (excess power) were highlighted, specifically looking at dive descents, ascents and level swimming. These behaviours were analysed regarding the vertical velocity, pitch angle, swim depth, time of day and how twisted the whale shark's swim track was.

We found high values of excess power when whale sharks descended at faster speeds than necessary, most likely to avoid a threat. Human interactions, from the tourism industry or the tagging process, may also be causing greater additional energetic costs to this species than expected. High values of excess power were recorded during periods associated with feeding and when the swim track also became more twisted. This effect was exacerbated when whale sharks swam near the surface, presumably because they must also overcome additional drag caused by wave action.

These results highlight how whale sharks using excess power to swim should be balanced by prey intake (either prey quality or quantity). Given that whale sharks are listed as endangered, and currently under threat from the increasingly challenging marine environment, it seems appropriate that we now examine how human interactions may affect their energy budget, providing better insight into areas crucial to their conservation.

Further application of excess power usage during longer-term tag deployments would be highly beneficial to examine what role this plays across sexes and outside of Ningaloo Reef. This should help our understanding of how the energy usage of whale sharks is affected by varying ecological conditions.

8. Introduction

Animal movement patterns, including factors such as step lengths and turn angles (Benhamou, 2007), speeds (Wilson *et al.*, 2015), gaits (Wampler & Popović, 2009) and home ranges (Gautestad & Mysterud, 1993), are complicated, and vary through space and time (Torres *et al.*, 2017). In general, natural selection is expected to exert strong pressure for animals to move by expending energy judiciously (Pyke, 1984; McNamara & Houston, 1997) and ultimately by moving in a way that promotes survival and lifetime reproductive success (Pianka, 1976; Dickinson, 2000). Understanding how animals move to minimise energy expenditure and the intrinsic and extrinsic factors that shape these movement patterns is crucial for elucidating their ecology and informing effective species management and conservation (Nathan *et al.*, 2008; Shaw, 2020).

Animal-attached tag technology is highly advantageous for observing behaviour in wild animals (Wilson *et al.*, 2008; Shillinger *et al.*, 2012; Cooke *et al.*, 2013; Jepsen *et al.*, 2015; Holton *et al.*, 2021). In particular, the use of accelerometers, can provide fine-scale measurements of body movements (Brown *et al.*, 2013; Hounslow *et al.*, 2019). This has been used to look at changes in effort associated with movement energetics with, in particular, Dynamic Body Acceleration (DBA) (Qasem *et al.*, 2012) being a powerful (linear) predictor of movement-related energy expenditure (Halsey *et al.*, 2009). DBA is calculated by subtracting the static acceleration component (due to gravity) from the raw data, using a running mean for each orthogonal acceleration channel, and then summing the remaining dynamic components across all channels, either vectorially (Vectorial Dynamic Body Acceleration – VeDBA) or as a simple sum (Overall Dynamic Body Acceleration - ODBA) (Wilson *et al.*, 2019). The resultant data is due to animal movement (Wilson *et al.* 2019).

8.2 Power Use for Movement

Swimming animals, such as the whale shark (*Rhincodon typus*), operate in a three-dimensional environment, adding a further level of complexity to the terrestrial scenario (Burt de Perera *et al.*, 2016). The cost of vertical travel in a fluid medium (water or air) is fundamentally different from that of horizontal, because of the energetic consequences of gravity (Gleiss *et al.*, 2010).

All species of shark lack a swim bladder and have therefore evolved large, lipid-rich livers to generate hydrostatic lift (Alexander, 1990). This adaptation has resulted in considerable

interspecific variation in buoyancy, ranging from negative to near neutral and even positive in some species (Bone & Roberts, 1969). Despite this, most sharks possess an overall body density greater than seawater, making them inherently negatively buoyant (Craik, 1978). To regulate their position in the water column, sharks have developed various behavioural adaptations. For instance, sand tiger sharks (*Carcharias taurus*) gulp air at the surface and store it in their stomachs, enabling them to temporarily achieve neutral buoyancy (Hussain, 1989).

A study by Wilson *et al.*, (2022) used DBA metrics to examine the energetic strategies of swimming in whale sharks. Specifically, they compared DBA values against the rate of change of depth of ascending sharks to build a functional relationship. They argued that a curve linking the lowest VeDBA points for various rates of change of depth (a lower convex polygon) describes the minimum power (P_{\min}) needed to swim for any given rate of change of depth. Adoption of the minimum power for movement (P_{\min}) is expected to be subjected to strong selection pressure, particularly in species like the whale shark, that operate at overall low metabolic rates (Meekan *et al.*, 2015; Wilson, 2022). Exploring the role of P_{\min} during key swimming behaviours is therefore valuable in understanding 'normal', energy-saving circumstances patterns of these animals.

A. Descending

When whale sharks descend the water column, their increased density compared to water produces a net downward force, which the shark can use to provide propulsion, allowing them to glide (Iosilevskii & Papastamatiou, 2016). Gliding is hydrodynamically very efficient because no energy is lost during tail beating (Weihs, 1973), and the energetic cost of descent is therefore expected to be near to that of the resting metabolic rate. Since no active propulsion is needed, P_{\min} as expressed in VeDBA metrics, is zero.

B. Level Travel

Having a higher body density than seawater (Craik, 1978), whale sharks swimming level (at a constant depth) must continuously swim to generate dynamic lift and counteract sinking (Gleiss *et al.*, 2010; Iosilevskii & Papastamatiou, 2016). The primary propulsion mechanism for sharks is their caudal fin, which generates the forward thrust (Sumikawa *et al.*, 2023). Lift is then produced by the pectoral fins, with water flow over them facilitated by the caudal propulsion (Compagno, 1986). Sharks use a range of strategies to reduce the energetic cost of

locomotion, such as utilising tidal (Papastamatiou *et al.*, 2021) and surface geostrophic currents (Sims *et al.*, 2003). However, these behaviours have not been confirmed for whale sharks (Sleeman *et al.*, 2010) but rather energy conservation primarily includes their slow swimming speed (Eckert and Stewart, 2001; Meekan *et al.*, 2015). As such, level swimming does incur a metabolic cost but although higher than descending, P_{\min} is expected to be minimal.

C. Ascent

For ascent in the water column, energy is necessary to overcome the force of gravity in the acquisition of potential energy because potential energy (PE) is given by;

$$PE = mgh \quad (1)$$

where m is the mass, g is the gravitational constant (9.81 m/s^2) and h is the height (depth) difference. Thus, with increasing pitch angle, the vertical component of the ascent is increased, resulting in a higher rate of gain of potential energy and a higher energetic cost (Gleiss *et al.*, 2010). At higher ascent angles, the lift generated by the pectoral fins is reduced, necessitating additional thrust by caudal propulsion to compensate, additionally increasing the drag coefficient through body undulations (Weihs, 1973). P_{\min} therefore represents the power value which minimises the cost of ascent for defined ascent angles, providing a comprehensive picture of the minimum energetic investment required by whale sharks to swim at any angle (Wilson *et al.*, 2022).

There is a considerable knowledge gap regarding the certain environmental scenarios that will cause whale sharks to deviate from minimum energy expenditure. Power increases will typically occur when animals observe trade-offs to maximise fitness (Houston & McNamara, 2013), including prey acquisition (Langerhans *et al.*, 2021), predator avoidance (Houston *et al.*, 1993) and the high energetic cost of reproduction (Hammerschlag *et al.*, 2018). The extent to which swimming behaviours deviate from minimum power can be examined by subtracting instantaneous VeDBA values from P_{\min} . This has been coined putative power above minimum (PPA_{\min}), a new metric used to describe periods when the extent to which animals invest more energy than necessary for minimum power travel (Wilson *et al.*, 2022). The authors use the terms ‘putative’ because, although there is good evidence to suggest that

VeDBA metrics scale linearly with metabolic rate in sharks (Byrnes *et al.*, 2021), the precise relationship between VeDBA metrics and the power needed to swim is not known for whale sharks.

8.3 Background Ecology of the Whale Shark

The whale shark is the world's largest species of fish (up to 18m), that filter feed on large quantities of plankton to sustain their energetic demand (McClain *et al.*, 2015). As opportunistic feeders, whale sharks repeatedly dive to scan the water column, adjusting their body angles to minimise either the horizontal or vertical transport costs (Gleiss *et al.*, 2010). Whale sharks can feed 'passively' by swimming slowly with their mouths open and filtering plankton (Taylor, 2007) or feed "actively" by gulping water when prey conditions are suboptimal (Nelson & Eckert, 2007; Ketchum *et al.*, 2012). Due to the overall inefficiency and energetically costly nature of these feeding mechanisms, whale sharks are more dependent on concentrated prey availability than other shark species (Meekan *et al.*, 2015).

At Ningaloo Reef, Western Australia, whale sharks form annual aggregation of juvenile males between March and August, thereby creating a valuable area for tagging studies to be performed (Meekan *et al.*, 2006). Additionally, the reliable aggregations and charismatic nature of whale sharks has also created a highly profitable tourism industry at Ningaloo Reef, where opportunities to snorkel and dive with whale sharks are numerous (Gallagher & Hammerschlag, 2011). Whale Sharks are migratory, travelling thousands of kilometres around the Pacific to take advantage of the seasonal blooms of phytoplankton (Heyman *et al.*, 200; Rowat & Gore, 2007). At Ningaloo reef, the bloom is believed to be caused by the warmer, southward-moving Leeuwin Current, interacting with the cooler, northward-moving Ningaloo Current (Xu *et al.*, 2016). This interaction forms a highly productive upwelling of nutrients, subsequently causing high phytoplankton biomass (Woo *et al.*, 2006).

It is understood that juveniles whale sharks utilise such shallow coastal areas for continued growth before retreating to deeper offshore waters as adults (Meekan *et al.*, 2015). In comparison, it is believed that juvenile females possess slower growth rates and continuously utilise deeper waters to attain a larger size (Meekan *et al.*, 2020). Therefore, segregation in size and sex by whale sharks at Ningaloo is related to their behavioural strategies, rather than the oceanographic features (Ketchum *et al.*, 2012).

8.3 Aims and Objectives

The aim of this study was to use data from accelerometers and depth sensors in animal-attached behavioural data-logging tags, deployed on the dorsal fin of whale sharks, to identify the circumstances under which whale sharks deviate from P_{\min} and instead display substantial PPA_{\min} .

The dynamics of energy expenditure and swim efficiency of a negatively buoyant animal are dependent on the power required for movement as a function of drag and velocity. The drag (D) experienced by such a body is:

$$D = 0.5 \times Cd \times \rho \times A \times v^2 \quad (2)$$

where Cd is the drag coefficient (depending on the shape of the swimmer and flow characteristics), ρ is the density of the fluid medium e.g. water (kg/m^3), A is the cross-sectional area of the swimmer in m^2 and v is the swim speed (m/s). The formula makes clear that the drag force increases with the square of the velocity, so the effect of drag is greatly intensified at greater velocities (Altringham & Johnson, 1990).

The relationship of power (P) to swim with respect to swim speed and drag is given by:

$$P = 0.5 \times Cd \times \rho \times A \times v^3 \quad (3)$$

where the power (the energy expended per second) is expressed in watts or joules per second. Since the power expenditure increases with the cube of the velocity, power usage is even more sensitive to speed than drag.

These two formulae explicitly show how changes in drag (such as will occur when a whale shark opens its mouth to feed) and speed affect the rate of energy expenditure (power) and point to two features that can account for high values of power usage above the minimum (PPA_{\min}).

Given the fundamental differences in energy expenditure associated with descent, level swimming and ascent, the study has been based on separating these three major kinematic parameters (Gleiss, *et al.*, 2010). We build on the current understanding of the effect of body

angles (Gleiss, *et al.*, 2010), depth (Watanabe *et al.*, 2019), time of day (Gleiss *et al.*, 2013) and tortuosity (Cade *et al.*, 2020; Wilson *et al.*, 2021), on whale shark energy expenditure, across the different behaviours. We hypothesise that PPA_{min} will increase with increasing speed and foraging effort, and that the combined effect on PPA_{min} will be magnified, as power increases with the cube of velocity.

9. Methodology

9.1. Study site

Fieldwork was conducted from the 5th of May to the 25th. However, due to a tag failure, data from fieldwork has not been included in this study. Therefore, all data were collected by ECOCEAN from May 2019 to May 2024 (Reynolds *et al.*, 2024) at Ningaloo Reef, Western Australia. Located along one of the narrowest sections of the Australian continental shelf, the 200m depth contour is less than 20 km offshore (Kobryn *et al.*, 2013). Nearly all of the reef area has been protected under state and federal legislation and has been inscribed as a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Site, Ningaloo Reef, Northwest Australia (Figure 1). This occurs within the International Union for Conservation of Nature (IUCN) Marine protected area (21° 59' 57.84" S, 113° 54' 33.62" E) (Reynolds *et al.*, 2024).

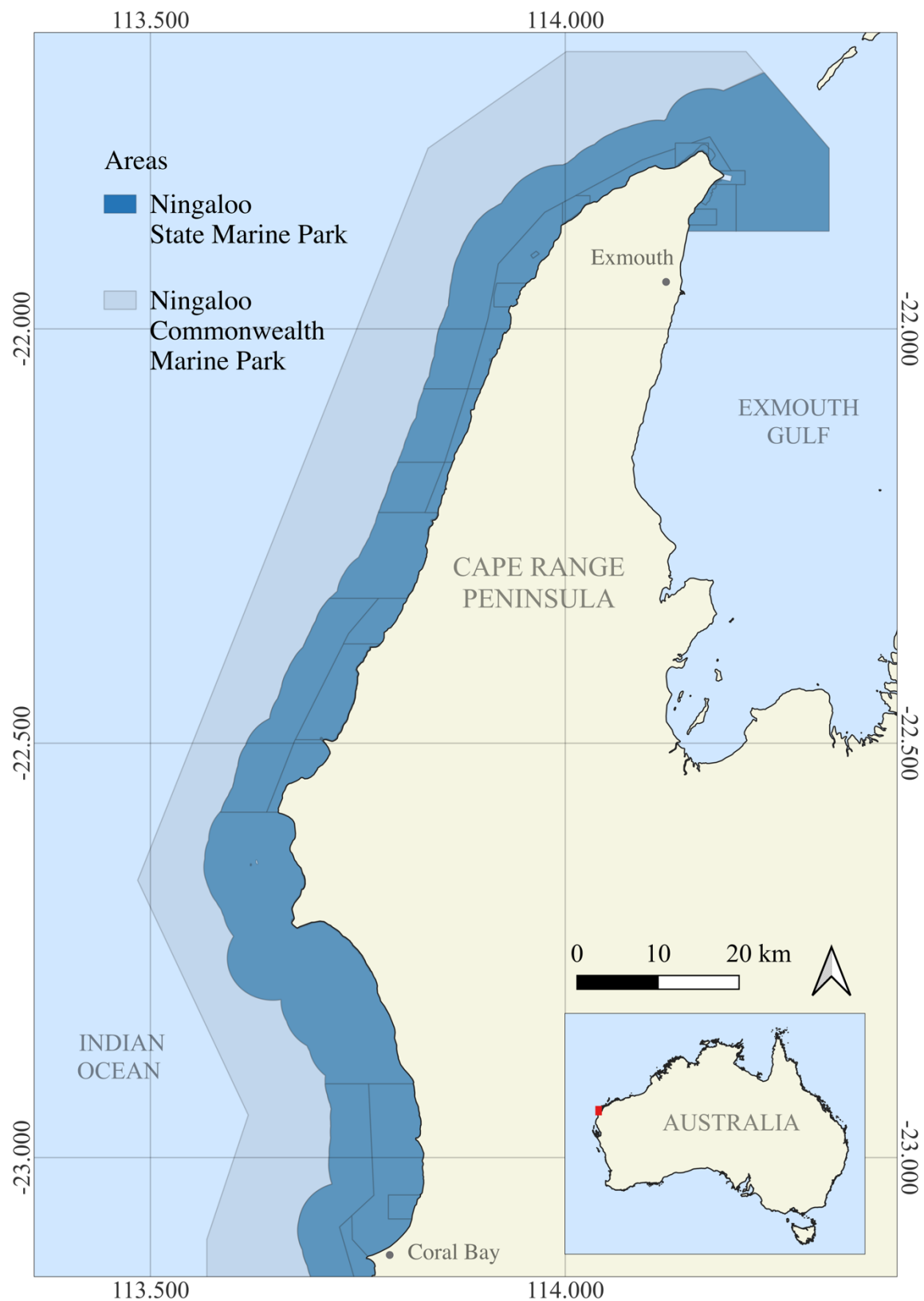


Figure 1. Study site at Ningaloo Reef, itself located within the Ningaloo State Marine Park and Ningaloo Commonwealth Marine Park, in North West Australia (Australian Bureau of Statistics, 2021).

9.2. Data Collection

Daily Diary (DD) Information

Data was collected with multi-sensor archival Daily Diary (DD) tags (Figure 2) (Wilson *et al.*, 2008; Wildbyte Technologies, 2024) (<http://www.wildbytetechnologies.com>). Tags were programmed to simultaneously record triaxial orthogonal acceleration, tri-axial orthogonal magnetic field intensity, pressure and temperature (Table 1), written onto a 2 Gb memory card.

Table 1. Description of primary metrics recorded by the DD.

Primary Metric	Description
Acceleration x	The triaxial acceleration in the x axis, ‘surge’. Measures the anterior, posterior acceleration with a measuring range of ± 16 g at 20 Hz.
Acceleration y	The triaxial accelerator y axis, sway. Measures the medio-lateral acceleration with a measuring range of ± 16 g at 20 Hz.
Acceleration z	The triaxial accelerator z axis, heave. Measures the dorsal-ventral acceleration with a measuring range of ± 16 g at 20 Hz.
Magnetic field intensity x	The triaxial magnetometer sensor in the x axis. Measures magnetic field intensity, ranging ± 0.88 G with a step resolution of 0.73 mG/LSB at 13 Hz.
Magnetometry y	The triaxial magnetometer sensor in the y axis. Measures magnetic field intensity, ranging ± 0.88 G, with a step resolution of at 0.73 mG/LSB at 13Hz.
Magnetometry z	The triaxial magnetometer sensor in the z axis. Measures magnetic field intensity, ranging ± 0.88 G, with a step resolution of at 0.73 mG/LSB at 13Hz.
Pressure	Water pressure (in mbar) with a sampling frequency of 4 Hz.
Temperature	Water temperature measured in $^{\circ}\text{C}$ at 4 Hz.
Time	The DD tag possesses an onboard Real Time Clock (RTC), which gives accurate timing (± 15 s/month), allowing sensor sample data to be allocated to precise days, hours, minutes and seconds (DD:HH:MM:SS).

The package was fitted with a continuous acoustic transmitter (V16P-5H, Innovasea), which allowed the sharks to be actively tracked by a research vessel (Figure. 2) (Reynolds *et al.*,

2024). The DD must be retrieved to obtain the data (Wilson *et al.*, 2008). Therefore, DDs were attached to a custom-made spring clamp fitted with a salt-water corroding galvanic system. In the instance that whale sharks could not be relocated during the study period, the spring clamp would release the tags after ~ 6 months.

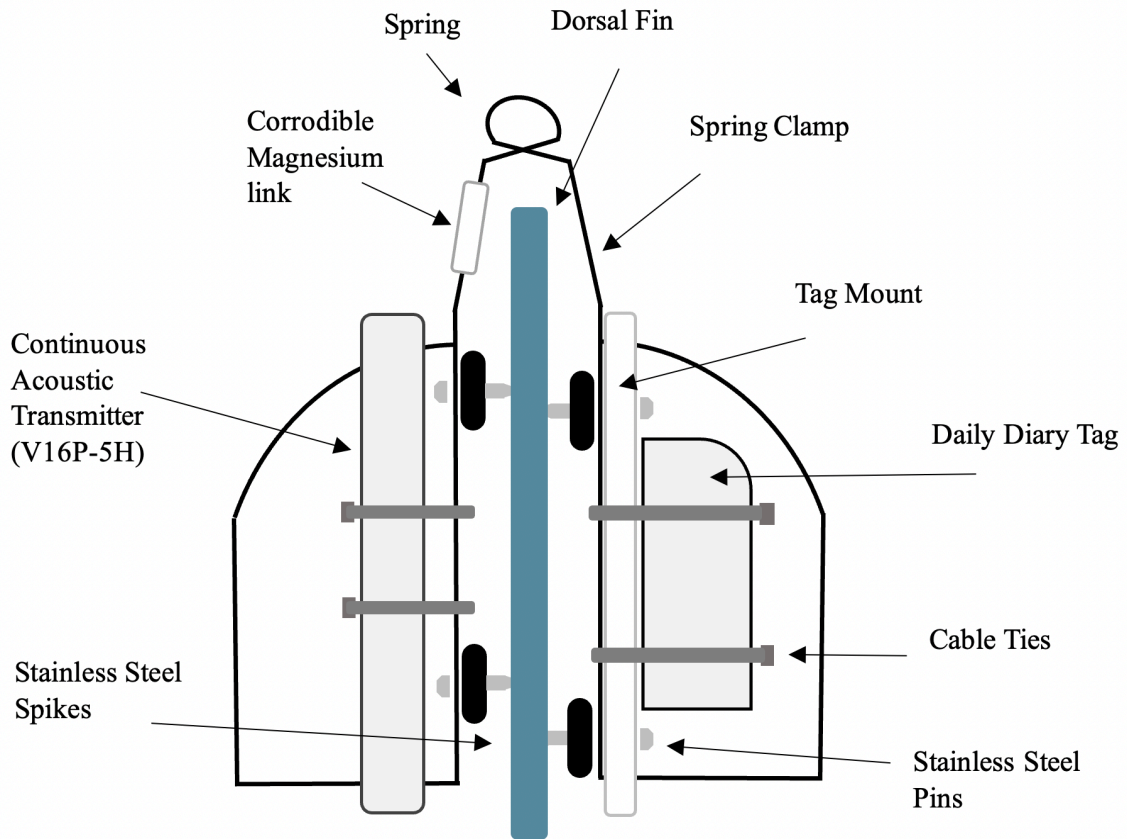


Figure 2. Schematic diagram of the custom-made spring clamp and stainless-steel pins, fitted with DD tag and acoustic transmitter. The tag is fitted around the front of the dorsal fin, secured by stainless steel spikes.

Tag Deployment Methodology

Tag deployment was divided into ‘short-term’ and ‘long-term’, with the distinction being based on whether tags were deployed and retrieved within one day or left on the shark for multiple days before later retrieval.

A spotter plane was used to initially locate whale sharks over Ningaloo Reef, before a research vessel approached a shark approximately 50 m in front. GPS coordinates of the whale shark at the time of tagging was recorded (Figure 3), shark size was estimated, sex

determined, and photographs taken so that all sharks could be identified using Shark book (<https://www.sharkbook.ai/>) (Arzoumanian *et al.*, 2005). Researchers then entered the water to manually deploy the tag onto the first dorsal fin of the whale shark (Figure 4) by using the spring clamp as the shark swam past (Reynolds *et al.*, 2024). As far as possible, care was taken to position the DD so that the orthogonal acceleration axes matched the primary axes of the shark's body (surge, heave and sway) (Figure 4).

For short-term deployments, the shark's location was monitored every 5 minutes by tracking the acoustic signals from a continuous transmitter, using a directional hydrophone (VH110, Innovasea) and an acoustic receiver (VR100, Innovasea), while following approximately 10 meters behind with the research vessel. This identified the proximity and heading of the shark with respect to the boat for GPS coordinates to be calculated from. After a decided period of time (which varied according to shark behaviour and weather), researchers re-entered the water and the fin clamp was manually detached from the whale sharks as it swam past. The memory card was then removed and the GPS coordinates of the detachment location were recorded.

For long-term deployments, the tag was deployed and left on the shark for an extended period between 14 to 39 days. When the whale shark was relocated, researchers or allocated members of the tourism industry re-entered the water and the fin clamp was manually detached from the whale sharks as it swam past (Reynolds *et al.*, 2024). The memory card was removed and the GPS coordinates of the detachment location were recorded.

Quantification of Tourism

During short-term deployments, whale sharks were involved in tourism interactions or “tourism days”, while during long-term deployments, referred to as “non-tourism days”, they were not. All tourism operators cooperated with the research program, providing confidence that no sharks tagged for long-term deployments had interacted with tourists until the tags were retrieved (Reynolds *et al.*, 2024).

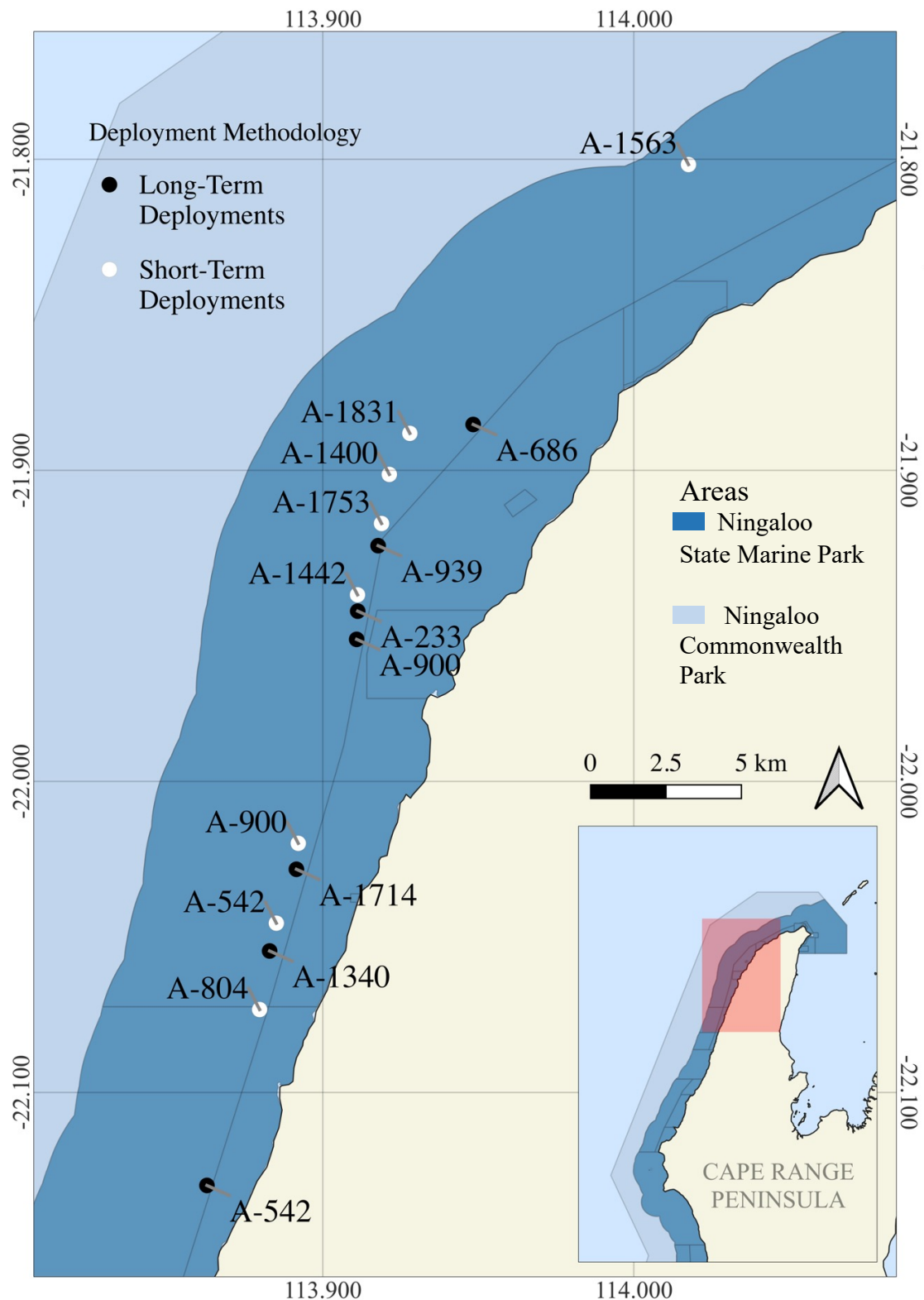


Figure 3. Deployment location of the long-term and short-term DD tags onto the whale sharks. Located across Ningaloo and Coral Bay, all deployments occurred within the Ningaloo State Marine Park, and Ningaloo Commonwealth Marine Park, in North West Australia (Australian Bureau of Statistics, 2021).

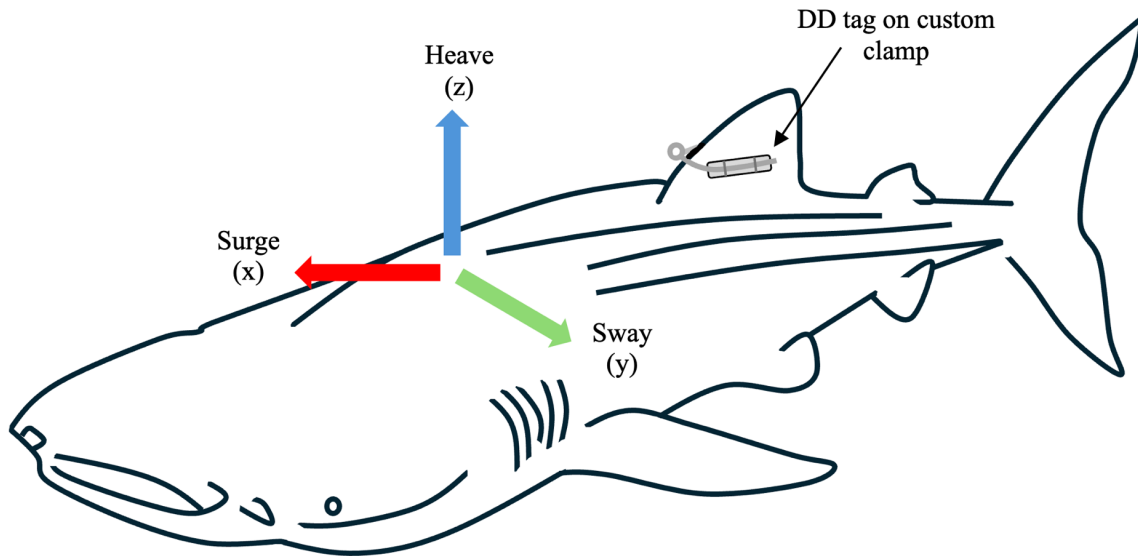


Figure 4. Schematic diagram of a whale shark, with the DD tag attached on the custom-made clamp, at the base of the first dorsal fin. The three arrows represent the position of the tag relative to the acceleration axis of the species body orientation and movement. The red arrow illustrates the surge (x-axis), blue the heave (z axis), and green the sway (y-axis).

Ethical Note

This study was endorsed by research permit RW3327/21 (Appendix I) for the experimental practice on animals, completed on the 30th of March 2021 and amended on the 28th of June 2023. In compliance with the Animal Welfare Act (2002) and the Australian code for the care and use of animals for scientific purposes (8th edition, 2013), this was approved by the Research Ethics & Integrity Office for Murdoch University.

9.3. Data Analysis

Once data was retrieved from the micro-Secure Digital Card, it was assessed using a Wildbytes-produced program; DDMT (*Wildbyte Technologies*, 2024) (<http://www.wildbytetechologies.com>). DDMT displays data graphically, with channels of primary data such as magnetometry and acceleration being presented in 2D, with sensor data on the y axis, and time on the x axis (Table 1). DDMT additionally creates powerful 3D plots for visualisation and examination of data trends and provides multiple algorithms for processing secondary metrics (Arkwright *et al.*, 2020) (Table 2).

Table 2. Description of secondary metrics created using DDMT

Secondary Metric	Description
<i>Vertical Velocity</i>	Travel by whale sharks up and down the water column was given by vertical velocity (m/s). This was calculated using the rate of change of pressure, since pressure equates linearly with water depth, and then converted to vertical speed. Vertical velocity was calculated over periods of one second (original pressure data at 20 Hz) within the ‘Differential channel’ option in DDMT (Whitney <i>et al.</i> , 2016).
<i>Vectorial dynamic body acceleration (VeDBA)</i>	A prime acceleration-based metric that is a good (linear) proxy for power (rate of energy expenditure) is vectorial dynamic body acceleration VeDBA (Qasem <i>et al.</i> 2011; Wilson <i>et al.</i> 2020) which has been validated for birds (Williams <i>et al.</i> , 2015, Stothart <i>et al.</i> , 2016), mammals (Halsey <i>et al.</i> , 2009) and fish (Gleiss <i>et al.</i> , 2010, Wright <i>et al.</i> , 2014). The triaxial sensor, recording raw acceleration of each orthogonal axis measures all accelerations, including that produced by gravity ($9.81 \text{ m/s}^2 = 1 \text{ g}$) as well as accelerations due to the movement of the animal. As acceleration is vectorial, possessing both direction and magnitude, total acceleration (A_{total}) is given by:

$$A_{\text{total}} = (Ax^2 + Ay^2 + Az^2)^{0.5} \quad (4)$$

The gravitational acceleration of a stationary animal has a vectorial sum of 1 g and to access this component, each axis in the raw data needs to be smoothed, nominally over 2 s (Shepard *et al.* 2008a) before the vectorial sum can be computed. Notably, the smoothed acceleration of specific axes also provides the information necessary to calculate animal pitch and roll (see below). To obtain the acceleration caused by movement of an animal, researchers use ‘dynamic body acceleration’ (DBA), which subtracts the gravitational component from the raw acceleration of each the acceleration axis (Shepard *et al.*, 2008b).

Vectorial dynamic body acceleration (VeDBA) is given by:

$$\text{VeDBA} = \sqrt{(\text{DBAX})^2 + (\text{DBAY})^2 + (\text{DBAZ})^2} \quad (5)$$

where ‘D’ describes the dynamic acceleration calculated by subtracting the gravitational acceleration from raw acceleration for each axis (x, y, z) (Wilson *et al.*, 2019). ‘V’ describes the vectorial summing of each component (Qasem *et al.*, 2012).

Pitch

Pitch (°) is derived from the smoothed acceleration data along the x-axis (surge), given by:

$$\text{Pitch} = \sin(\text{smoothedAccX}) \quad (6)$$

A pitch angle of 0 ° represents level travel. The angle of inclination or declination is relative to the earth’s gravitational plane and therefore shows the angle of ascent and descent in the water column by an animal (Gunner *et al.*, 2021a).

Dead

reckoning

Dead reckoned paths are three-dimensional paths of an animal’s movement (Gunner *et al.*, 2021a). They are calculated using vectorial calculation on heading, speed, movement angle (pitch) and change in depth data from DD-tagged animals (Gunner *et al.* 2021a). VeDBA is considered a good proxy for speed (Bidder *et al.*, 2015) and the pressure data can give 3D relevance to visualise movement. However, drift from in water currents causes the relationship between the powered direction of travel and the vectoral travel path to become inaccurate (Wilson *et al.*, 2008). To correct this, ‘Verified Points’ from GPS coordinates recorded during the deployment, detachment and acoustic monitoring are programmed in DDMT to reconstruct more accurate movement paths (Gunner *et al.*, 2021b). The complete process of dead-reckoning (which can be performed within DDMT) is complex and described in detail by Gunner *et al.* (2021a).

9.4. Data Corrections

It is essential that any data collected from the DD is corrected, allowing “true” data to be analysed. DDMT possesses processing algorithms to adjust for minor irregularities in the DD placement on an animal and any movement that might occur in tag positioning throughout the deployment.

Magnetometer corrections

With respect to derivation of animal heading, hard and soft iron deposits in the environment surrounding the DD cause distortions and locational shifts in the magnetic field (Gunner *et al.*, 2020). To deal with this, prior to deployment, a magnetometry calibration is created by rotating the DD 360° in both vertical and horizontal axes, so that the normalised orientation of the *X, Y, Z* axes are accounted for (Williams *et al.*, 2017; Bidder *et al.*, 2015). Using DDMT, the “initiate magnetometer correction” algorithm presents a sphere of normalised data (of the calibrated data), creating a reference frame for subsequent movement data. An ellipsoid-fitting algorithm and correction factor adjusts for offsets and distortions – so that it is perfectly spherical, and position data on each axis at the true origin (Figure 5) (Wilson *et al.*, 2020; Walker *et al.*, 2015).

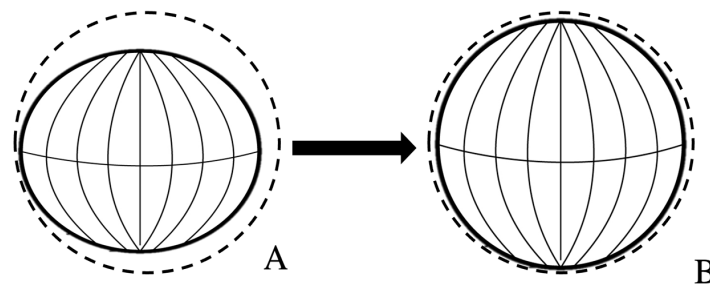


Figure 5. Schematic diagram of magnetometer data corrected in the “magnetometry sphere”, transforming (A) raw data that is distorted and offset, to (B) normalised and centred data at each axis at the true origin.

Accelerometer corrections

Acceleration values are affected by changes in tag orientation (Wilson *et al.*, 2019). By creating a 'smoothed accel sphere' - a 3D plot of the smoothed acceleration data, also known as a 'g-sphere' (Wilson *et al.*, 2016) - the data distribution can be analysed to identify periods

when sharks were traveling at a constant depth, indicating level movement. For a perfectly aligned DD, in this situation, the surge and sway axes should each have gravitational components of 0 g , the heave would have a component of 1 g and the distribution of the data points should be on the North pole of the g-sphere (Figure 6) (Wilson *et al.*, 2016). If they are not, DDMT can be used to rotate the data so that this occurs, correcting all the acceleration data within the file accordingly. In this manner, all shark pitch data were also corrected.

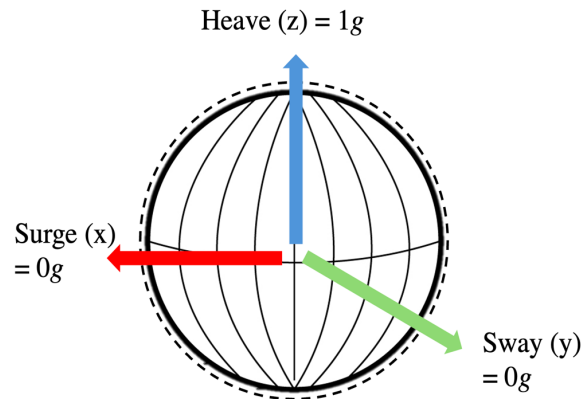


Figure 6. Schematic diagram of corrected acceleration data in a ‘smoothed accel sphere’, adjusted so that the surge and sway axes have gravitational components of 0 g , and the heave has a component of 1 g . This should be the situation when the shark is swimming horizontally.

Pitch Corrections

Where the tags are incorrectly orientated on the dorsal fin, erroneous accelerometer values are produced, causing significant error for the derived pitch metrics calculated (Garde *et al.*, 2022). To correct this, the pitch angle for instances where the whale shark was swimming at a constant depth and vertical velocity was zero, was subtracted from all pitch estimates (Andrzejczek *et al.*, 2019). To correct the tag shifting on the dorsal fin due to DD inflections and wave action throughout the deployment, the pitch angle had to be continuously monitored by visualising the data for every “split” and repeating the correction process.

9.5. Calculation of the Minimum Power Line (P_{min})

Since sharks are denser than seawater (Craig, 1978), movement down the water column does not require power. Instead, they can glide (Papastamatiou *et al.*, 2018). By contrast, the faster they move up the water column (either due to increasing speed or travel angle or both), the

more power they must invest. The minimum power required for power increment with vertical velocity has been termed P_{\min} (Wilson *et al.*, 2022) and can be described by the lowest VeDBA points on the graph for any given vertical velocity (for ascents only). In a graph of VeDBA versus vertical velocity, the minimum power line effectively ‘sits under’ the lowest points.

To create this relationship, points plotted where vertical velocity was >0 m/s and all outliers at the 95% confidence interval were removed (Wilson *et al.* 2022). Of the remaining points, a line under the convex hull of the points was plotted, consisting of two piecewise linear curves, joined left to right. To the vertices of the bottom of the curve, a quadratic function was calculated as:

$$VeDBA = a + b * \text{vertical velocity}^2 \quad (7)$$

with the function describing the relationship with a significant fit ($R^2 > 0.7$) (Figure 7). This approach was adopted for all sharks, which showed appreciable intraspecific variation (Figure 8).

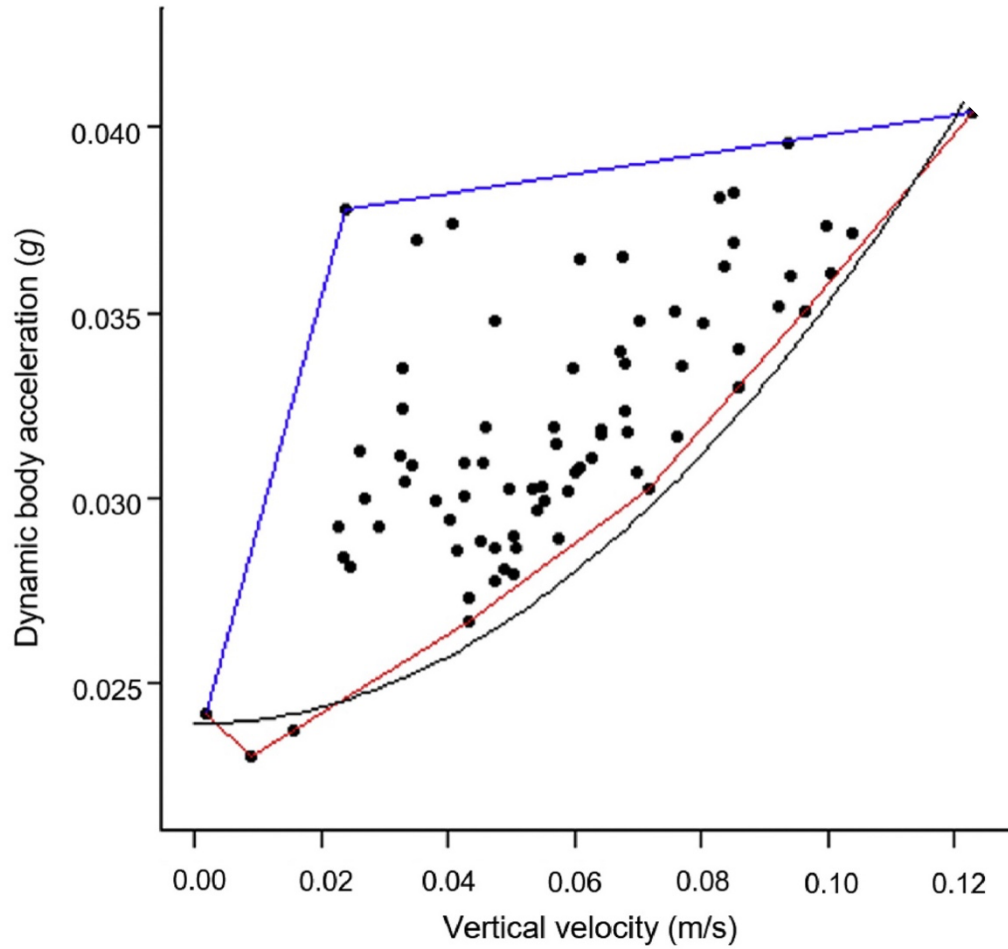


Figure 7. Calculation of the minimum power line for VeDBA increment with vertical velocity for a single whale shark. Dots represent VeDBA (expressed as DBA) versus vertical velocity (rate of change of depth), with the removal of 95% confidence interval outliers. Red represents the bottom of the convex hull, two piece-wise linear lines. Blue represents the top of the convex hull. Black represents the quadratic function: $VeDBA = a + b * \text{vertical velocity}^2$. Taken from (Wilson *et al.*, 2022).

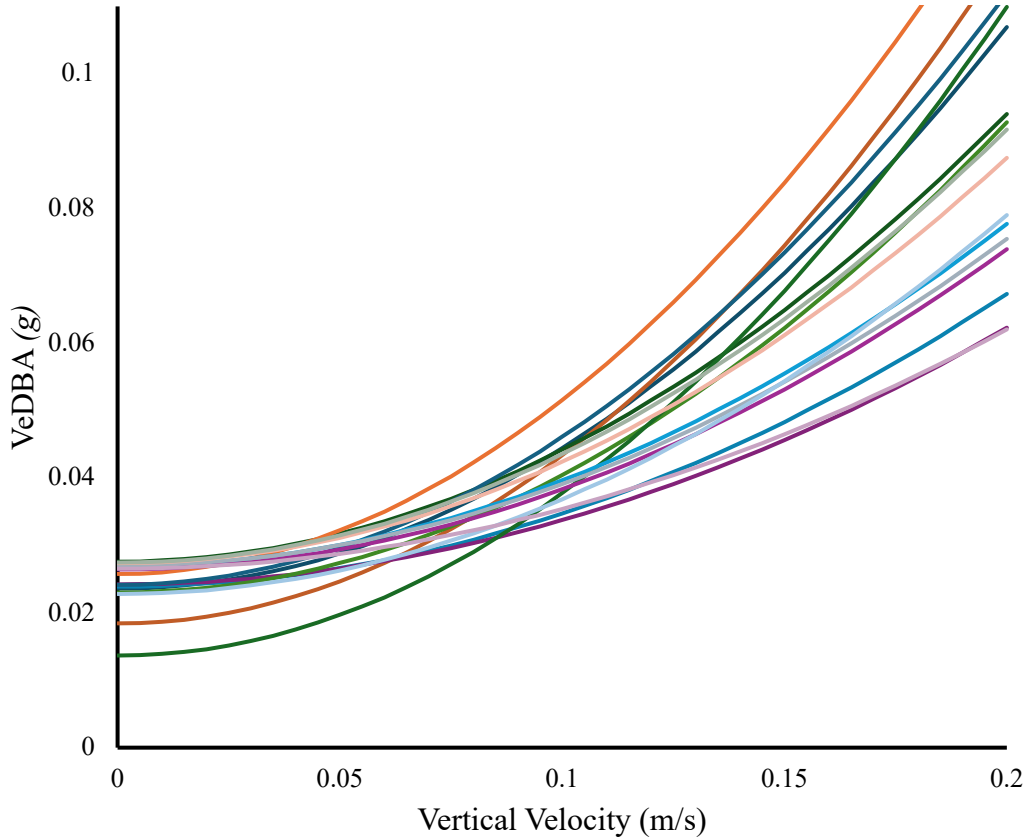


Figure 8. Minimum power lines with respect to vertical velocity for various individual whale sharks, calculated using the quadratic function $VeDBA = a + b * \text{vertical velocity}^2$. Power is represented by the vectorial dynamic body acceleration (VeDBA), a metric which has been repeatedly shown to provide a good linear proxy for metabolic power (see text). Each line represents an individual whale shark used in this study (by colour).

9.6. Calculation of Substantial Putative Power above Minimum (PPA_{min})

PPA_{min} is the VeDBA-based value describing the numerical extent to which points are above the minimum power line. PPA_{min} was extracted from the data once the minimum power line had been calculated per individual, by subtracting VeDBA from P_{min} . To reduce noise from DD inflections and wave action, PPA_{min} was smoothed across 10 data points (executed within DDMT).

The objective of this study was to determine the circumstances under which whale sharks perform behaviours that are energetically higher than that required (minimum power use). It was therefore important to determine at which point power usage could be considered ‘substantially’ above P_{min} . To do this, a $(P_{min} + \phi)$ line was created that represented an upward

y-shift in the P_{\min} line, where ϕ was a given value of VeDBA. The value of ϕ determined how far the $(P_{\min} + \phi)$ line moved up the y-axis and this changed the proportion of points above it (Figure 9). By plotting different $P_{\min} + \phi$ lines, with varying ϕ -values, the relationship between ϕ and the proportion (%) of points above the line could be visualised. Four percentages were inspected (5%, 10%, 25% and 50%), and overall, the line at which 50% of VeDBA points sat above the P_{\min} line was determined to be the most appropriate in displaying PPA_{\min} values that were appreciably far from the P_{\min} line, while still leaving good variability in VeDBA values above this line (Figure 9). Due to the appreciable intraspecific variation in P_{\min} lines (Figure 9), this 50% line was calculated for each whale shark (Appendix II).

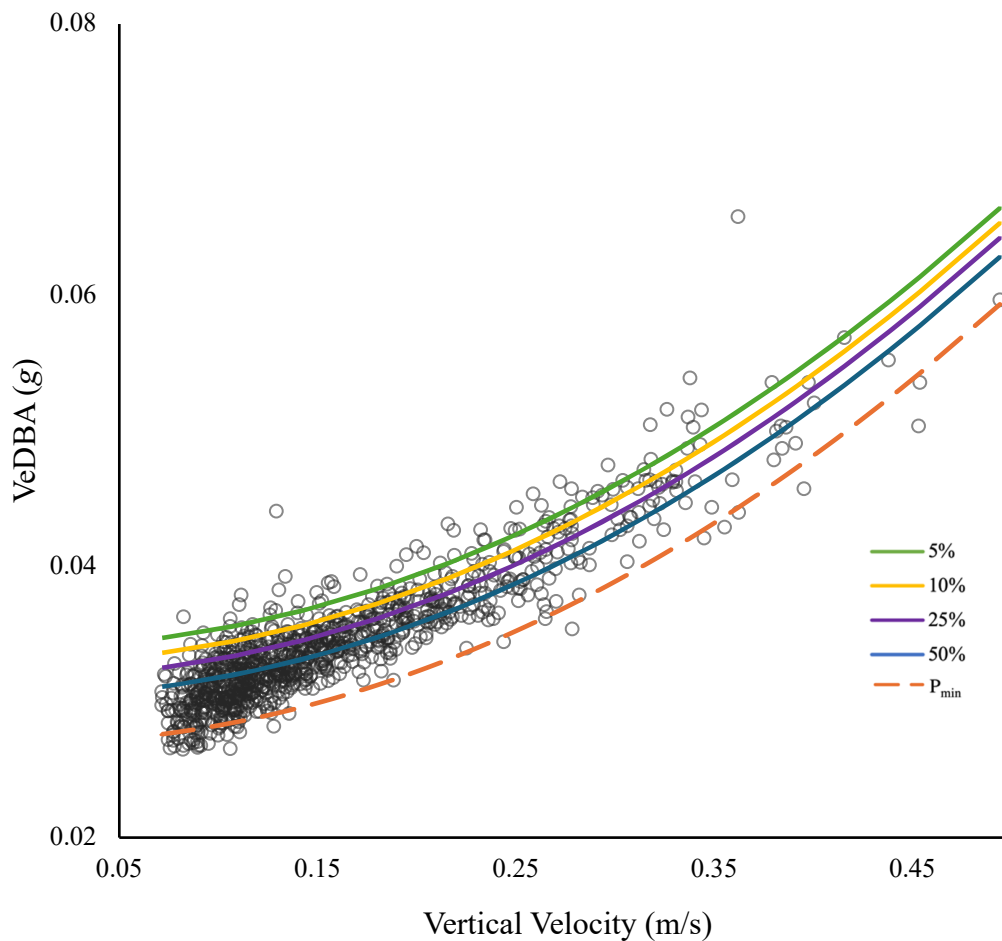


Figure 9. Calculation of the line at which PPA_{\min} is considered ‘substantial’. The y-intercept for the quadratic function has been adjusted to move P_{\min} up the y-axis. The line in which 50% of points remain above P_{\min} was selected as the best representation of considerable VeDBA values while still maintaining a good range of values for any given vertical velocity.

DDMT has a Boolean algorithm function, ‘Behaviour Builder’ which is used to identify defined behaviours (Wilson *et al.*, 2018). Using this function, incidences above substantial PPA_{min} were highlighted as; *If* (PPAM.smoothed > 0) *then* ‘Mark Events’. All data was merged over 1 second (20 events), and any periods lasting greater than 10 seconds were converted to ‘Bookmarks’. Bookmarks contain data for all metrics, for every second, which can then be exported.

9.7. Derivation of Additional Variables

All bookmarks were compiled using R Studio (R Core Team, 2022). Additional calculations were performed on the exported metrics to derive additional variables (Table 3). For each incidence of PPA_{min} , data was averaged across all available seconds, yielding a single data point per incident. The duration of each PPA_{min} incident was then also calculated by summing the total number of seconds. To reduce any outliers that occur when using the ‘Behaviour Builder’ function, incidents of PPA_{min} were limited to durations below the 95% percentile. Due to the size, data was downloaded by “split” (also allowing for pitch to be continuously monitored).

Table 3. Description of additional variables calculated in R Studio.

Additional Variable	Description
<i>Depth</i>	Depth in metres was calculated from the primary metric; pressure in hbar, multiplied by 9.93 to account for the change in hydrostatic pressure associated with depth in saltwater.
<i>Hour</i>	The primary metric Time was categorised by hour using the “lubridate” package (Grolemund, & Wickham, 2011).
<i>Absolute velocity</i>	<p>Absolute velocity can be calculated if the vertical velocity and dive or return to surface angle is known using:</p> $S = \frac{\Delta d}{\sin(\theta - \frac{\pi}{180})} \quad (8)$ <p>The vertical velocity is multiplied by the sine of the pitch, to obtain the absolute velocity in m/s (Gunner <i>et al.</i>, 2021a). The resultant speed should be only positive and can only account for travel when pitch angles are substantial</p>

since minor errors in pitch angle result in huge variation in speed estimates when pitch is close to 0 °. Data was therefore limited to periods where pitch was $\geq 10^\circ$, and $\leq -10^\circ$.

Tortuosity Tortuosity is the extent to which an animal twists and turns along its movement path. For whale sharks, increased tortuosity has been attributed to increased foraging efforts as the most parsimonious behavioural explanation (Cade *et al.*, 2020). There are various methods to calculate it (Troup *et al.*, 2020). Tortuosity (T) was derived from dead reckoned paths via:

$$T = 1 - \frac{\text{Straight Line Distance between Positions p1 and p2}}{\text{Total Distance Travelled between Positions p1 and p2}} \quad (9)$$

in which the straight-line distance travelled between positions p1 and p2 is calculated and divided by the total distance travelled between positions p1 and p2, over the duration of each PPA_{min} event. This produces a value between 0 and 1, with 0 being the straightest and 1 being the most tortuous (Reynolds *et al.*, 2024).

9.8. Behavioural Characterisation

This study aimed to assess how PPA_{min} varied with different movements. For this, data was divided into three major movements: *Descent*, *Level Travel* and *Ascent*, based on kinematic parameters. Taken from Gleiss *et al.* (2010), these are defined as; (1.) descent = pitch angle $< -10^\circ$ and vertical velocity $< -0.05 \text{ m/s}^{-1}$, (2.) level travel = pitch angle $> -10^\circ$ & $< 10^\circ$, vertical velocity $< 0.05 \text{ m/s}^{-1}$ & $> -0.05 \text{ m/s}^{-1}$, and (3.) ascent = pitch angle $> 10^\circ$ and vertical velocity $> 0.05 \text{ m/s}^{-1}$ (Figure 10).

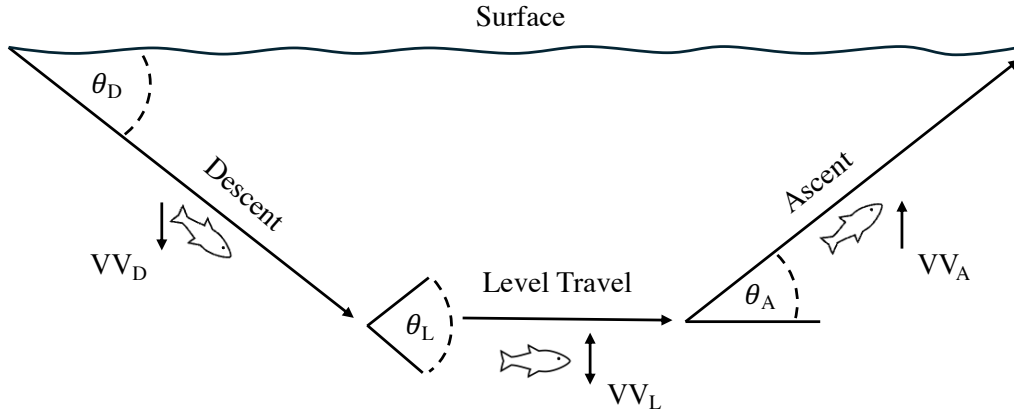


Figure 10. Schematic representation of the pitch angle and vertical velocity associated with each kinematic/behavioural category. Whereby descent = pitch angle (θ_D) $< -10^\circ$ and vertical velocity (VV_D) $< -0.05 \text{ m/s}^{-1}$. Level travel = pitch angle (θ_L) $> -10^\circ$ & $< 10^\circ$ and vertical velocity (VV_L) $< 0.05 \text{ m/s}^{-1}$ & $> -0.05 \text{ m/s}^{-1}$. Ascent = pitch angle (θ_A) $> 10^\circ$ and vertical velocity (VV_A) $> 0.05 \text{ m/s}^{-1}$.

9.9. Statistical Analysis

Data analyses and presentation were performed using R studio (R Core Team, 2022) and Origin(Pro) “Version 2022”. The level of significance was set at $P = 0.05$.

The distribution of the response variable PPA_{\min} , was determined using the *fit.dist* function from the “fitdistrplus” package (Delignette-Muller *et al.*, 2015). Observation of a Cullen and Frey graph (Appendix III) and comparison of Akaike information criteria (AICs) scores between distribution types were used to determine the best fit (Appendix IV). An Anderson Darling test was then used to confirm if the response variable had a normal distribution or not.

The Mann-Whitney U test was used to observe differences between PPA_{\min} and short term and long-term deployment types ($n = 2$) (nominal).

The Kruskal Wallis test was firstly used to observe differences in PPA_{\min} between different sharks (Shark ID) ($n = 15$) (nominal) and repeated between deployment groups. Secondly, this was used to observe how PPA_{\min} differed between the three behavioural/kinematic groups.

To observe the non-linear responses of PPA_{min} during each kinematic/behavioural category, three Generalised Additive Mixed Models (GAMMs) were constructed using the “*mgcv*” package (Wood, 2011). GAMMs were selected as the model of choice as they allow for nonlinear responses in the data, providing the flexibility needed to capture complex patterns whilst accounting for intraspecific variation and ununiform sampling.

For each behavioural category, PPA_{min} was modelled against the explanatory variables: vertical velocity and pitch angle (Table 2), depth, and time of day (Table 3). Tortuosity was also examined to explore whether incidences of PPA_{min} can be used to identify feeding (Table 3). Due to the large proportion of data calculated at level travel (between -10° and 10°), absolute velocity calculations showed a substantial level of error and were thus not included in any models.

A gamma error distribution with a log link was used to account for the gamma distribution of the data. Shark ID was included as a random effect to account for intraspecific differences and to avoid pseudo-replication, while the explanatory variables were set as fixed effects. The hour of the day was treated with cyclic smoothers ($bs = cc$), due to its circular nature. Thin-plate splines ($bs = tp$) were chosen as the basis type, whilst the number of smoothed terms (k) was set to 10, to enhance the “wiggleness” of the smooth variables, without overfitting (Wood, 2003).

For each kinematic/behavioural category, an additive model with all the explanatory variables was constructed, of which all possible combinations were then evaluated using the *dredge* function from the “*MuMin*” package (Burnham, 2002) (Appendix V-VII). The model used was chosen by a balance between lowest AIC and ΔAIC (to a threshold of >2) and observation of plots, using the *gam.check* function from the “*nlme*” package (Pinheiro *et al.*, 2024) to determine the most parsimonious model that best described the relationship of the covariates (Table 4). As we hypothesised that an increased speed would have a magnified effect on PPA_{min} when accompanied by the increased drag from feeding and the additional interactive effect of (Vertical Velocity \times Tortuosity) was included.

For the model describing level travel that included Time as a covariate, a decline of autocorrelation was observed with increasing lag, Using the auto-correlation function, in the

“nlme” package. Correlation structure was added to account for serial dependence of the behaviour of each shark, modelled as lag = 1, as a fixed term (corAR1) (Table 4).

Table 4. Final GAMM model selection for descent, level travel and ascent, based on the lowest ΔAIC value. The additional interaction for ascent and descent has been italicised.

Behaviour	Model Type	Response Variables	Explanatory Variables	Random Effect	Cor Effect
Descent	Gamma distribution, log link	PPA _{min}	~ VV + Pitch Angle + Tortuosity + <i>(VV × Tortuosity)</i>	(Shark ID = ~1)	N/A
Level Travel	Gamma distribution, log link	PPA _{min}	~ Depth + Time + Tortuosity + Pitch Angle	(Shark ID = ~1)	corAR1 (form = ~1 SharkID)
Ascent	Gamma distribution, log link	PPA _{min}	~ VV + Pitch Angle + Tortuosity + <i>(VV × Tortuosity)</i>	(Shark ID = ~1)	N/A

10.Results

10.1. PPA_{min} Summary Statistics

In total, 15 whale sharks were tagged, 7 as long-term deployments, and 8 as short-term deployments. All tagged sharks were male with lengths ranging from 6-8 m (mean 7.1 m) (Table 5).

The duration of tag deployments varied from 39 days, 22 hours, 56 mins to 1hr, 52 mins, constituting a total of 181 hours and 4 minutes of fine scale daily diary data. All tags were successfully recovered, except for A-233 that suffered a battery failure. Behavioural characteristics varied largely by shark and deployment type, including the depth range, pitch angle and vertical velocity per behaviour (Table 6).

Table 5. Details of all the whale sharks observed in the study, divided into short-term and long-term deployment types.

Shark ID	Shark Length (m)	Sex	Deployment Date (DD.MM.YY)	Deployment Time (HH:MM:SS)
Short-Term Deployments				
A-542	7.5	Male	08.06.20	09:29:10
A-1753	6	Male	13.05.21	09:29:00
A-900	7	Male	24.04.21	09:59:08
A-804	7.5	Male	11.06.20	10:32:25
A-1442	7	Male	09.05.21	09:31:24
A-1563	6	Male	06.05.21	09:39:50
A-1831	6	Male	07.06.20	09:52:00
A-1400	7	Male	12.05.21	09:34:03
Long-Term Deployments				
A-233	7.5	Male	13.05.21	13:46:00
A-1340	8	Male	26.04.21	13:06:13
A-542	7.5	Male	27.04.21	13:52:23
A-1714	8	Male	03.05.21	13:13:50
A-939	8	Male	14.05.21	13:40:00
A-686	6.5	Male	01.05.21	13:27:57
A-900	7	Male	24.04.21	14:05:00

Table 6. Summary statistics of behavioural characteristics including tag duration, duration of time spent at PPA_{min} per deployment and dive characteristics, calculated for all whale sharks and organised by behaviour.

Shark ID	Deployment Duration (DD: HH: MM)	PPA _{min} Duration (%)	Range of Depth Use (m)	Mean Depth (m)	Ascent		Level Travel		Descent	
					Mean Vertical Velocity (m/s ⁻¹)	Mean Pitch Angle (°)	Mean Vertical Velocity (m/s ⁻¹)	Mean Pitch Angle (°)	Mean Vertical Velocity (m/s ⁻¹)	Mean Pitch Angle (°)
Short-Term Deployments										
A-542	00:01:52	61	3.8 to 33.1	4.9±3.5	0.3 ± 0.05	21.0±5.5	-0.0002±0.01	0.3±1.7	-0.19±0	-15.03±0
A-1753	00:03:42	18.7	4.1 to 41.1	5.5±5.10	0.31 ±0.05	26.0 ±6.7	1.0e-05±0.008	-1.4 .8	-0.41±0.0	-22.0±0.0
A-900	00:03:58	42	2.9 to 35.6	3.5±2.6	0.26±0.07	20.3±2.78	-0.0007±0.01	-0.34±1.6	-0.1±0.0	-11.2±0
A-804	00:04:01	10.6	3.7 to 27.8	5.2±4.4	0.315±0.05	24.6 ±6.3	0.0006±0.007	-0.2±1.21	0.0	0.0
A-1442	00:04:03	20.8	4.4 to 66.3	6.3±6.9	0.28 ±0.08	20.7 ±10.2	0.002±0.013	-2.4±0.93	-0.4± 0.1	-28.6±13.1
A-1563	00:04:14	15.4	4.3 to 8.31	5.0±0.8	0.0	0.0	-0.002±0.014	0.04±1.01	-0.131±0.0	-11.05±0.0
A-1831	00:04:17	52	3.5 to 44.6	4.5±4.8	0.3±0.05	22.7 ± 4.2	-0.0009±0.009	-0.27±1.13	-0.64±0.0	-24.49±0.0
A-1400	00:04:33	29.1	4.7 to 38.5	6.9±5.54	0.301±0.05	21.6±4.7	9.2e-05 ± 0.013	-0.38±1.3	-0.3±0.0	17.39±0.0
Long-Term Deployments										
A-233	25:02:48	12.9	0.4 to 176.2	35.3±30.9	0.3±0.1	13.1±3.5	0.004 ± 0.02	0.71±4.0	-0.32±0.2	-15.7±6.5
A-1340	14:22:16	13.6	1.0 to 228.8	24.3±33.5	0.3±0.09	13.0±2.9	0.0007±0.02	-0.7±3.2	-0.24±0.16	-16.2±6.07
A-542	15:00:05	17.6	2.2 to 44.7	82.9±53.7	0.6±0	16.3 ±4.5	-0.0005±0.02	0.7 ± 4.7	-1.0±0.72	-14.6±3.7
A-1714	17:20:57	21.6	0.6 to 156.7	19.3±23.7	0.16±0.10	4.5±4.5	0.002±0.02	0.3±3.6	-0.3±0.3	-15.9±5.6
A-939	21:21:22	25.2	0.4 to 175.5	20.1±23.2	0.2±0.1	15.0±4.9	0.002±0.02	1.6±3.6	-0.2±0.2	-16.4±6.1
A-686	22:20:00	18.6	0.2 to 206.0	15.0±23.5	0.86±0.31	14.2±3.7	0.0003±0.02	0.2±3.3	-0.9±0.8	-16.9±6.3
A-900	39:22:56	19.6	0.5 to 173.4	27.2±27.8	0.14 ±0.07	15.1 ±3.7	-0.002±0.02	0.9±3.4	-0.2±0.16	-16.2±7.2

Mean PPA_{min}

In total, 106,052 incidences of PPA_{min} were recorded, 1,348 during short-term deployments (1.2 %), and 104,704 during long-term deployments (98.7 %), whilst the percentage of PPA_{min} recorded per tag deployment varied from 19% to 61%, with a mean of 25.2%. Across all PPA_{min} incidences, mean PPA_{min} was 0.013 g (± 0.010 SD), ranging from 2.41e-20 to 0.205 g. The duration of these incidences ranged for 10 to 136 s, with a mean of 27.6 s (± 23.7 SD). The distribution of PPA_{min} showed a unimodal, highly right-skewed density distribution that was best described as gamma (Appendix IV) (Figure 11), and non-parametric (Anderson Darling, $A = 5528.2$, $p < 2.2e-16$).

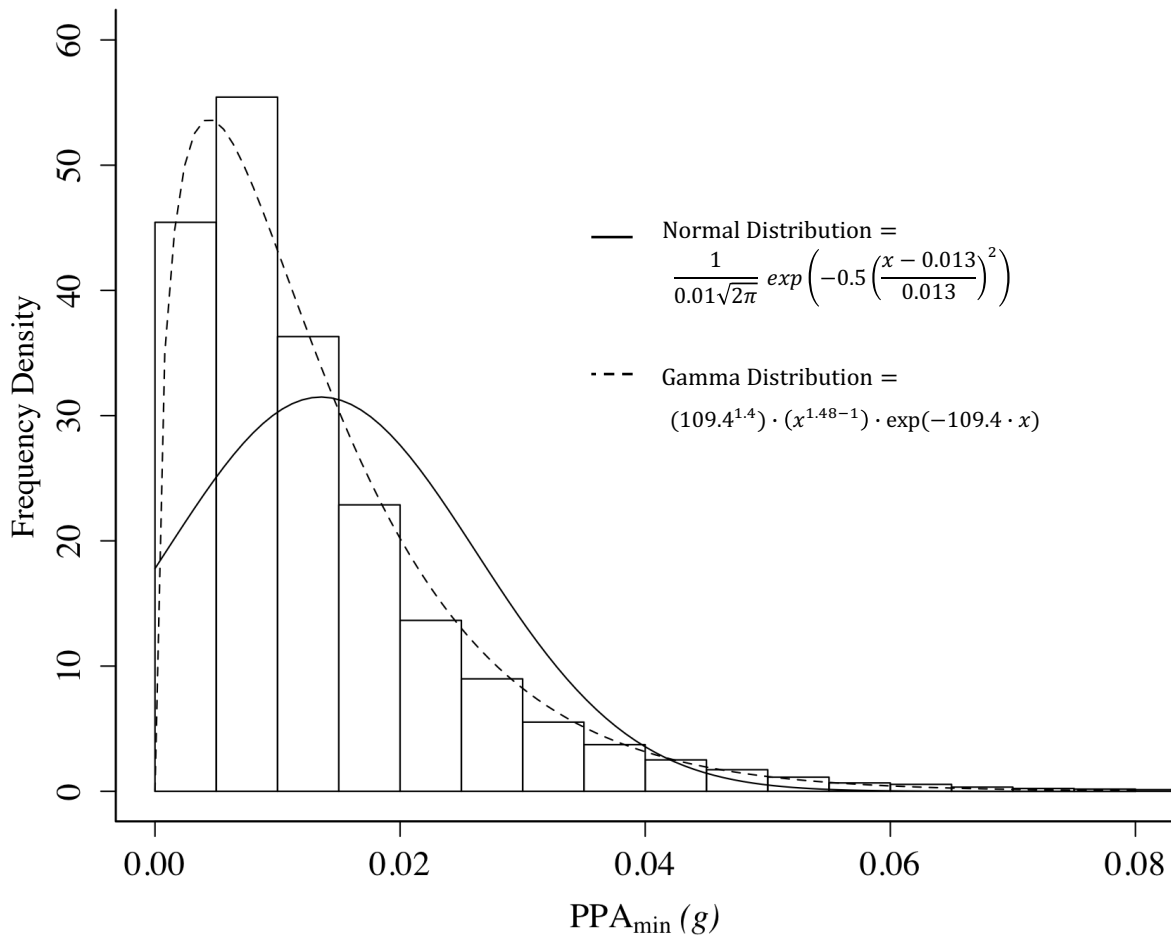


Figure 11. The relative density of total PPA_{min} of all sharks, comparing a normal distribution to a gamma distribution, to determine the best fit for the data.

Intraspecific Variation

Mean PPA_{min} was significantly different between deployment types; short-term or “tourism days” and long-term or “non-tourism days” (Mann-Whitney U Test; $W = 49640295$, $p < 2.2e-16$), decreasing from $0.017\text{ g} (\pm 0.011\text{ SD})$ for short-term deployments to $0.013\text{ g} (\pm 0.013\text{ SD})$ for long-term deployments (Figure 12).

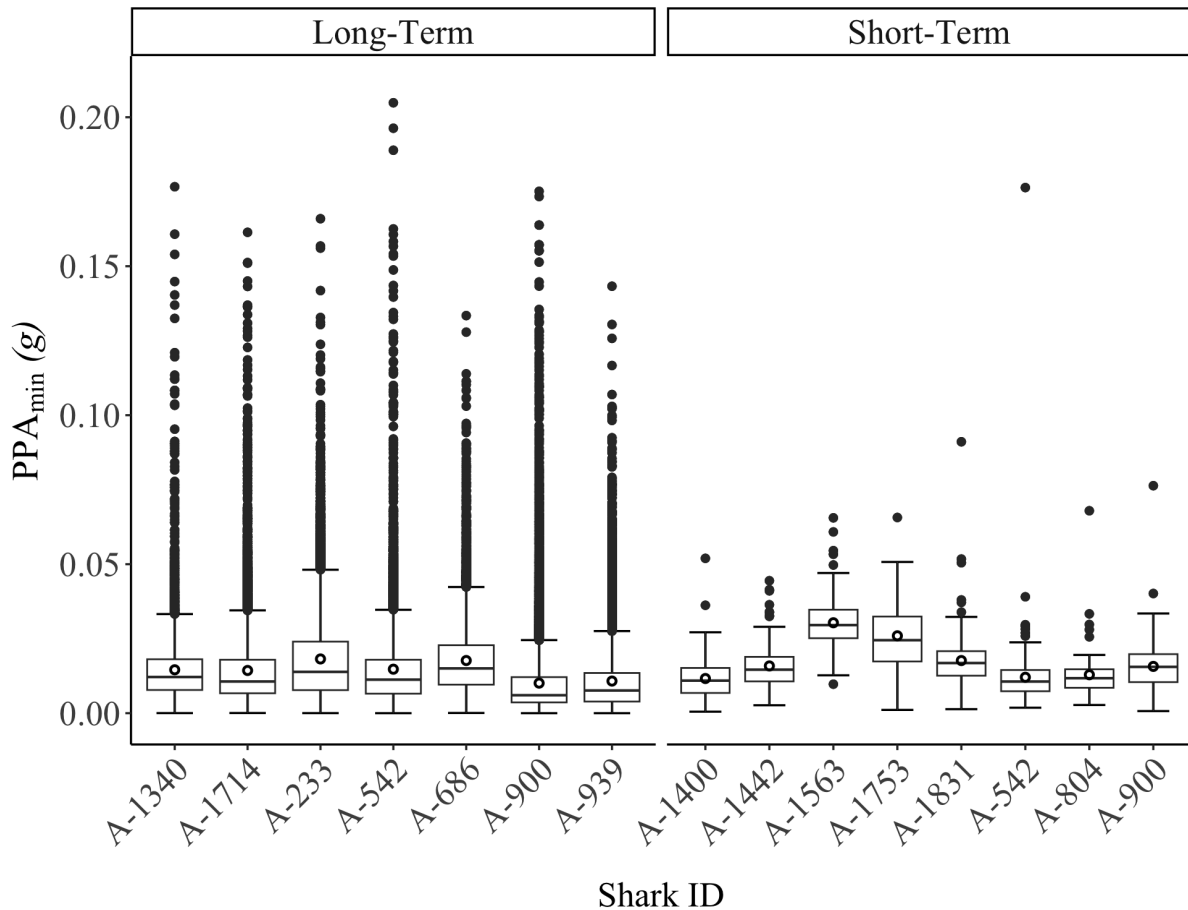


Figure 12. Box-and-whisker plot depicting the distribution of PPA_{min} per whale shark, divided by short-term or “tourism days” and long-term or “non-tourism days”, showing the large intraspecific variation. The box describes 50% of the data, with whiskers showing the top and bottom 25% intervals. The black centre line represents the median value, the clear circle represents the mean value, and black circles represent any outliers.

PPA_{min} also indicated a high level of intra-specific variation, with mean values ranging from $0.010\text{ g} (\pm 0.011\text{ SD})$ to $0.030\text{ g} (\pm 0.049\text{ SD})$ (Figure 12). Between deployment methods also indicated a significant level of intra-specific variation, but this was more marked between long-term deployments (Kruskal Wallis, $\chi^2 = 13391$, $DF = 6$, $p < 2.2e-16$) than short-term deployments ($\chi^2 = 461.58$, $DF = 7$, $p < 2.2e-16$).

10.2. Analysis of PPA_{min} by Behaviour

Categorisation by behaviour accounted for 90.41% (95,890) of incidences of PPA_{min} . PPA_{min} values for long term deployments varied significantly (Kruskal Wallis, $\chi^2 = 933.9$, $DF = 2$, $p < 2.2e-16$) (Figure 13). PPA_{min} was slightly higher during ascents (Mean $0.0161g \pm 0.0094$ SD) than during level travel (Mean $0.0160g \pm 0.021$ SD), whilst PPA_{min} for descents was considerably lower (Mean $0.012g \pm 0.011$ SD) (Figure 13). However, for short term deployments, PPA_{min} was instead highest during descents (Mean $0.028g \pm 0.021$ SD), followed by ascents (Mean $0.017g \pm 0.011$ SD), and lastly level travel (Mean $0.016g \pm 0.0096$ SD), but the variation was insignificant (Kruskal Wallis, $\chi^2 = 2.7$, $DF = 2$, $p < 0.256$).

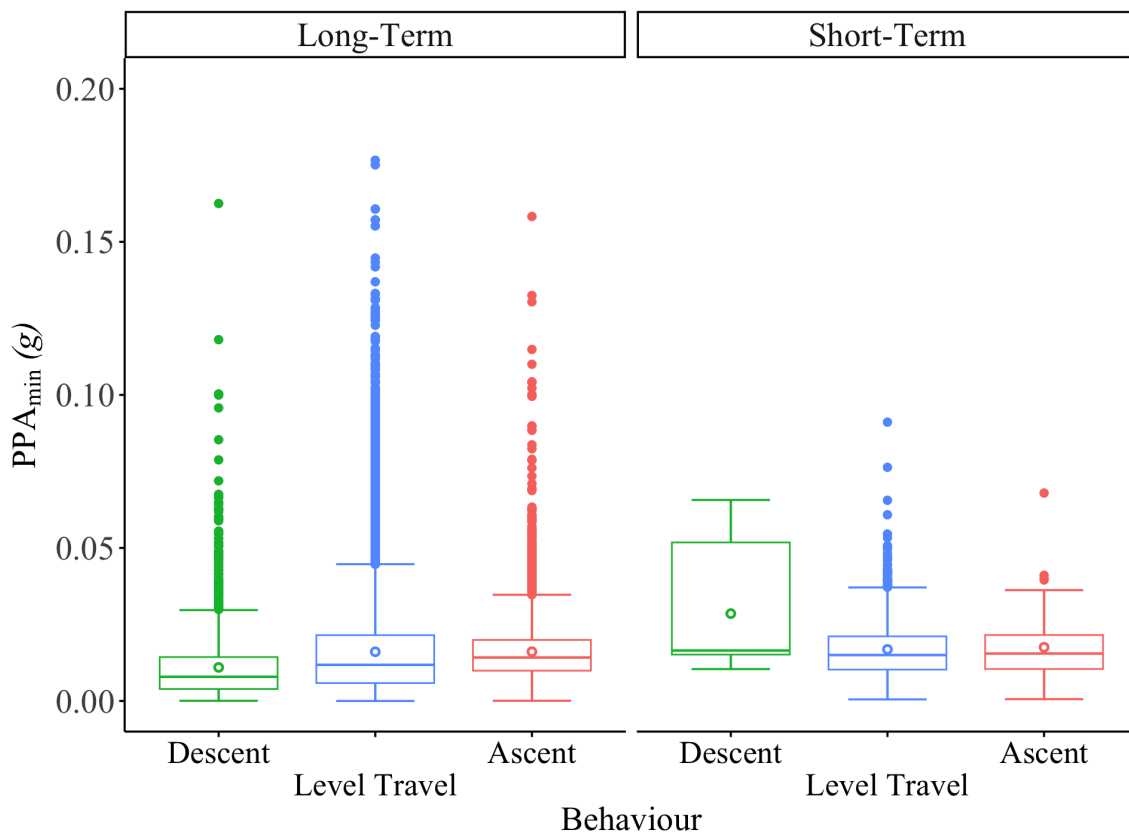


Figure 13. Box and whiskers plot of the distribution of PPA_{min} by behavioural/kinematic categories. according to Gleiss *et al.* (2010) and divided by short-term or “tourism days” and long-term or “non-tourism days”. The box describes 50% of the data, with whiskers showing the top and bottom 25% intervals. The black centre line represents the median value, the clear circle represents the mean value, and black circles represent any outliers.

Highlighted incidences of PPA_{min} during descents were indicative of a constant negative ($< -10^\circ$) pitch angle, accompanied by a substantial change in the vertical velocity (Figure 14). However, across all incidences of PPA_{min} , this behaviour was observed for the least amount of the total time (1.27 %). Incidences of PPA_{min} during ascents showed a similar pattern (pitch angle $> 10^\circ$) but were observed more frequently than descents (9.68 %) (Figure 15). PPA_{min} during level travel showed substantial variability, and multiple incidences were often highlighted over prolonged periods (Figure 16). This behaviour was thus observed for a considerably greater proportion of total PPA_{min} events (89.03 %).

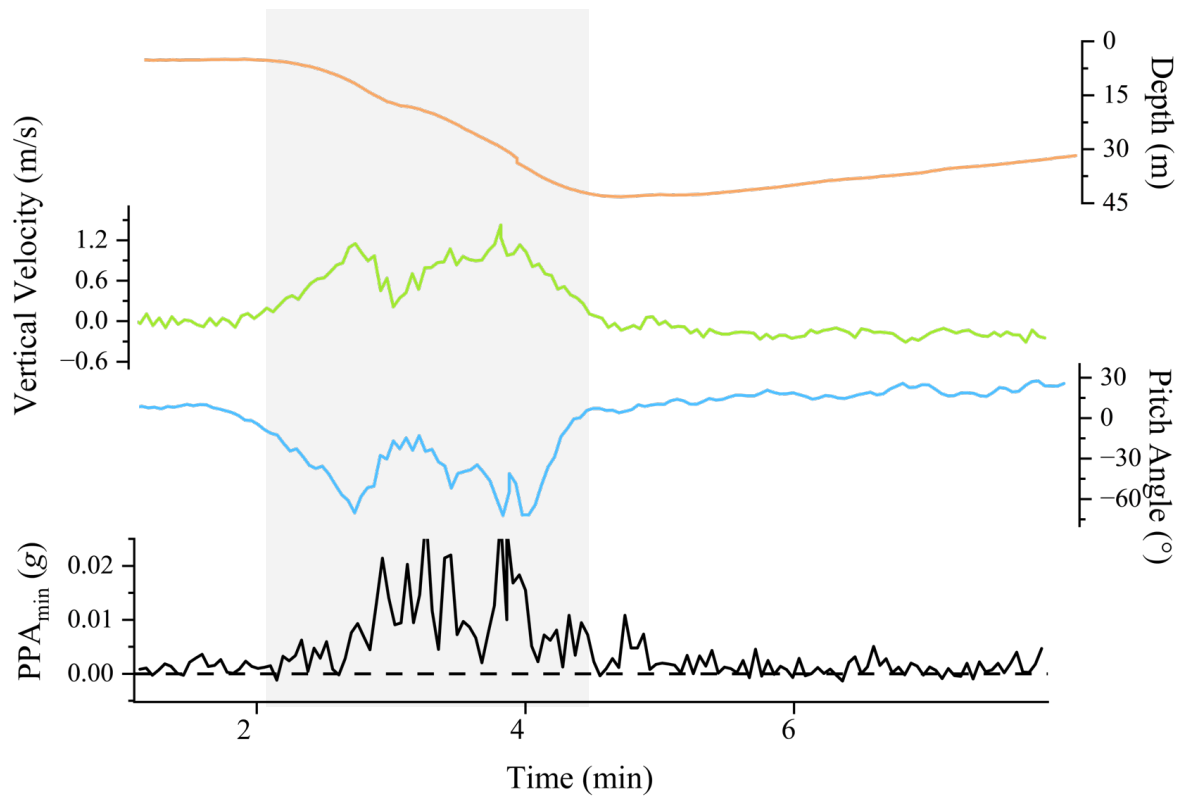


Figure 14. Example of incidences of PPA_{min} during the descent phase (highlighted in grey) of a typical dive, by a whale shark. Lasting around 2 minutes the descent starts at 5 m depth, before the animal travels down to 43 m. PPA_{min} has been highlighted during a substantial, constant decrease in the pitch angle and vertical velocity.

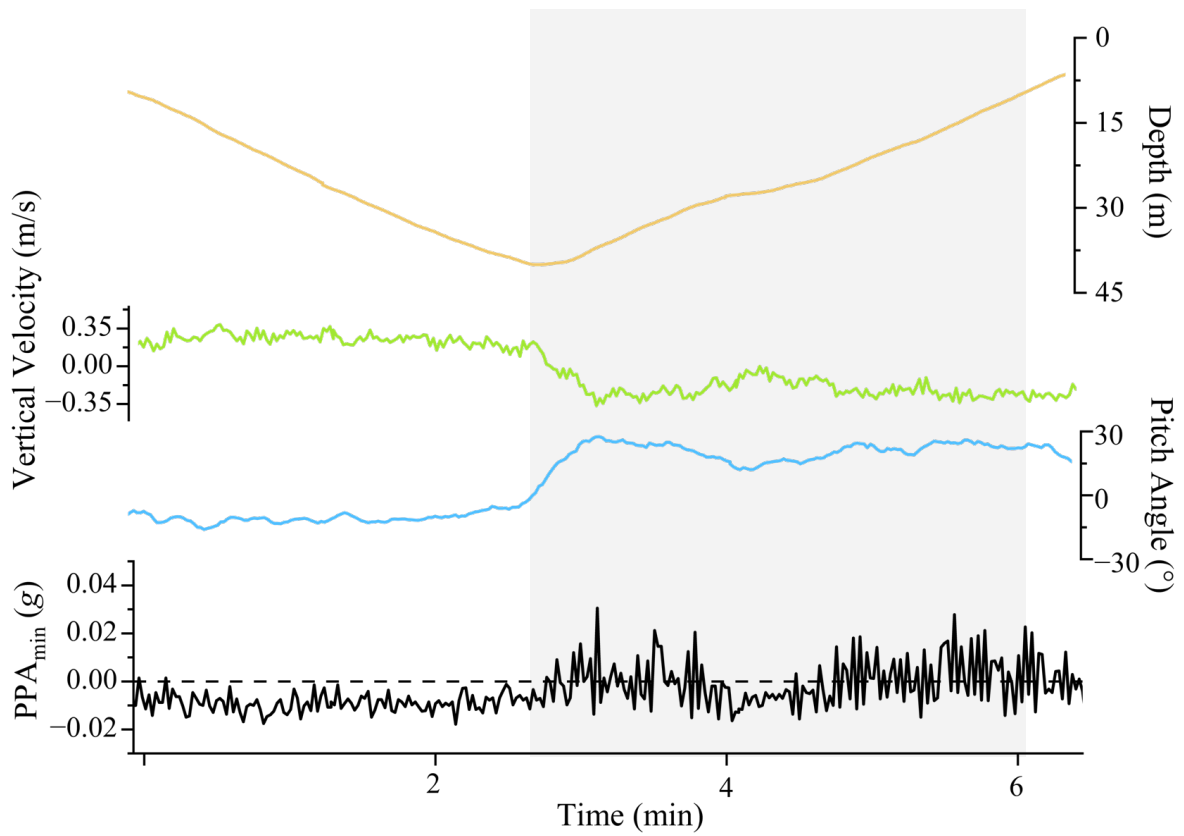


Figure 15. Example of incidences of PPA_{min} during the ascent phase (highlighted in grey) of a typical dive by a whale shark. Lasting around 4 minutes, the shark descends to around 43 m, then ascends back to 4 m. PPA_{min} has been highlighted during a substantial, constant increase in the pitch angle, and constant decrease in vertical velocity.

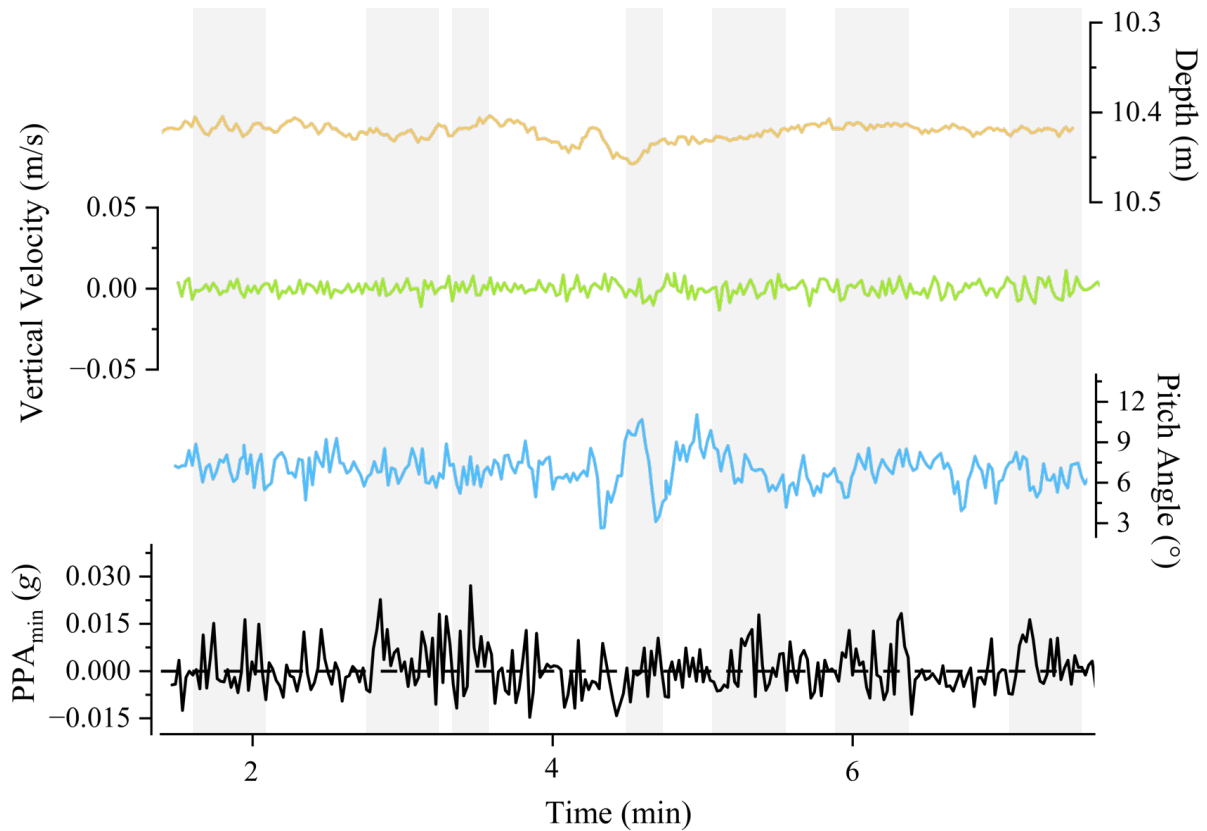


Figure 16. Example of incidences of PPA_{min} (highlighted in grey) recorded during level travel through the water column, by a whale shark swimming at around 10.4 m deep. Over an 8-minute period, seven incidences of PPA_{min} have been highlighted, indicative of a spike above 0 g for periods greater than 10 seconds.

GAMMs

A. Descent Model

Incidences of PPA_{min} during descents in the water column, occurred with varying pitch angles, ranging from -10 to -57.2 ° (Mean -16.06 ° \pm 6.45 SD), showing an almost linear, positive relationship with steeper descent angles (GAMM, $F = 28.85$, effective degree of freedom (edf) = 2.82, $p < 2e-16$) (Figure 17a).

Incidences of PPA_{min} were also observed over varying vertical velocities, ranging from -0.05 to -3.43 m/s⁻¹ (Mean -0.38 m/s⁻¹ \pm 0.49 SD), showing a significant, non-linear, but overall positive relationship with faster vertical movement (GAMM, $F = 5.91$, edf = 5.65, $p < 2e-16$) (Figure 17b).

Movement paths were predominantly straight (Mean 0.0075 ± 0.041 SD) and PPA_{\min} showed no significant increase or decrease with increasing tortuosity (GAMM, $F = 0.67$, $edf = 1$, $p = 0.41$) and showed no interactive effect with vertical velocity (GAMM, $p = 0.98$, $F = 0.009$, $edf = 1.854$) (Figure 17c).

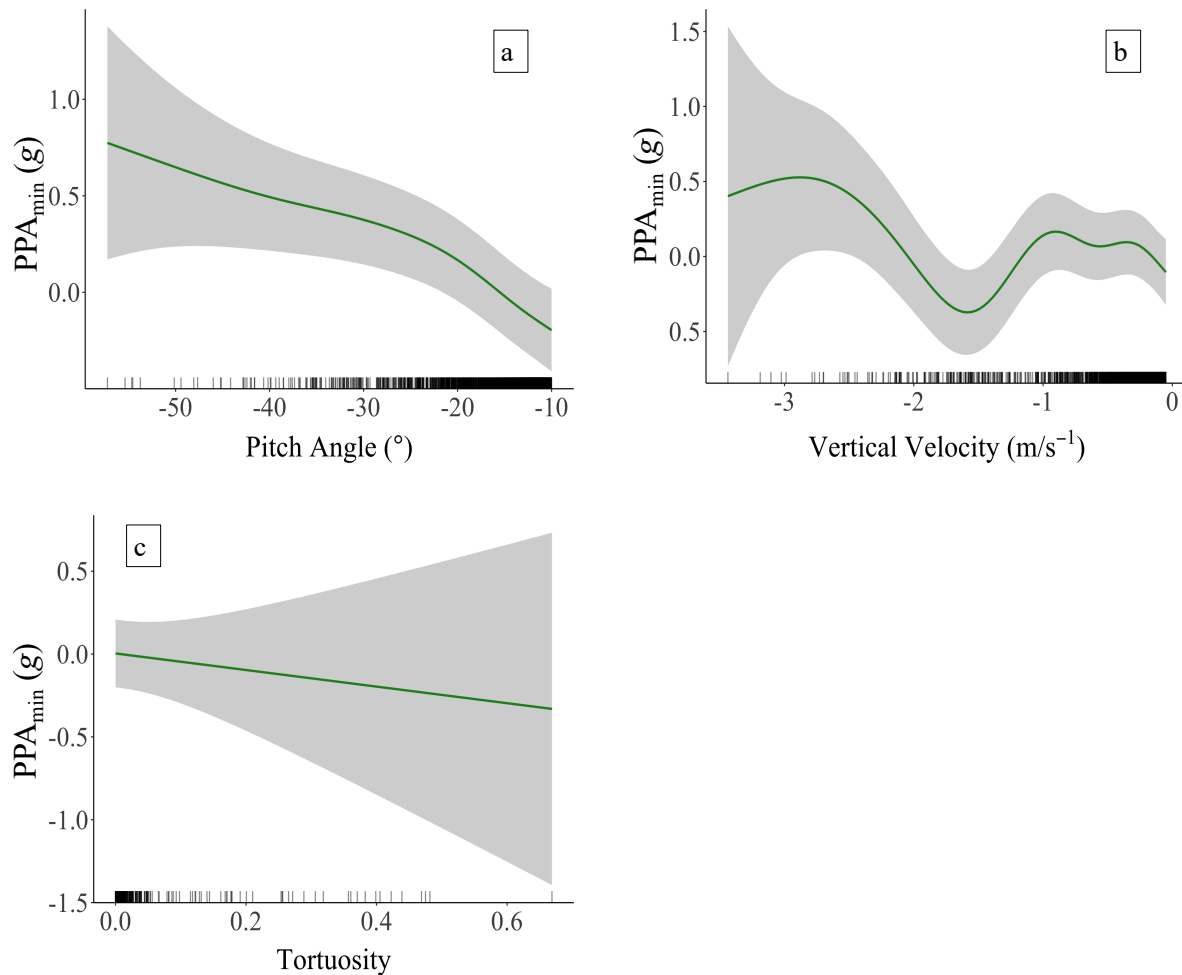


Figure 17. GAMM outputs for descent in the water column, showing the covariates: a. pitch angle, b. vertical velocity, and c. tortuosity. The X axis shows the values of the explanatory variables, and the Y-axis shows PPA_{\min} after smoothing of each variable, accounting for the non-linear relationship. The grey area represents the 95% confidence intervals around each smoothed term, and black ticks along the bottom (rug plot) represent the distribution of the covariates.

B. Level Travel Model

PPA_{\min} during level travel in the water column, showed a significant, non-linear relationship with the pitch angle (GAMM, $F = 11.40$, $edf = 5.28$, $p < 2e-16$) (Figure 18a).

PPA_{min} also showed considerable variability over a 24-hour cycle, showing a significant, non-linear relationship with the time of day (GAMM, $p < 2e-16$, $F = 19.78$, $edf = 7.06$). PPA_{min} gradually increased between at 0:00 h (0.012 ± 0.011 SD) and 10:00 h (0.013 ± 0.01 SD) but showed a clear peak at sunrise ($\sim 05:00$) of 0.012 g (± 0.011 SD) and sunset ($\sim 18:00$) of 0.018 g (± 0.015 SD) (Figure 18b).

PPA_{min} showed a significant, non-linear relationship with tortuosity (GAMM, $F = 21.53$, $edf = 7.65$, $p < 2e-16$) (Figure 18c). However, overall, movement paths during level travel were predominantly straight (Mean 0.006 ± 0.035 SD).

Lastly, PPA_{min} during level travel varied considerably throughout the water column (Figure 18d), showing a significant, non-linear, but overall negative correlation with increasing depth (GAMM, $F = 402.86$, $edf = 8.91$, $p < 2e-16$) (Figure 18d). PPA_{min} was substantially higher in the top 50 m of the water column, where the greatest proportion of time was spent (91.5 %) (during level travel). PPA_{min} decreased from 0.014 g (± 0.011 SD) at depths less than 50 m, to 0.0076 g (± 0.009 SD) at depths deeper than 50 m. Furthermore, the highest PPA_{min} value of 0.016 g (± 0.011 SD) was observed closest to the water surface (between 0.3 and 2 m), where 59.78 % of time was spent when swimming level.

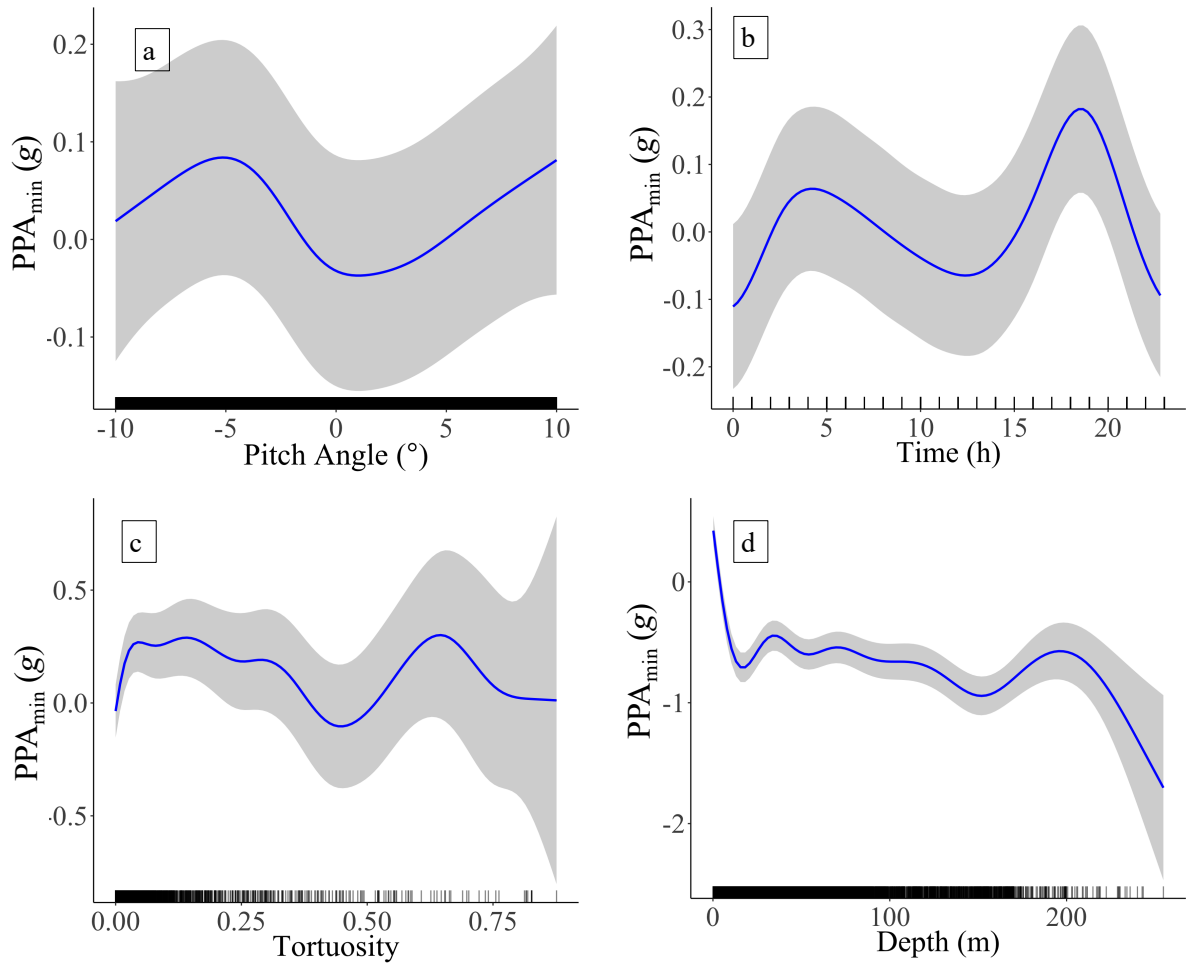


Figure 18. GAMM outputs for level travel in the water column, showing the covariates a. pitch angle, b. time, c. tortuosity, and d. depth. The X axis shows the values of the explanatory variables, and the Y-axis shows PPA_{min} after smoothing of each variable, accounting for the non-linear relationship. The grey area represents the 95% confidence intervals around each smoothed term, and black ticks along the bottom (rug plot) represent the distribution of the covariates.

C. Ascent Model

Incidences of PPA_{min} during ascent in the water column occurred at varying pitch angles, ranging from 10 to 41.7 ° (Mean 14.8 ° (± 4.19 SD)), showing a linear, positive relationship with steeper ascent angles (GAMM, $F = 34049$, $edf = 1$, $p < 2e-16$) (Figure 19a).

Incidences of PPA_{min} were also observed over varying vertical velocities, ranging from 0.05 to 2.37 m/s^{-1} (Mean 0.52 $m/s^{-1} \pm 0.35$ SD), slower than that of descents, showing a significant, non-linear, but overall positive relationship with faster vertical movement (GAMM, $F = 75.38$, $edf = 8.51$, $p < 2e-16$) (Figure 19b).

Whilst movement paths during ascents were predominantly straight (Mean 0.0048 ± 0.024 SD), PPA_{\min} showed a significant non-linear relationship with tortuosity (GAMM, $F = 11.26$, $\text{edf} = 7.01$, $p < 2e-16$), that showed a greatest increase between 0.3 and 0.5, but again showed no interactive effect with vertical velocity (GAMM, $p = 0.73$, $F = 0.315$, $\text{edf} = 2.05$) (Figure 19c).

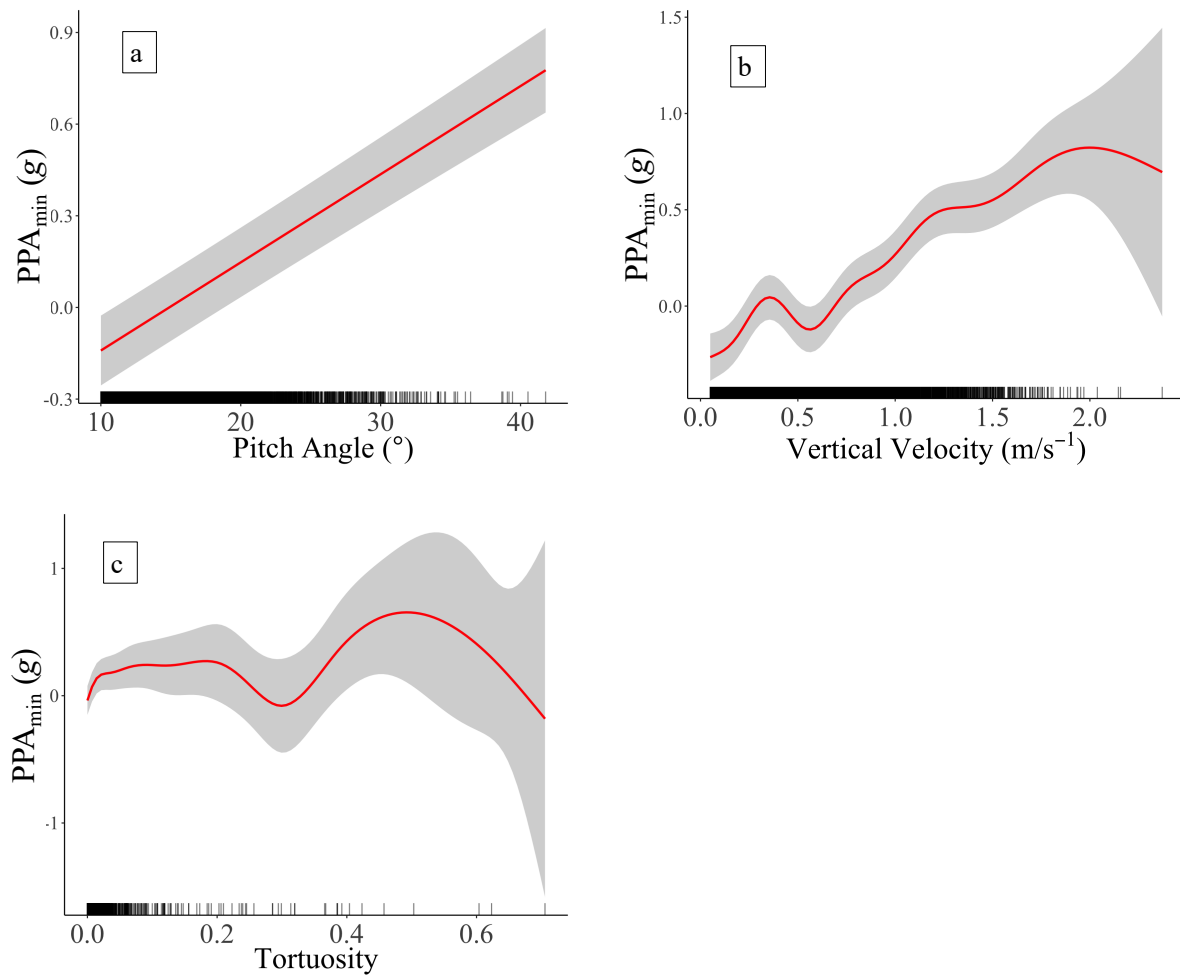


Figure 19. GAMM outputs for ascent in the water column, showing the covariates a. pitch angle, b. vertical velocity, and c. tortuosity. The X axis shows the values of the explanatory variables, and the Y-axis shows PPA_{\min} after smoothing of each variable, accounting for the non-linear relationship. The grey area represents the 95% confidence intervals around each smoothed term, and black ticks along the bottom (rug plot) represent the distribution of the covariates.

10.3 Observation of Instances of Considerable PPA_{min}

On several occasions, instances of exceptionally high PPA_{min} (> 0.1 g) were observed throughout the data, lasting between 5 - 10 s. All these instances coincided with substantial changes in body motions across the three axis (Fig 20). This occurred throughout the water column, with no appreciable change in vertical velocity or pitch angle.

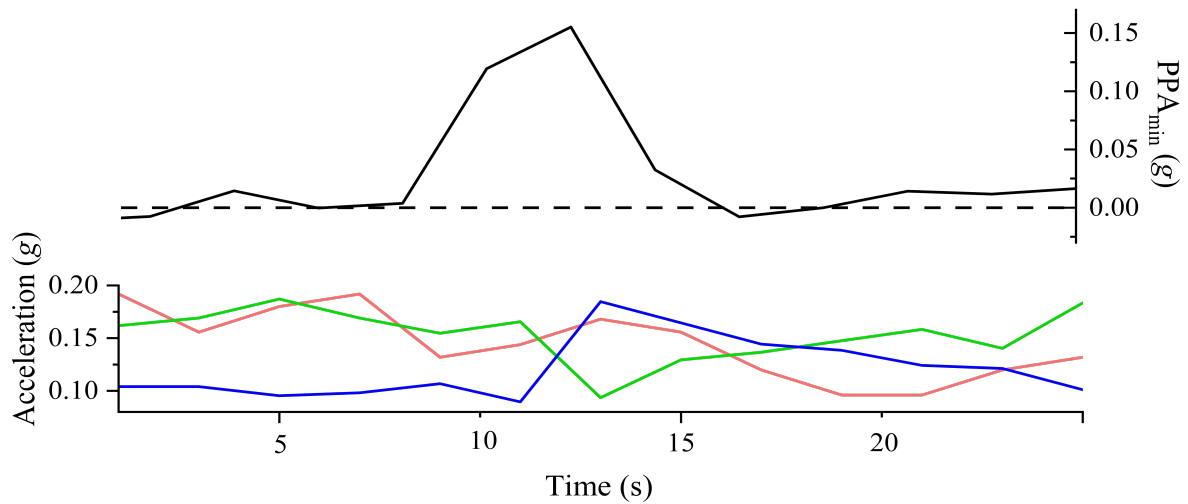


Figure 20. Examples of an instance of exceptionally high PPA_{min} , recorded during level travel near the surface (at 5 m), in which the whale shark performed no substantive change in pitch angle or vertical velocity but was accompanied by a substantive change in acceleration on the X (red), Y (green) and Z (blue) axes.

11. Discussion

Certain environmental scenarios are expected to cause whale sharks to deviate from seemingly prudent energy expenditure (Wilson *et al.* 2022). The energy expenditure and swimming efficiency of negatively buoyant animals directly depends on their drag and velocity, with drag increasing with the square of speed and power increasing with the cube of speed – see equation 2 and 3. This emphasises how factors like mouth opening and velocity influence energy use beyond the minimum required. The results demonstrated that PPA_{min} values during descents are likely due to increased speed, whilst PPA_{min} during level travel and ascents are likely due to increases in the drag coefficient when the whale shark opens its mouth to feed and/or from surface drag. Our results suggest that factors including tourism and research practices are also likely linked to recorded PPA_{min} values, providing insight for future studies regarding environmental cues and regulatory practices.

11.1 Conditions Leading to Appreciable PPA_{min}

Appreciable PPA_{min} values were observed across all three swimming behaviours (descent, level swimming and ascent) and factors that are responsible for this have been proposed.

A. Descent

Whale sharks typically move slowly, with ‘normal’ speeds recorded as ~3.9 km/hour (Eckert and Stewart, 2001), accompanied by low tail beat frequency (Cade *et al.*, 2020). However, as power to swim increases with the cube of the velocity (Altringham & Johnston, 1990), we would expect to see high PPA_{min} values as being likely linked to increases in speed (Wilson *et al.* 2022). Mean PPA_{min} for descents (0.028 g) during short-term deployments was substantially higher than any other behaviours observed. Flight behaviour is a common reaction to threat for fish (Zaccone, 2017). With whale sharks spending the greatest amount of time swimming at the surface, fast descent is expected to be an appropriate antipredator strategy (Martin, 2007). We suggest that the speed at which they descend, will depend on the severity of the threat as documented for multiple bird (Ydenberg & Dill, 1986) and fish species (Domenici, 2010). Whilst pitch angle and vertical velocity for descent remained relatively continuous across sharks, we recorded PPA_{min} values as high as 0.163 g for descent, suggesting a high-speed perception to a severely threatening situation. As such, high PPA_{min} values during descent are particularly informative.

Evidence of predation of whale sharks at Ningaloo has been recorded from large predatory species, such as tiger sharks (*Galeocerdo cuvier*), and orcas (*Orcinus orca*) (Fitzpatrick *et al.*, 2006). Whilst little is known about antipredatory behaviours of whale sharks (Martin, 2007), the principal strategy observed is banking, whereby whale sharks roll and present their backs towards a threat (Quiros, 2007). This behaviour would be accompanied by a substantial shift on the sway (y) axis, which was not detected in the data.

Data collected during short-term deployments, or “tourism days”, showed a higher mean PPA_{min} value of 0.017 g, compared to 0.013 g during long-term “non-tourism days” deployments, suggesting the higher PPA_{min} was caused by an overall disturbance. Unlike other tourism destinations, such as Thailand, Madagascar, Mozambique and Indonesia (Ziegler & Dearden, 2021), Ningaloo Reef is highly regulated by the Western Australian State Government (1993) that limits swimmers, boats and proximity to the whale sharks (Reynolds., *et al* 2024; Davis *et al.*, 1997). Despite this, disturbance from boats, snorkellers, and divers, has been widely recorded (Taylor, 2007; Speed *et al.*, 2008; Womersley *et al.*, 2022). It could therefore be suggested that this disturbance was directly due to the presence of tourists (Reynolds., *et al* 2024) or the proximity to the research vessel (Gunn *et al.*, 1999), thus causing the energetically expensive rapid descents. However, this concurs somewhat with previous studies that have shown albeit minimal, increase in VeDBA values in swimming whale sharks exposed to snorkelling tourists (Barry *et al.*, 2023).

Given their large size and low energy intake rates, it is appropriate that whale sharks should be particularly cautious about “overspending” their energy budget (Meekan *et al.*, 2015). The extent of tourism should therefore be carefully monitored with respect to sustained rises in PPA_{min}. Additionally, following a whale shark with a research vessel, should potentially be conducted with further ethical consideration to minimise disturbance, as prolonged tracking could be contributing to the unnecessary expenditure.

The degree to which externally attached devices alters whale shark behaviour can generally be categorised into two main effects: the initial trauma with any behavioural changes from the attachment and handling until the animal acclimates (Sundström, 2002), and the lasting impact of the increased drag (Gleiss *et al.*, 2009; Grusha & Patterson, 2018). The increased values of PPA_{min} during short-term deployments may therefore also reflect an initial “skittish” reaction to the tag – in addition to the disturbance from the research vessel and tourists

(Jepson *et al.*, 2015). Over time, the whale shark becomes accustomed, leading to the reduction in PPA_{min} and further suggesting the tag is not having a substantial impact on the whale sharks overall drag coefficient - owing to the small cross-sectional surface area of the tag-package relative to the size of the shark (Gleiss *et al.*, 2009; Bannasch *et al.*, 1994). For short-term deployments, this may suggest an inaccurate representation of the general mean behaviour in DBA-based metrics, as they do not account for this acclimation period. Furthermore, the discomfort associated raises ethical concerns regarding the use of externally attached tags for a short period of data collection. Given the importance of tagging for whale shark research (Hammerschlag *et al.*, 2014), future studies would benefit from a quantification of the impacts of the tagging procedure and behavioural changes to not only increase confidence that data is representative, but that minimal physiological cost is incurred by the animal (Gleiss *et al.*, 2009).

B. Level Travel

Overall, P_{min} for horizontal travel is generally expected to be the same at all depths, except when sharks are within 2.5 body diameters of the water surface. Here, like all animals, they are subject to additional drag in the form of “surface drag”, whereby animals inevitably create small waves, incurring increased drag, even when fully submerged (Alexander, 2003). The results supported this, with PPA_{min} substantially higher at the surface (0.3 – 2 m depth). In total, whale sharks spent 59.78 % of the total time in this region, so the expectation is that the surface drag is an appreciable energetic component of their daily energy expenditure. Whales sharks are known to occasionally feed at the water surface (Eckert & Stewart, 2001; Nelson & Eckert, 2007; Brunnschweiler *et al.*, 2009; Motta *et al.*, 2010; Cade *et al.*, 2020). However, given the increased energetic costs of such surface swimming, it is interesting to consider why whale sharks might swim near the surface, when not for feeding. Current hypotheses suggest possible trade-offs for short-term optimality, such as navigation (Klimley *et al.*, 2001), thermoregulation (Thums *et al.*, 2013; Tyminski *et al.*, 2015) or scanning the water column for prey encounters (Gunn *et al.*, 1999), although these remain speculative.

The literature presents a wide variety of whale shark feeding behaviours, but there is significant inconsistency in their characterisation (Nelson & Eckert, 2007; Motta *et al.*, 2010; Ketchum *et al.*, 2012; Cade *et al.*, 2020; Dove & Pierce, 2022). Despite this, three main feeding behaviours can be identified.

Whale sharks can feed ‘Passively’ (termed ‘continuous ram feeding’ (Nelson & Eckert, 2007)), by swimming slowly with their mouths open so water can pass through the mouth and over the gills, filtering the plankton (Taylor, 2007). This will increase the drag (by increasing the drag coefficient ‘Cd’) and may incur additional drag due to the flow of water through the gills and gill rakers (Cade *et al.*, 2020; Motta *et al.*, 2010). Hence, it has been suggested that variations in energy expenditure (and hence PPA_{min}) will be due to different degrees of mouth openings (Gleiss *et al.*, 2010). Whilst, it has been proposed that whale sharks may passively feed during descent glides to reduce this energetic cost of the added drag (Gleiss *et al.*, 2010), feeding is most predominantly characterised by slow forward locomotion (Nelson & Eckert, 2007; Motta *et al.*, 2010; Dove & Pierce, 2022), as observed during level travel.

The act of “active” feeding (termed ‘dynamic suction feeding’ or ‘surface ram filter feeding’ (Nelson & Eckert, 2007; Dove & Pierce, 2022)), occurs where whale sharks swim purposefully forward, actively taking in large gulps of water before closing their mouths for a few seconds, and then expelling the water out of their gill slits (Nelson & Eckert, 2007; Ketchum *et al.*, 2012). The mouth-opening (leading to higher drag) combined with the greater propulsion, is certainly likely to increase PPA_{min} (Ketchum *et al.*, 2012; Gudger, 1941). Such active feeding is also known to occur at the surface, where whale sharks may even actively gulp water from the incoming waves (Figure 18d). Gulping at the surface is expected to increase drag and hence travel costs (Ketchum *et al.*, 2012). However, observations of this behaviour are rare at Ningaloo (Gleiss *et al.*, 2013) and would most likely coincide with the dorsal fin breaking the surface, bringing with it confounds for the use of DBA as a metric for energy expenditure (Reynolds *et al.*, 2017). Despite the reduced swimming efficiency of feeding for sustained periods of time, whale sharks require relatively low prey intake to meet their feeding costs, largely due to their substantial body size, helping justify these associated higher costs (Yowell & Vinyard, 1993; Cade *et al.*, 2020).

For many free-ranging predators, including thresher sharks (*Alopias vulpinus*) and blacktip reef sharks (*Carcharhinus melanopterus*), movement patterns often alternate between tortuous and longer, straight-line paths as part of prey-search strategies (Papastamatiou *et al.*, 2011; Fallows *et al.*, 2013). Since turning requires more energy than straight-line travel (Wilson *et al.*, 2013), this facet of behaviour will also tend to increase PPA_{min} . As direct observations of whale shark feeding behaviours, such as an open mouth, were not possible for this study, tortuosity has been interpreted as the most parsimonious indicator of feeding

(Cade *et al.*, 2020). However, increased track tortuosity has been attributed to other behavioural functions, namely predator avoidance in species such as Atlantic Tarpon (*Megalops atlanticus*) that move slower and more convoluted paths underneath vegetation and faster in risky open habitats (Hammerschlag *et al.*, 2012). However, such behaviours are characteristic of shallow, structured environments and are unlikely to apply to the pelagic whale shark. Tortuosity has also been shown to increase in response to human disturbances, with the presence of tourists prompting more frequent directional changes in whale sharks (Montero-Quintana *et al.*, 2018; Reynolds, 2024). Despite this, no significant difference in tortuosity was detected between deployment types in this study (Appendix IX). Other potential influences of movement patterns, such as courtship and copulation, have not yet been documented in whale sharks and therefore also cannot be linked to track tortuosity (Martin, 2007).

A final form of feeding behaviour is known as “lunge-feeding”, identified by Montero-Quintana *et al.* (2021), where whale sharks encircle an aggregation of prey, such as anchovies or krill, before surging through it (Taylor & Pearce, 1999). This behaviour occurs with the mouth open (thus increasing drag) and greatly increased speed (which also increases the required swim power, which increases with the cube of the velocity – see equation 3), as they accelerate through the prey. It is notable that presumed incidences of such encircling behaviour in the data with high PPA_{min} were also accompanied by greater track tortuosity (Figure 18c). This makes intuitive sense, because aggregations that induce lunge feeding are highly localised (Montero-Quintana *et al.*, 2021).

Whilst lunge feeding appears exceptionally energetically costly, a major benefit is that whale sharks can capture a large abundance of large mobile prey, and exploit a greater diversity of functional groups, helping to offset the metabolic cost (Dove & Pierce, 2022). However, overall mean tortuosity throughout the tracks was low, suggesting a preference for predominantly straight travel paths (Reynolds, 2024), and highlighting the rarity this feeding behaviour (Montero-Quintana *et al.*, 2021). Where high PPA_{min} values coincide with high tortuosity, it may provide insight into areas where lunge feeding is most likely to be occurring, indicating potential hotspots of profitable prey abundance (Liu *et al.*, 2015), an idea of particular interest for species working on an energetic “knife’s edge” (Sims, 1999).

PPA_{min} was highest in the top 50 m of the water column, decreasing with increasing depth beyond this point. A preference for feeding in shallow waters by whale sharks has been widely documented by biotelemetry studies (Motta *et al.*, 2010; Tyminski *et al.*, 2015; Rowat & Gore, 2007; Taylor, 2007). At Ningaloo, the study site coincides with warmer surface waters associated with nutrient-rich upwellings, forming large planktonic aggregations (Hanson & McKinnon, 2009; Copping *et al.*, 2018). Therefore, the top 50 metres of the water column represents a localised area of productivity (Rowat & Gore, 2007), which would explain why whale sharks in this study spent 91.5 % of their time swimming horizontally, at this depth (Mori, 1998). However, whale sharks are certainly not limited to this region (Figure 18c), being documented as exploiting prey throughout the water column, particularly when surface prey densities are suboptimal (Rowat & Gore, 2007).

Prey availability, as a function of depth, varies with the time of day for a multitude of species (Mehner, 2012), so it is not surprising that it influences whale shark feeding behaviours (Gleiss *et al.*, 2013). Planktivorous Diel Vertical Migrations (DVM) occur with changes in ambient light levels, regulating hourly vertical movements. Observation of depth usage varied throughout the 24 h cycle, but sharks were overall found shallower during the day (Appendix VIII), likely reflecting a reverse DVM pattern (Graham *et al.*, 2005; Gleiss *et al.*, 2013; Tyminski *et al.*, 2015). However, vertical movements by whale sharks are highly variable depending on the local prey distribution (Graham *et al.*, 2005) and could be governed by additional factors such as thermoregulation (Carey *et al.*, 1990). Mean PPA_{min} steadily increased throughout the day, and most notably peaked at 05:00 h and 18:00 h (Figure 18b). Planktonic accumulations into shallower waters at night is thought to reduce predation pressure from visual predators (Sims *et al.*, 2005; Shepard *et al.*, 2006; Motta *et al.*, 2010). In response to this movement, whale shark foraging is often highest at sunrise and sunset, attributed to active feeding on large aggregations of tropical krill swarms, causing the increase in PPA_{min} at sunset (Taylor, 2007; Gleiss *et al.*, 2013).

C. Ascent

Mean PPA_{min} was highest during upward travel through the water column for long-term deployments (0.0161 g), representing a substantial deviation from P_{min}. As flight behaviour is better characterised by descent, we suggest that higher PPA_{min} during ascent is more likely to be indicative of feeding activity, either active, passive or lunge, depending on the localised abundance of prey (Tyminski *et al.*, 2015; Cade *et al.*, 2020)

11.2. Instances of Exceptionally High PPA_{min}

The highest incidence of PPA_{min} observed in this study was 0.205 g, over seven times greater than the overall average of 0.03 g. Instances of such exceptionally high PPA_{min} values would be so metabolically costly, that it is worth considering other behavioural or environmental factors to justify them.

Inspection of PPA_{min} showed occasional sharp peaks, typically lasting no more than 10 s, but picked up in the data as substantive changes in the overall body motion (acceleration channels X, Y and Z) (Wilson et., 2022). However, rather than being due to high-speed swimming, this behaviour has been attributed to ‘gill clearing’, whereby whale sharks close their gill slits and “cough”, flushing water and particles from their mouths (Nelson & Eckert, 2007), creating a body shudder stemming from the underbelly (Taylor, 2007). This is likely picked up as a 'vibration' by the accelerometers on the dorsal fin, and presumably does not align with particularly high metabolic costs.

Interference from other marine animals during archival tag deployments can occur when predators attempt to consume or interact with the tagging equipment, leading to distorted movement data being recorded (Tolentino *et al.*, 2017). This phenomenon may include the ingestion of the whole tagged fish, such as has been documented for Atlantic salmon *Salmo salar* (Lacroix, 2014) and albacore (*Thunnus alalunga*) (Cosgrove *et al.*, 2015). However, this has also been documented for predatory fish, such as white marlin (*Tetrapturus albidus*), biting the tag (Kerstetter *et al.*, 2004). We consider that exceptionally high PPA_{min} values may indeed be due to interference from other fish, rather than representing the true whale sharks' movements.

11.3 Intraspecific variation

PPA_{min} in this study showed appreciable intra-specific variation, possibly due to variations in shark size (Wilson., *et al* 2022) but it is unclear how this relates to PPA_{min} derived from acceleration metrics because no explicit study has yet related VeDBA signals to mass/size in any species. However, difficulties with DBA metrics have been noted in 'large' animals such as whales (Martín López., *et al* 2022). In this study, there was relatively little difference in animal size (Table 5) so size considerations may not play a substantive role.

11.4 Recommendations for Future Research

The value in determining the circumstances for PPA_{\min} events depends on the quantity of data that can be inspected (Wilson *et al.* 2022). Data collection was limited to the duration of the tag's deployment, dictated by battery life, the risk of damage, and recovery (Mate *et al.*, 2016; Hart *et al.*, 2021; Holten *et al.*, 2021). Short-term tags are therefore especially constrained, with a maximum deployment of under 5 hours (Reynolds *et al.*, 2024).

This study presents a dataset restricted to one location, with no appreciable variation in the environment or ecosystem. Whale Sharks are migratory and move between Australia, Indonesia and New Zealand before returning to Ningaloo annually (Wilson *et al.*, 2005, Sleeman *et al.*, 2010, Sequeira *et al.*, 2013; Reynolds *et al.*, 2022). Ningaloo Reef is bathymetrically constrained, with the deepest depth recorded by the whale sharks in this study as 228.8m and 980 m previously (Wilson *et al.*, 2005). However, in the Mozambique Channel, deep diving behaviour has been recorded, with whale sharks entering the Bathypelagic zone and reaching a maximum depth of 1286 m. Whilst the function of deep dives remains largely unknown, a deeper vertical search for prey opportunities and thermoregulation after prolonged surface feeding have been suggested (Brunnschweiler *et al.*, 2009; Araujo *et al.*, 2020). To generalise findings in tagging studies, longer-term deployments across different locations would be highly advantageous in capturing a wider range of environmental cues.

Due to the large sexual segregation of whale sharks at Ningaloo Reef, the possibility of sampling bias towards juvenile males cannot be excluded (Meekan *et al.*, 2020). Females are larger, occurring offshore at Ningaloo where they do not take advantage of the increased productivity of shallower waters (Ketchum *et al.*, 2012; Meekan *et al.*, 2020). Difference in resting metabolic rates, feeding behaviours and disturbance levels across habitats will likely be reflected in both P_{\min} and PPA_{\min} . Furthermore, very little is known about courtship and mating behaviours of whale sharks (Martin, 2007; Norman & Stevens, 2007). However, in other species of shark such as tiger sharks (*Galeocerdo cuvier*), the act of reproduction and subsequent gestation period is very energetically costly (Hammerschlag *et al.*, 2018). Deployments of tags on female whale sharks and the application of PPA_{\min} would therefore also be highly advantageous in identifying poorly researched behaviours and understanding the wider scope of whale shark energetics.

Whilst the large body size of whale sharks does provide a level of thermal inertial (Nakamura *et al.*, 2020), ocean warming because of anthropogenic climate warming will directly challenge the energetic balance of whale sharks (Reynolds, *et al.*, 2025). The metabolic rates of organism's scales allometrically with body mass, causing a greater increase in the absolute energetic requirements for larger species with ocean warming, likely reflecting overall higher P_{\min} values (Gillooly, 2001). Additionally, it has been estimated that the mean daily energetic requirement for a 7m whale shark in Australian waters will rise from $\sim 18,100 \text{ kJ day}^{-1}$ under current temperatures, to a projected $\sim 19,700 \text{ kJ day}^{-1}$, equating to an increase in zooplankton from 13.4 kg to 14.5 kg (Reynolds, *et al.*, 2024). However, increased metabolic demand may not be met by feeding, with mean global zooplankton biomass estimated to fall by 14% this century (Kwiatkowski *et al.*, 2018). With an increase in foraging effort to sustain metabolic demand, an increase in PPA_{\min} would also be expected. Future research should focus on developing the relationship between modelled energetic budgets (Reynolds, *et al.*, 2024), thermal physiology (Nakamura *et al.*, 2020) and the effect of behavioural compensation strategies (Araujo *et al.*, 2020) in whale sharks to better predict how these changes may impact the long-term survival and distribution of whale sharks.

Large planktivorous sharks are considered to operate under an energetic “knife edge” (Sims, 1999), where small changes in energy expenditure can have disproportionately negative effects on their energy budget (Meekan *et al.*, 2015). Due to their large size, slow growth, and late maturation (Wintner, 2000; Rowat & Brooks, 2012), whale sharks are particularly susceptible to overexploitation (Dove & Pierce, 2022). This is of particular concern as the species is listed as Endangered and Largely Depleted by the IUCN (Dove & Pierce, 2022). The study of energetically expensive behaviours (as manifest by PPA_{\min}) is therefore particularly important, especially where they result from human activities. As a result, this research provides essential insights into energetic budgets that may limit the whale shark's capacity to cope with increasing anthropogenic stressors, necessary to inform targeted conservation strategies and guide the development of regulatory practices.

12. Conclusions

Energy expenditure and swimming efficiency in whale sharks is closely tied to the power required for movement through water, which is fundamentally regulated by the drag and speed. This study reveals significant variability in PPA_{min} expenditure across different swimming behaviours, caused by the interactive response of both environmental and physiological factors. As power usage increases with the cube of swim speed, values of high PPA_{min} likely correspond to speed increases, principally observed during rapid retreats down the water column. During ascent and level travel, we propose that high PPA_{min} values are due to an increase in the drag coefficient, which occur when the whale shark opens its mouth to feed and/or from surface drag. As this drag force increases with the square of the velocity (Altringham & Johnson, 1990), the effect of drag is greatly intensified when whale shark feed at increased velocities. The study's findings point to the importance of external factors, such as prey availability and sensitivity to human activity in influencing PPA_{min} and thus a whale shark's energy budget. We suggest that future research would largely benefit from longer and more varied deployments to capture a wider range of environmental influences, explore the impact of ocean warming on energetic budgets (Reynolds, *et al.*, 2024), and emphasise the importance of ethical considerations when handling whale sharks (Gleiss *et al.*, 2009).

13. References

- Alexander, R. M. (1990). Size, Speed and Buoyancy Adaptations in Aquatic Animals. *Integrative and Comparative Biology*, 30(1), 189–196. <https://doi.org/10.1093/icb/30.1.189>
- Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton University Press.
- Altringham, J., & Johnston, I. A. (1990). Modelling Muscle Power Output in a Swimming Fish. *Journal of Experimental Biology*, 148(1), 395–402. <https://doi.org/10.1242/jeb.148.1.395>
- Andrzejaczek, S., Gleiss, A. C., Lear, K. O., Pattiaratchi, C. B., Chapple, T. K., & Meekan, M. G. (2019). Biologging Tags Reveal Links Between Fine-Scale Horizontal and Vertical Movement Behaviors in Tiger Sharks (*Galeocerdo cuvier*). *Frontiers in Marine Science*, 6. <https://doi.org/10.3389/fmars.2019.00229>
- Andrzejaczek, S., Mikles, C. S., Dale, J. J., Castleton, M., & Block, B. A. (2023). Seasonal and Diel Habitat Use of Blue Marlin Makaira Nigricans in the North Atlantic Ocean. *ICES Journal of Marine Science*, 80, 1002–1015. <https://doi.org/10.1093/icesjms/fsad020>
- Andrzejaczek, S., Vély, M., Jouannet, D., Rowat, D., & Fossette, S. (2021). Regional Movements of Satellite-tagged Whale Sharks *Rhincodon Typus* in the Gulf of Aden. *Ecology and Evolution*, 11(9), 4920–4934. <https://doi.org/10.1002/ece3.7400>
- Araujo, G., Labaja, J., Snow, S., Huveneers, C., & Ponzo, A. (2020a). Changes in Diving Behaviour and Habitat Use of Provisioned Whale sharks: Implications for Management. *Scientific Reports*, 10(1). <https://doi.org/10.1038/s41598-020-73416-2>
- Arkwright, A. C., Archibald, E., Fahlman, A., Holton, M. D., Crespo-Picazo, J. L., Cabedo, V. M., Duarte, C. M., Scott, R., Webb, S., Gunner, R. M., & Wilson, R. P. (2020).

Behavioral Biomarkers for Animal Health: A Case Study Using Animal-Attached Technology on Loggerhead Turtles. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00504>

Arzoumanian, Z., Holmberg, J., & Norman, B. (2005). An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *Journal of Applied Ecology*, 42(6), 999–1011. <https://doi.org/10.1111/j.1365-2664.2005.01117.x>

Australian Bureau of Statistics. (2021, July 20). Digital Boundary Files | Australian Bureau of Statistics. [www.abs.gov.au](https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/access-and-downloads/digital-boundary-files). <https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/access-and-downloads/digital-boundary-files>

Bannasch, R., Wilson, R. P., & Culik, B. (1994). Hydrodynamic Aspects of Design and Attachment of A Back-Mounted Device in Penguins. *Journal of Experimental Biology*, 194(1), 83–96. <https://doi.org/10.1242/jeb.194.1.83>

Barry, C., Legaspi, C., Clarke, T. M., Araujo, G., Bradshaw, C. J. A., Gleiss, A. C., Meyer, L., & Huveneers, C. (2023). Estimating the energetic cost of whale shark tourism. *Biological Conservation*, 284, 110164. <https://doi.org/10.1016/j.biocon.2023.110164>

Benhamou, S. (2007). How Many Animals Really Do The Levy Walk? *Ecology*, 88(8), 1962–1969. <https://doi.org/10.1890/06-1769.1>

Bidder, O. R., Walker, J. S., Jones, M. W., Holton, M. D., Urge, P., Scantlebury, D. M., Marks, N. J., Magowan, E. A., Maguire, I. E., & Wilson, R. P. (2015). Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. *Movement Ecology*, 3(1). <https://doi.org/10.1186/s40462-015-0055-4>

- Bone, Q., & Roberts, B. L. (1969). The Density of Elasmobranchs. *Journal of the Marine Biological Association of the United Kingdom*, 49(4), 913–937.
<https://doi.org/10.1017/s0025315400038017>
- Brown, D. D., Kays, R., Wikelski, M., Wilson, R., & Klimley, A. (2013). Observing the Unwatchable through Acceleration Logging of Animal behaviour. *Animal Biotelemetry*, 1(1), 20. <https://doi.org/10.1186/2050-3385-1-20>
- Brunnschweiler, J. M., Baensch, H., Pierce, S. J., & Sims, D. W. (2009). Deep-diving Behaviour of a Whale shark *Rhincodon Typus* during long-distance Movement in the Western Indian Ocean. *Journal of Fish Biology*, 74(3), 706–714.
<https://doi.org/10.1111/j.1095-8649.2008.02155.x>
- Burt de Perera, T., Holbrook, R. I., & Davis, V. (2016). The Representation of Three-Dimensional Space in Fish. *Frontiers in Behavioral Neuroscience*, 10, 40.
<https://doi.org/10.3389/fnbeh.2016.00040>
- Byrnes, E. E., Lear, K. O., Brewster, L. R., Whitney, N. M., Smukall, M. J., Armstrong, N. J., & Gleiss, A. C. (2021). Accounting for body mass effects in the estimation of field metabolic rates from body acceleration. *The Journal of Experimental Biology*, 224(7), jeb.233544. <https://doi.org/10.1242/jeb.233544>
- Cade, D. E., Levenson, J. J., Cooper, R., de la Parra, R., Webb, D. H., & Dove, A. D. M. (2020). Whale Sharks Increase Swimming Effort While Filter feeding but Appear to Maintain High Foraging Efficiencies. *Journal of Experimental Biology*, 223(11).
<https://doi.org/10.1242/jeb.224402>
- Carey, F. G., Scharold, J. V., & Kalmijn, Ad. J. (1990). Movements of Blue Sharks (*Prionace glauca*) in Depth and Course. *Marine Biology*, 106(3), 329–342.
<https://doi.org/10.1007/bf01344309>

- Compagno, L. J. V. (1986). *Sharks of the world. an Annotated and Illustrated Catalogue of Shark Species Known to Date*. 71(2), 295–295.
<https://doi.org/10.1002/iroh.19860710229>
- Cooke, S. J., Midwood, J. D., Thiem, J. D., Klimley, P., Lucas, M. C., Thorstad, E. B., Eiler, J., Holbrook, C., & Ebner, B. C. (2013). Tracking animals in freshwater with electronic tags: past, present and future. *Animal Biotelemetry*, 1(1), 5.
<https://doi.org/10.1186/2050-3385-1-5>
- Copping, J. P., Stewart, B. D., McClean, C. J., Hancock, J., & Rees, R. (2018). Does Bathymetry Drive Coastal Whale Shark (*Rhincodon typus*) aggregations? *PeerJ*, 6, e4904. <https://doi.org/10.7717/peerj.4904>
- Cosgrove, R., Arregui, I., Arrizabalaga, H., Goni, N., & Neilson, J. D. (2015). Predation of pop-up Satellite Archival Tagged Albacore (*Thunnus alalunga*). *Fisheries Research*, 162, 48–52. <https://doi.org/10.1016/j.fishres.2014.09.003>
- Craik, J. C. A. (1978). The lipids of six species of shark. *Journal of the Marine Biological Association of the United Kingdom*, 58(4), 913–921.
<https://doi.org/10.1017/s002531540005685x>
- Davis, D., Banks, S., Birtles, A., Valentine, P., & Cuthill, M. (1997). Whale Sharks in Ningaloo Marine Park: Managing Tourism in an Australian Marine Protected Area. *Tourism Management*, 18(5), 259–271. [https://doi.org/10.1016/s0261-5177\(97\)00015-0](https://doi.org/10.1016/s0261-5177(97)00015-0)
- Davis, V. A., Holbrook, R. I., & Burt de Perera, T. (2018). The influence of locomotory style on three-dimensional spatial learning. *Animal Behaviour*, 142, 39–47.
<https://doi.org/10.1016/j.anbehav.2018.06.002>

- Dickinson, M. H. (2000). How Animals Move: An Integrative View. *Science*, 288(5463), 100–106. <https://doi.org/10.1126/science.288.5463.100>
- Domenici, P. (2010). Context-dependent Variability in the Components of Fish Escape response: Integrating Locomotor Performance and Behavior. *Journal of Experimental Zoology*, 313A(2), 59–79. <https://doi.org/10.1002/jez.580>
- Dove, A. D. M. (2015). Foraging and Ingestive Behaviours of Whale Sharks, *Rhincodon typus*, in Response to Chemical Stimulus Cues. *The Biological Bulletin*, 228(1), 65–74. <https://doi.org/10.1086/bblv228n1p65>
- Dove, Alistair. D. M., & Pierce, Simon. J. (2022). *Whale Sharks : biology, ecology, and Conservation*. Crc Press, Taylor & Francis Group.
- Eckert, S. A., & Stewart, B. S. (2001). Telemetry and Satellite Tracking of Whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the North Pacific Ocean. *Developments in Environmental Biology of Fishes*, 20, 299–308. https://doi.org/10.1007/978-94-017-3245-1_17
- Fallows, C., Gallagher, A. J., & Hammerschlag, N. (2013). White Sharks (*Carcharodon carcharias*) Scavenging on Whales and Its Potential Role in Further Shaping the Ecology of an Apex Predator. *PLoS ONE*, 8(4), e60797. <https://doi.org/10.1371/journal.pone.0060797>
- Fitzpatrick, B., Meekan, M., & Richards, A. (2006). Shark Attacks on a Whale Shark (*Rhincodon typus*) at Ningaloo Reef...: Ingenta Connect. *Bulletin of Marine Science*, 78(2).
- Gallagher, A. J., & Hammerschlag, N. (2011). Global Shark currency: the distribution, frequency, and Economic Value of Shark Ecotourism. *Current Issues in Tourism*, 14(8), 797–812. <https://doi.org/10.1080/13683500.2011.585227>

- Garde, B., Wilson, R. P., Fell, A., Cole, N. C., Tatayah, V., Holton, M. D., Rose, K., Metcalfe, R. S., Robotka, H., Wikelski, M., Tremblay, F., Whelan, S., Elliott, K. H., & Emily. (2022). Ecological inference using data from accelerometers needs careful protocols. *Methods in Ecology and Evolution*, 13(4), 813–825.
<https://doi.org/10.1111/2041-210x.13804>
- Gautestad, A. O., & Mysterud, I. (1993). Physical and Biological Mechanisms in Animal Movement Processes. *The Journal of Applied Ecology*, 30(3), 523.
<https://doi.org/10.2307/2404192>
- Gillooly, J. F. (2001). Effects of Size and Temperature on Metabolic Rate. *Science*, 293(5538), 2248–2251. <https://doi.org/10.1126/science.1061967>
- Gleiss, A. C., Norman, B., Liebsch, N., Francis, C., & Wilson, R. P. (2009). A new prospect for tagging large free-swimming sharks with motion-sensitive data-loggers. *Fisheries Research*, 97(1-2), 11–16. <https://doi.org/10.1016/j.fishres.2008.12.012>
- Gleiss, A. C., Norman, B., & Wilson, R. P. (2010). Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Functional Ecology*, 25(3), 595–607. <https://doi.org/10.1111/j.1365-2435.2010.01801.x>
- Gleiss, A. C., Potvin, J., & Goldbogen, J. A. (2017). Physical trade-offs Shape the Evolution of Buoyancy Control in Sharks. *Proceedings of the Royal Society B: Biological Sciences*, 284(1866), 20171345. <https://doi.org/10.1098/rspb.2017.1345>
- Gleiss, A. C., Wilson, R. P., & Shepard, E. L. C. (2010). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, 2(1), 23–33. <https://doi.org/10.1111/j.2041-210x.2010.00057.x>

- Gleiss, A. C., Wright, S., Liebsch, N., Wilson, R. P., & Norman, B. (2013). Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo Reef. *Marine Biology*, 160(11), 2981–2992. <https://doi.org/10.1007/s00227-013-2288-3>
- Graham, R. T., Roberts, C. M., & Smart, J. C. R. (2005). Diving Behaviour of Whale Sharks in Relation to a Predictable Food Pulse. *Journal of the Royal Society Interface*, 3(6), 109–116. <https://doi.org/10.1098/rsif.2005.0082>
- Grolemund, G., & Wickham, H. (2011). Dates and Times Made Easy with lubridate. In *Journal of Statistical Software* (Vol. 40, Issue 3, pp. 1–25). <https://www.jstatsoft.org/v40/i03/>
- Grusha, D. S., & Patterson, M. R. (2018). *Quantification of Drag and Lift Imposed by Pop-Up Satellite Archival Tags and Estimation of the Metabolic Cost to Cownose Rays (Rhinoptera Bonasus)*. W&M ScholarWorks. <https://scholarworks.wm.edu/vimsarticles/567/>
- Gunn, J. S., Stevens, J. D., Davis, T. L. O., & Norman, B. M. (1999). Observations on the short-term Movements and Behaviour of Whale Sharks (*Rhincodon Typus*) at Ningaloo Reef, Western Australia. *Marine Biology*, 135(3), 553–559. <https://doi.org/10.1007/s002270050656>
- Gunner, R., Holton, M. D., Scantlebury, M., Louis, English, H. M., Williams, H. J., Hopkins, P., Quintana, F., Gómez-Laich, A., Luca Börger, Redcliffe, J., Yoda, K., Yamamoto, T., Ferreira, S. M., Govender, D., Viljoen, P., Bruns, A., Bell, S. H., Marks, N. J., & Bennett, N. C. (2021). Dead-reckoning animal movements in R: a reappraisal using Gundog.Tracks. *Animal Biotelemetry*, 9(1). <https://doi.org/10.1186/s40317-021-00245-z>

- Gunner, R., Wilson, R. P., Holton, M. D., Scott, R. J., Hopkins, P., & Duarte, C. M. (2020). A new direction for differentiating animal activity based on measuring angular velocity about the yaw axis. *Ecology and Evolution*, 10(14), 7872–7886. <https://doi.org/10.1002/ece3.6515>
- Halsey, L. G., Shepard, E. L. C., Quintana, F., Gomez Laich, A., Green, J. A., & Wilson, R. P. (2009). The Relationship between Oxygen Consumption and Body Acceleration in a Range of Species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 152(2), 197–202. <https://doi.org/10.1016/j.cbpa.2008.09.021>
- Hammerschlag, N., Cooke, S. J., Gallagher, A. J., & Godley, B. J. (2014). Considering the Fate of Electronic tags: Interactions with Stakeholders and User Responsibility When Encountering Tagged Aquatic Animals. *Methods in Ecology and Evolution*, 5(11), 1147–1153. <https://doi.org/10.1111/2041-210x.12248>
- Hammerschlag, N., Skubel, R. A., Sulikowski, J., Irschick, D. J., & Gallagher, A. J. (2018). A Comparison of Reproductive and Energetic States in a Marine Apex Predator (the Tiger Shark, *Galeocerdo cuvier*). *Physiological and Biochemical Zoology*, 91(4), 933–942. <https://doi.org/10.1086/698496>
- Hanson, C. E., & McKinnon, A. D. (2009). Pelagic Ecology of the Ningaloo region, Western Australia: Influence of the Leeuwin Current. *Journal of the Royal Society of Western Australia*, 92, 129–137.
- Hart, K. M., Guzy, J. C., & Smith, B. J. (2021). Drivers of realized satellite tracking duration in marine turtles. *Movement Ecology*, 9(1). <https://doi.org/10.1186/s40462-020-00237-3>
- Hays, G. C. (2003). A Review of the Adaptive Significance and Ecosystem Consequences of Zooplankton Diel Vertical Migrations. *Hydrobiologia*, 503(1-3), 163–170. <https://doi.org/10.1023/b:hydr.00000008476.23617.b0>

- Heyman, W., Graham, R., Kjerfve, B., & Johannes, R. (2001). Whale Sharks *Rhincodon Typus* Aggregate to Feed on Fish Spawn in Belize. *Marine Ecology Progress Series*, 215, 275–282. <https://doi.org/10.3354/meps215275>
- Holton, M. D., Wilson, R. P., Teilmann, J., & Siebert, U. (2021). Animal tag technology keeps coming of age: an engineering perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1831), 20200229. <https://doi.org/10.1098/rstb.2020.0229>
- Hounslow, J. L., Brewster, L. R., Lear, K. O., Guttridge, T. L., Daly, R. C., Whitney, N. M., & Gleiss, A. C. (2019). Assessing the effects of sampling frequency on behavioural classification of accelerometer data. *Journal of Experimental Marine Biology and Ecology*, 512, 22–30. <https://doi.org/10.1016/j.jembe.2018.12.003>
- Houston, A. I., & McNamara, J. M. (2013). Foraging currencies, metabolism and behavioural routines. *Journal of Animal Ecology*, 83(1), 30–40. <https://doi.org/10.1111/1365-2656.12096>
- Houston, A. I., McNamara, John. M., & Hutchinson, John. M. (1993). General Results concerning the trade-off between Gaining Energy and Avoiding Predation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 341(1298), 375–397. <https://doi.org/10.1098/rstb.1993.0123>
- Hussain, S. M. (1989). Buoyancy Mechanism and Density of Sand Tiger Sharks (*Eugomphodus taurus*). *Indian Journal of Fisheries*, 36(3), 266–268.
- Iosilevskii, G., & Papastamatiou, Y. P. (2016). Relations between morphology, Buoyancy and Energetics of Requiem Sharks. *Royal Society Open Science*, 3(10), 160406. <https://doi.org/10.1098/rsos.160406>

- Jeanniard-du-Dot, T., Guinet, C., Arnould, J. P. Y., Speakman, J. R., & Trites, A. W. (2016). Accelerometers can measure total and activity-specific energy expenditures in free-ranging marine mammals only if linked to time-activity budgets. *Functional Ecology*, 31(2), 377–386. <https://doi.org/10.1111/1365-2435.12729>
- Jepsen, N., Thorstad, E. B., Havn, T., & Lucas, M. C. (2015). The Use of External Electronic Tags on fish: an Evaluation of Tag Retention and Tagging Effects. *Animal Biotelemetry*, 3(1). <https://doi.org/10.1186/s40317-015-0086-z>
- Kerstetter, D., Polovina, J., & Graves, J. (2004). Evidence of Shark Predation and Scavenging on Fishes Equipped with Pop-up Satellite Archival Tags. *Fishery Bulletin*, 102(4). https://nsuworks.nova.edu/cgi/viewcontent.cgi?article=1552&context=occ_facarticles
- Ketchum, J. T., Galván-Magaña, F., & Klimley, A. P. (2012). Segregation and Foraging Ecology of Whale sharks, *Rhincodon typus*, in the Southwestern Gulf of California. *Environmental Biology of Fishes*, 96(6), 779–795. <https://doi.org/10.1007/s10641-012-0071-9>
- Klimley, P. A., Beavers, S. C., Curtis, T. H., & Jorgensen, S. J. (2002). Movements and Swimming Behavior of Three Species of Sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*, 63(2), 117–135. <https://doi.org/10.1023/a:1014200301213>
- Kobryn, H. T., Wouters, K., Beckley, L. E., & Heege, T. (2013). Ningaloo Reef: Shallow Marine Habitats Mapped Using a Hyperspectral Sensor. *PLoS ONE*, 8(7), e70105. <https://doi.org/10.1371/journal.pone.0070105>
- Kruskal, W. H., & Wallis, W. A. (1952). Use of Ranks in One-Criterion Variance Analysis. *Journal of the American Statistical Association*, 47(260), 583–621.

- Kwiatkowski, L., Aumont, O., & Bopp, L. (2018). Consistent Trophic Amplification of Marine Biomass Declines under Climate Change. *Global Change Biology*, 25(1), 218–229. <https://doi.org/10.1111/gcb.14468>
- Lacroix, G. L. (2014). Large Pelagic Predators Could Jeopardize the Recovery of Endangered Atlantic Salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(3), 343–350. <https://doi.org/10.1139/cjfas-2013-0458>
- Langerhans, R. B., Goins, T. R., Stemp, K. M., Riesch, R., Araújo, M. S., & Layman, C. A. (2021). Consuming Costly Prey: Optimal Foraging and the Role of Compensatory Growth. *Frontiers in Ecology and Evolution*, 8. <https://doi.org/10.3389/fevo.2020.603387>
- Liu, X., Xu, N., & Jiang, A. (2015). Tortuosity entropy: a Measure of Spatial Complexity of Behavioral Changes in Animal Movement. *Journal of Theoretical Biology*, 364, 197–205. <https://doi.org/10.1016/j.jtbi.2014.09.025>
- Martin, R. A. (2007). A Review of Behavioural Ecology of Whale Sharks (*Rhincodon typus*). *Fisheries Research*, 84(1), 10–16. <https://doi.org/10.1016/j.fishres.2006.11.010>
- Mate, B. R., Irvine, L. M., & Palacios, D. M. (2016). The Development of an Intermediate-duration Tag to Characterize the Diving Behavior of Large Whales. *Ecology and Evolution*, 7(2), 585–595. <https://doi.org/10.1002/ece3.2649>
- McClain, C. R., Balk, M. A., Benfield, M. C., Branch, T. A., Chen, C., Cosgrove, J., Dove, A. D. M., Gaskins, L. C., Helm, R. R., Hochberg, F. G., Lee, F. B., Marshall, A., McMurray, S. E., Schanche, C., Stone, S. N., & Thaler, A. D. (2015). Sizing ocean giants: patterns of intraspecific size variation in marine megafauna. *PeerJ*, 3, e715. <https://doi.org/10.7717/peerj.715>

- McNamara, John M., & Houston, Alasdair I. (1997). Currencies For Foraging Based on Energetic Gain. *The American Naturalist*, 150(5), 603–617.
<https://doi.org/10.1086/286084>
- Meekan, M. G., Fuiman, L. A., Davis, R., Berger, Y., & Thums, M. (2015). Swimming Strategy and Body Plan of the world's Largest fish: Implications for Foraging Efficiency and Thermoregulation. *Frontiers in Marine Science*, 2.
<https://doi.org/10.3389/fmars.2015.00064>
- Meekan, M. G., Taylor, B. M., Lester, E., Ferreira, L. C., Sequeira, A. M. M., Dove, A. D. M., Birt, M. J., Aspinall, A., Brooks, K., & Thums, M. (2020). Asymptotic Growth of Whale Sharks Suggests Sex-Specific Life-History Strategies. *Frontiers in Marine Science*, 7. <https://doi.org/10.3389/fmars.2020.575683>
- Meekan, M., Bradshaw, C., Press, M., McLean, C., Richards, A., Quaschnick, S., & Taylor, J. (2006). Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, 319, 275–285.
<https://doi.org/10.3354/meps319275>
- Mehner, T. (2012). Diel Vertical Migration of Freshwater Fishes - Proximate triggers, Ultimate Causes and Research Perspectives. *Freshwater Biology*, 57(7), 1342–1359.
<https://doi.org/10.1111/j.1365-2427.2012.02811.x>
- Montero-Quintana, A. N., Ocampo-Valdez, C. F., Vázquez-Haikin, J. A., Sosa-Nishizaki, O., & Osorio-Beristain, M. (2021). Whale Shark (*Rhincodon typus*) Predatory Flexible Feeding Behaviors on Schooling Fish. *Journal of Ethology*, 40(1), 117–117.
<https://doi.org/10.1007/s10164-021-00737-8>
- Montero-Quintana, A. N., Vázquez-Haikin, J. A., Merklings, T., Blanchard, P., & Osorio-Beristain, M. (2018). Ecotourism impacts on the behaviour of whale sharks: an

experimental approach. *Oryx*, 54(2), 1–6.
<https://doi.org/10.1017/s0030605318000017>

Mori, Y. (1998). The Optimal Patch Use in Divers: Optimal Time Budget and the Number of Dive Cycles during Bout. *Journal of Theoretical Biology*, 190(2), 187–199.
<https://doi.org/10.1006/jtbi.1997.0550>

Motta, P. J., Maslanka, M., Hueter, R. E., Davis, R. L., de la Parra, R., Mulvany, S. L., Habegger, M. L., Strother, J. A., Mara, K. R., Gardiner, J. M., Tyminski, J. P., & Zeigler, L. D. (2010). Feeding anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding off the Yucatan Peninsula, Mexico. *Zoology*, 113(4), 199–212. <https://doi.org/10.1016/j.zool.2009.12.001>

Nakamura, I., Matsumoto, R., & Sato, K. (2020). Body Temperature Stability in the Whale shark, the world's Largest Fish. *The Journal of Experimental Biology*, 223(11), jeb210286. <https://doi.org/10.1242/jeb.210286>

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105(49), 19052–19059.
<https://doi.org/10.1073/pnas.0800375105>

Nelson, J. D., & Eckert, S. A. (2007). Foraging Ecology of Whale Sharks (*Rhincodon typus*) within Bahía De Los Angeles, Baja California Norte, México. *Fisheries Research*, 84(1), 47–64. <https://doi.org/10.1016/j.fishres.2006.11.013>

Norman, B. (2002). *Review of Current and Historical Research on the Ecology of Whale Sharks (Rhincodon typus), and Applications to Conservation through Management of the Species*. Unpublished Report for the WA Department of Conservation and Land Management, Perth. <https://library.dbca.wa.gov.au/static/FullTextFiles/071172.pdf>

- Norman, B. M., & Stevens, J. D. (2007). Size and Maturity Status of the Whale Shark (*Rhincodon typus*) at Ningaloo Reef in Western Australia. *Fisheries Research*, 84(1), 81–86. <https://doi.org/10.1016/j.fishres.2006.11.015>
- Norman, B. M., Whitty, J. M., Beatty, S. J., Reynolds, S. D., & Morgan, D. L. (2017). Do They Stay or Do They go? Acoustic Monitoring of Whale Sharks at Ningaloo Marine Park, Western Australia. *Journal of Fish Biology*, 91(6), 1713–1720. <https://doi.org/10.1111/jfb.13461>
- Papastamatiou, Y. P., Cartamil, D. P., Lowe, C. G., Meyer, C. G., Wetherbee, B. M., & Holland, K. N. (2011). Scales of orientation, directed walks and movement path structure in sharks. *Journal of Animal Ecology*, 80(4), 864–874. <https://doi.org/10.1111/j.1365-2656.2011.01815.x>
- Papastamatiou, Y. P., Iosilevskii, G., Di Santo, V., Huveneers, C., Hattab, T., Planes, S., Ballesta, L., & Mourier, J. (2021). Sharks surf the slope: Current updrafts reduce energy expenditure for aggregating marine predators. *Journal of Animal Ecology*, 90(10), 2302–2314. <https://doi.org/10.1111/1365-2656.13536>
- Papastamatiou, Y. P., Iosilevskii, G., Leos-Barajas, V., Brooks, E. J., Howey, L. A., Chapman, D. D., & Watanabe, Y. Y. (2018). Optimal swimming strategies and behavioral plasticity of oceanic whitetip sharks. *Scientific Reports*, 8(1). <https://doi.org/10.1038/s41598-017-18608-z>
- Pianka, Eric. R. (1976). Natural Selection of Optimal Reproductive Tactics. *American Zoologist*, 16(4), 775–784. <https://doi.org/10.1093/icb/16.4.775>
- Pyke, G. H. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, 15, 523–575. <https://www.jstor.org/stable/pdf/2096959.pdf?refreqid=fastly->

default%3A71a61654c0872c8b89f2a9609cd9409f&ab_segments=&origin=&initiator
=&acceptTC=1

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C., & Wilson, R. (2012). Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? *PLoS ONE*, 7(2), e31187. <https://doi.org/10.1371/journal.pone.0031187>

QGIS.org, %Y. QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>

Quiros, A. L. (2007). Tourist Compliance to a Code of Conduct and the Resulting Effects on Whale Shark (*Rhincodon typus*) Behavior in Donsol, Philippines. *Fisheries Research*, 84(1), 102–108. <https://doi.org/10.1016/j.fishres.2006.11.017>

Reynolds, S. D., Franklin, C. E., Norman, B. M., Richardson, A. J., Everett, J. D., Schoeman, D. S., White, C. R., Lawson, C. L., Pierce, S. J., Rohner, C. A., Bach, S. S., Comezzi, F. G., Diamant, S., Jaidah, M. Y., Robinson, D. P., & Dwyer, R. G. (2024). Effects of climate warming on energetics and habitat of the world's largest marine ectotherm. *The Science of the Total Environment*, 951, 175832–175832. <https://doi.org/10.1016/j.scitotenv.2024.175832>

Reynolds, S. D., Norman, B. M., Beger, M., Franklin, C. E., & Dwyer, R. G. (2017). Movement, distribution and marine reserve use by an endangered migratory giant. *Diversity and Distributions*, 23(11), 1268–1279. <https://doi.org/10.1111/ddi.12618>

Reynolds, S. D., Norman, B. M., Franklin, C. E., Bach, S. S., Comezzi, F. G., Diamant, S., Jaidah, M. Y., Pierce, S. J., Richardson, A. J., Robinson, D. P., Rohner, C. A., & Dwyer, R. G. (2022). Regional variation in anthropogenic threats to Indian Ocean whale sharks. *Global Ecology and Conservation*, 33, e01961. <https://doi.org/10.1016/j.gecco.2021.e01961>

- Reynolds, S. D., Redcliffe, J., Norman, B. M., Wilson, R. P., Holton, M., Franklin, C. E., & Dwyer, R. G. (2024). Swimming with humans: Biotelemetry Reveals Effects of “gold Standard” Regulated Tourism on Whale Sharks. *Journal of Sustainable Tourism*, 1–20. <https://doi.org/10.1080/09669582.2024.2314624>
- Rowat, D., & Brooks, K. S. (2012). A Review of the biology, Fisheries and Conservation of the Whale Shark *Rhincodon Typus*. *Journal of Fish Biology*, 80(5), 1019–1056. <https://doi.org/10.1111/j.1095-8649.2012.03252.x>
- Rowat, D., & Gore, M. (2007). Regional Scale Horizontal and Local Scale Vertical Movements of Whale Sharks in the Indian Ocean off Seychelles. *Fisheries Research*, 84(1), 32–40. <https://doi.org/10.1016/j.fishres.2006.11.009>
- Sequeira, A. M. M., Mellin, C., Meekan, M. G., Sims, D. W., & Bradshaw, C. J. A. (2013). Inferred Global Connectivity of Whale Shark *Rhincodon Typus* Populations. *Journal of Fish Biology*, 82(2), 367–389. <https://doi.org/10.1111/jfb.12017>
- Shaw, A. K. (2020). Causes and Consequences of Individual Variation in Animal Movement. *Movement Ecology*, 8(1). <https://doi.org/10.1186/s40462-020-0197-x>
- Shepard, E., Wilson, R. P., Halsey, L. G., Quintana, F., Agustina Gómez Laich, Gleiss, A. C., Liebsch, N., Myers, A. A., & Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology*, 4, 235–241. <https://doi.org/10.3354/ab00104>
- Shepard, E. L. C., Ahmed, M. Z., Southall, E. J., Witt, M. J., Metcalfe, J. D., & Sims, D. W. (2006). Diel and Tidal Rhythms in Diving Behaviour of Pelagic Sharks Identified by Signal Processing of Archival Tagging Data. *Marine Ecology Progress Series*, 328, 205–213. <https://doi.org/10.3354/meps328205>

- Shepard, E., Wilson, R., Quintana, F., Gómez Laich, A., Liebsch, N., Albareda, D., Halsey, L., Gleiss, A., Morgan, D., Myers, A., Newman, C., & McDonald, D. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research*, 10, 47–60. <https://doi.org/10.3354/esr00084>
- Shillinger, G., Bailey, H., Bograd, S., Hazen, E., Hamann, M., Gaspar, P., Godley, B., Wilson, R., & Spotila, J. (2012). Tagging through the stages: technical and ecological challenges in observing life histories through biologging. *Marine Ecology Progress Series*, 457, 165–170. <https://doi.org/10.3354/meps09816>
- Sims, D. W. (1999). Threshold Foraging Behaviour of Basking Sharks on zooplankton: Life on an Energetic knife-edge? *Proceedings of the Royal Society B: Biological Sciences*, 266(1427), 1437. <https://doi.org/10.1098/rspb.1999.0798>
- Sims, David. W., Southall, Emily. J., Tarling, G. A., & Metcalfe, J. D. (2005). Habitat-specific Normal and Reverse Diel Vertical Migration in the plankton-feeding Basking Shark. *Journal of Animal Ecology*, 74(4), 755–761. <https://doi.org/10.1111/j.1365-2656.2005.00971.x>
- Sleeman, J. C., Meekan, M. G., Wilson, S. G., Polovina, J. J., Stevens, J. D., Boggs, G. S., & Bradshaw, C. J. A. (2010). To go or not to go with the flow: Environmental influences on whale shark movement patterns. *Journal of Experimental Marine Biology and Ecology*, 390(2), 84–98. <https://doi.org/10.1016/j.jembe.2010.05.009>
- Speed, C. W., Meekan, M. G., Rowat, D., Pierce, S. J., Marshall, A. D., & Bradshaw, C. J. A. (2008). Scarring Patterns and Relative Mortality Rates of Indian Ocean Whale Sharks. *Journal of Fish Biology*, 72(6), 1488–1503. <https://doi.org/10.1111/j.1095-8649.2008.01810.x>
- Stothart, M. R., Elliott, K. H., Wood, T., Hatch, S. A., & Speakman, J. R. (2016). Counting calories in cormorants: dynamic body acceleration predicts daily energy expenditure

measured in pelagic cormorants. *The Journal of Experimental Biology*, 219(14), 2192–2200. <https://doi.org/10.1242/jeb.130526>

Sumikawa, H., Naraoka, Y., Obayashi, Y., Fukue, T., & Miyoshi, T. (2023). Fluid dynamic properties of shark caudal fin morphology and its relationship to habitats. *Ichthyological Research*, 71(2), 294–304. <https://doi.org/10.1007/s10228-023-00933-1>

Taylor, J. G. (2007). Ram filter-feeding and nocturnal feeding of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Fisheries Research*, 84(1), 65–70. <https://doi.org/10.1016/j.fishres.2006.11.014>

Taylor, J. G., & Pearce, A. F. (1999). Ningaloo Reef currents: Implications for Coral Spawn dispersal, Zooplankton and Whale Shark Abundance. *Journal of the Royal Society of Western Australia*, 82, 57–65.

Thums, M., Meekan, M., Stevens, J., Wilson, S., & Polovina, J. (2013). Evidence for Behavioural Thermoregulation by the world's Largest Fish. *Journal of the Royal Society Interface*, 10(78), 20120477. <https://doi.org/10.1098/rsif.2012.0477>

Tolentino, E. R., Howey, R. P., Howey, L. A., Jordan, L. K. B., Grubbs, R. D., Brooks, A., Williams, S., Brooks, E. J., & Shipley, O. N. (2017). Was my science project eaten? A novel approach to validate consumption of marine biologging instruments. *Animal Biotelemetry*, 5(1). <https://doi.org/10.1186/s40317-016-0117-4>

Torres, L. G., Orben, R. A., Tolkova, I., & Thompson, D. R. (2017). Classification of Animal Movement Behavior through Residence in Space and Time. *PLOS ONE*, 12(1), e0168513. <https://doi.org/10.1371/journal.pone.0168513>

Troup, G., Doran, B., Au, J., King, L. E., Douglas-Hamilton, I., & Heinsohn, R. (2020). Movement tortuosity and speed reveal the trade-offs of crop raiding for African

elephants. *Animal Behaviour*, 168, 97–108.
<https://doi.org/10.1016/j.anbehav.2020.08.009>

Tyminski, J. P., de la Parra-Venegas, R., González Cano, J., & Hueter, R. E. (2015). Vertical Movements and Patterns in Diving Behavior of Whale Sharks as Revealed by Pop-Up Satellite Tags in the Eastern Gulf of Mexico. *PLOS ONE*, 10(11), e0142156.
<https://doi.org/10.1371/journal.pone.0142156>

Walker, J. S., Jones, M. W., Laramée, R. S., Holton, M. D., Shepard, E. L., Williams, H. J., Scantlebury, D. M., Marks, N. J., Magowan, E. A., Maguire, I. E., Bidder, O. R., Di Virgilio, A., & Wilson, R. P. (2015). Prying into the intimate secrets of animal lives; software beyond hardware for comprehensive annotation in “Daily Diary” tags. *Movement Ecology*, 3(1). <https://doi.org/10.1186/s40462-015-0056-3>

Wampler, K., & Popović, Z. (2009). Optimal gait and form for animal locomotion. *ACM Transactions on Graphics*, 28(3), 1. <https://doi.org/10.1145/1531326.1531366>

Watanabe, Y. Y., Payne, N. L., Semmens, J. M., Fox, A., & Huveneers, C. (2019). Swimming strategies and energetics of endothermic white sharks during foraging. *The Journal of Experimental Biology*, 222(4), jeb185603.
<https://doi.org/10.1242/jeb.185603>

Weihs, D. (1973). *Mechanically Efficient Swimming Techniques for Fish with Negative Bouyancy*. EliScholar – a Digital Platform for Scholarly Publishing at Yale.
https://elischolar.library.yale.edu/journal_of_marine_research/1268

Whitney, N. M., White, C. F., Gleiss, A. C., Schwieterman, G. D., Anderson, P., Hueter, R. E., & Skomal, G. B. (2016). A novel method for determining post-release mortality, behavior, and recovery period using acceleration data loggers. *Fisheries Research*, 183, 210–221. <https://doi.org/10.1016/j.fishres.2016.06.003>

Wildbyte Technologies. (2024). Wildbytetechnologies.com.

<http://wildbytetechnologies.com/tags.html>

Williams, H. J., Holton, M. D., Shepard, E. L. C., Largey, N., Norman, B., Ryan, P. G., Duriez, O., Scantlebury, M., Quintana, F., Magowan, E. A., Marks, N. J., Alagaili, A. N., Bennett, N. C., & Wilson, R. P. (2017). Identification of animal movement patterns using tri-axial magnetometry. *Movement Ecology*, 5(1). <https://doi.org/10.1186/s40462-017-0097-x>

Williams, H. J., Shepard, E. L. C., Duriez, O., & Lambertucci, S. A. (2015). Can accelerometry be used to distinguish between flight types in soaring birds? *Animal Biotelemetry*, 3(1). <https://doi.org/10.1186/s40317-015-0077-0>

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P. M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Geraldi, N. R., Duarte, C. M., Scott, R., Strano, M. S., Robotka, H., Eizaguirre, C., Fahlman, A., & Shepard, E. L. C. (2019). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, 89(1), 161–172. <https://doi.org/10.1111/1365-2656.13040>

Wilson, R. P., Griffiths, I. W., Legg, P. A., Friswell, M. I., Bidder, O. R., Halsey, L. G., Lambertucci, S. A., & Shepard, E. L. C. (2013). Turn costs change the value of animal search paths. *Ecology Letters*, 16(9), 1145–1150. <https://doi.org/10.1111/ele.12149>

Wilson, R. P., Holton, M. D., Agustina di Virgilio, Williams, H. J., Emily, Lambertucci, S. A., Quintana, F., Juan Emilio Sala, Balaji, B., Eun Sun Lee, Srivastava, M., Scantlebury, D., & Duarte, C. M. (2018). Give the machine a hand: A Boolean time-based decision-tree template for rapidly finding animal behaviours in multisensor data. *Methods in Ecology and Evolution*, 9(11), 2206–2215. <https://doi.org/10.1111/2041-210x.13069>

- Wilson, R. P., Holton, M. D., Walker, J. S., Shepard, E. L. C., Scantlebury, D. M., Wilson, V. L., Wilson, G. I., Tysse, B., Gravenor, M., Ciancio, J., McNarry, M. A., Mackintosh, K. A., Qasem, L., Rosell, F., Graf, P. M., Quintana, F., Gomez-Laich, A., Sala, J.-E., Mulvenna, C. C., & Marks, N. J. (2016). A spherical-plot solution to linking acceleration metrics with animal performance, state, behaviour and lifestyle. *Movement Ecology*, 4(1). <https://doi.org/10.1186/s40462-016-0088-3>
- Wilson, R. P., Reynolds, S., Potts, J. R., Redcliffe, J., Holton, M. D., Buxton, A., Kayleigh, & Norman, B. (2022). Highlighting when animals expend excessive energy for travel using dynamic body acceleration. *IScience*, 25(9), 105008–105008. <https://doi.org/10.1016/j.isci.2022.105008>
- Wilson, R. P., Rose, K., Metcalfe, R. S., Holton, M. D., Redcliffe, J., Gunner, R., Börger, L., Loison, A., Jezek, M., Painter, M. S., Vaclav Silovský, Marks, N., Garel, M., C. Toïgo, Marchand, P., Bennett, N. C., McNarry, M. A., Mackintosh, K. A., M. Rowan Brown, & D. Michael Scantlebury. (2021). Path tortuosity changes the transport cost paradigm in terrestrial animals. *Ecography*, 44(10), 1524–1532. <https://doi.org/10.1111/ecog.05850>
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving Towards Acceleration for Estimates of activity-specific Metabolic Rate in free-living animals: the Case of the Cormorant. *Journal of Animal Ecology*, 75(5), 1081–1090. <https://doi.org/10.1111/j.1365-2656.2006.01127.x>
- Wilson, R. P., Williams, H. J., Holton, M. D., Agustina di Virgilio, Luca Börger, Potts, J. R., Gunner, R., Arkwright, A., Fahlman, A., Bennett, N. C., Abdulaziz Alagaili, Cole, N. C., Duarte, C. M., & Scantlebury, D. M. (2020). An “orientation sphere” visualization for examining animal head movements. *Ecology and Evolution*, 10(10), 4291–4302. <https://doi.org/10.1002/ece3.6197>

- Wilson, R. S., Husak, J. F., Halsey, L. G., & Clemente, C. J. (2015). Predicting the Movement Speeds of Animals in Natural Environments. *Integrative and Comparative Biology*, 55(6), 1125–1141. <https://doi.org/10.1093/icb/icv106>
- Wilson, R., Shepard, E., & Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research*, 4, 123–137. <https://doi.org/10.3354/esr00064>
- Wilson, S. G., Polovina, J. J., Stewart, B. S., & Meekan, M. G. (2005). Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. *Marine Biology*, 148(5), 1157–1166. <https://doi.org/10.1007/s00227-005-0153-8>
- Wintner, S. P. (2000). Preliminary Study of Vertebral Growth Rings in the Whale shark, *Rhincodon typus*, from the East Coast of South Africa. *Environmental Biology of Fishes*, 59(4), 441–451. <https://doi.org/10.1023/a:1026564707027>
- Womersley, F. C., Humphries, N. E., Queiroz, N., Vedor, M., da Costa, I., Furtado, M., Tyminski, J. P., Abrantes, K., Araujo, G., Bach, S. S., Barnett, A., Berumen, M. L., Bessudo Lion, S., Braun, C. D., Clingham, E., Cochran, J. E. M., de la Parra, R., Diamant, S., Dove, A. D. M., & Dudgeon, C. L. (2022). Global collision-risk hotspots of marine traffic and the world’s largest fish, the whale shark. *Proceedings of the National Academy of Sciences*, 119(20). <https://doi.org/10.1073/pnas.2117440119>
- Woo, M., Pattiaratchi, C., & Schroeder, W. (2006). Summer surface circulation along the Gascoyne continental shelf, Western Australia. *Continental Shelf Research*, 26(1), 132–152. <https://doi.org/10.1016/j.csr.2005.07.007>
- Wright, S., Metcalfe, J., Hetherington, S., & Wilson, R. (2014). Estimating activity-specific Energy Expenditure in a Teleost fish, Using Accelerometer Loggers. *Marine Ecology Progress Series*, 496, 19–32. <https://doi.org/10.3354/meps10528>

- Xu, J., Lowe, R. J., Ivey, G. N., Jones, N. L., & Zhang, Z. (2016). Ocean Transport Pathways to a World Heritage Fringing Coral Reef: Ningaloo Reef, Western Australia. *PLOS ONE*, 11(1), e0145822. <https://doi.org/10.1371/journal.pone.0145822>
- Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. *Advances in the Study of Behavior*, 16, 229–249. [https://doi.org/10.1016/s0065-3454\(08\)60192-8](https://doi.org/10.1016/s0065-3454(08)60192-8)
- Yowell, D. W., & Vinyard, G. L. (1993). An energy-based Analysis of particulate-feeding and filter-feeding by Blue tilapia, *Tilapia Aurea*. *Environmental Biology of Fishes*, 36(1), 65–72. <https://doi.org/10.1007/bf00005980>
- Zaccone, G. (2017). *Fish Defenses Vol. 1*. CRC Press.
- Ziegler, J., & Dearden, P. (2021). Whale Shark Tourism as an Incentive-Based Conservation Approach. *CRC Press EBooks*, 199–238. <https://doi.org/10.1201/b22502-10>

14. Appendices

Appendix I – Ethics Permit statement for Brad Norman (2021 and 2023), Murdoch University

www.murdoch.edu.au

Dr Brad Norman
Harry Butler Institute
Murdoch University

Tuesday, 30 March 2021

Dear Brad,

ANIMAL ETHICS

Protocol ID.	852
Permit No.	RW3327/21
Protocol Title	Elucidating the behaviour of the endangered whale shark (Rhincodon typus) for conservation and management

At its meeting on the 23 March 2021, the Animal Ethics Committee, Murdoch University, considered the above application.

It has been granted **OUTRIGHT** approval. Work using animals may commence.

Special Condition/s of Approval for this Permit

- External Investigators are required to provide a signature to confirm their involvement in the permit. Please distribute the attached form for completion by Prof Rory Wilson and return to the Research Ethics & Integrity Office.
- Samantha Reynolds must complete an online Working with Animals training module and attend an Animal Care & Ethics Workshop or provide evidence of equivalent training in animal ethics before she can be added as a co-investigator. Enrolment for the Working with Animals training module can be accessed via <https://canvas.instructure.com/enroll/XRBCXP> and must be completed prior to online attendance at the workshop. Registration for the next online workshop can be done by contacting animal.ethics@murdoch.edu.au.
- A copy of the current licence to use animals in WA is attached. This must be carried by researchers on any field trips.
- Provide a copy of the DBCA permit to the Animal ethics office when available.

The approval of this project requires you to adhere to the conditions outlined in this letter and to comply with the Animal Welfare Act (2002) and the *Australian code for the care and use of animals for scientific purposes* (8th edition, 2013).

Investigators must maintain records of the care and use of animals and Chief Investigators must provide to the AEC an Annual Report which is due in January each year.

Location	Impact	Species Code	Animal Species	Number Requested	Number Approved
WA	3. Minor conscious intervention	30	Whale shark	60	60

The Research Ethics and Integrity Office wish you every success for your research.



On behalf of the Animal Ethics Committee

cc: A/Prof David Morgan, Samantha Reynolds, Prof Rory Wilson

Standard Conditions for Teaching and Research

Responsibilities of Chief Investigators:

Investigators and teachers have personal responsibility for all matters related to the welfare of the animals they use and must act in accordance with all requirements of the Australian code for the care and use of animals for scientific purposes (current edition). This responsibility begins when an animal is allocated to a project and ends with its fate at the completion of the project.

In addition, the AEC requires Chief Investigators to:

1. Provide the Research Ethics & Integrity Office with a copy of any current licences and permits associated with the project e.g. from Department of Biodiversity, Conservation and Attractions (DBCA); Fisheries; DPIRD etc.
2. Ensure all personnel associated with the project have completed Animal Care and Ethics (ACE) registration with the Research Ethics & Integrity Office.
3. Provide prompt notification to the Research Ethics & Integrity Office immediately any unforeseen or adverse event occurs.
4. Ensure accurate records of the use of animals are maintained.
5. Where personnel from other Institutions are involved in the project, or when premises of another Institution are being utilised, that Institution must be advised of the project and must provide approval or formally delegate approval of the proposal.

Permits:

- Permits are valid for three years from the date of AEC approval providing a satisfactory annual report is submitted and approved by February of each year.
- Permits may be closed by a Chief Investigator with the submission of a Closure Annual Report or by an AEC directive.
- Investigators may be added to a permit following the submission of an amendment form and providing the investigator meets ACE registration and competency requirements. All forms are available on the Research Ethics & Integrity website.
- Please quote your ethics permit number in all correspondence.

Permits are treated in confidence. To enable the institution to fulfil requirements under the Animal Welfare Act WA (2002), information contained in your permit may be released to appropriate personnel at any collaborating institution. In addition, selected information from the application may also be provided to authorised personnel within the appropriate School or Faculty at Murdoch University. Commercial or patentable information should be clearly separated and marked "Commercial-in-Confidence".

Licences:

The Licence to use animals for scientific purposes in WA is obtained from the Department of Primary Industries and Regional Development (DPIRD) by the Research Ethics & Integrity Office on behalf of the University. The University is also licensed in most other states in Australia. It is a requirement that licences are available for public scrutiny. Therefore, you must ensure that the relevant licence is:

- a. Displayed wherever animals are used for scientific purposes, e.g. in your laboratory
- b. Carried by investigators in the field, e.g. in the car or boat.

Dr Brad Norman
College of Science, Health, Engineering and Education
Murdoch University

Wednesday, 28 June 2023

Dear Brad,

ANIMAL ETHICS – Amendment

Protocol ID.	852
Permit No.	RW3327/21
Protocol Title	Elucidating the behaviour of the endangered whale shark (Rhincodon typus) for conservation and management

Amendment details:

1. Use of UAV (drone) to observe 20 whale sharks.
2. Collection of morphometric measurements from these observations.

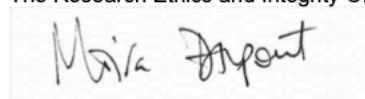
Thank you for your reply to my letter dated 9th June 2023 regarding the AEC response to the above Permit Amendment Application. The committee's concerns have all been addressed and the permit amendment now has **OUTRIGHT** approval. Amended work using animals may continue.

The approval of this project amendment requires you to adhere to the conditions outlined in this letter and to comply with the Animal Welfare Act (2002) and the *Australian code for the care and use of animals for scientific purposes* (8th edition, 2013).

Investigators must maintain records of the care and use of animals and Chief Investigators must provide to the AEC an Annual Report which is due in January each year.

Location Impact		Species Code	Animal Species	Number Requested	Number Approved
WA	3. Minor conscious intervention	30	Whale shark	60	60
WA	1. Observational use with no or minor interference	30	Whale shark	20	20

The Research Ethics and Integrity Office wish you every success for your research.



Dr Moira Desport
Animal Ethics Adviser

Research and Innovation

Animal Ethics
Research Ethics & Integrity Office

90 South Street, Murdoch
Western Australia 6150

T +61 8 9360 7366

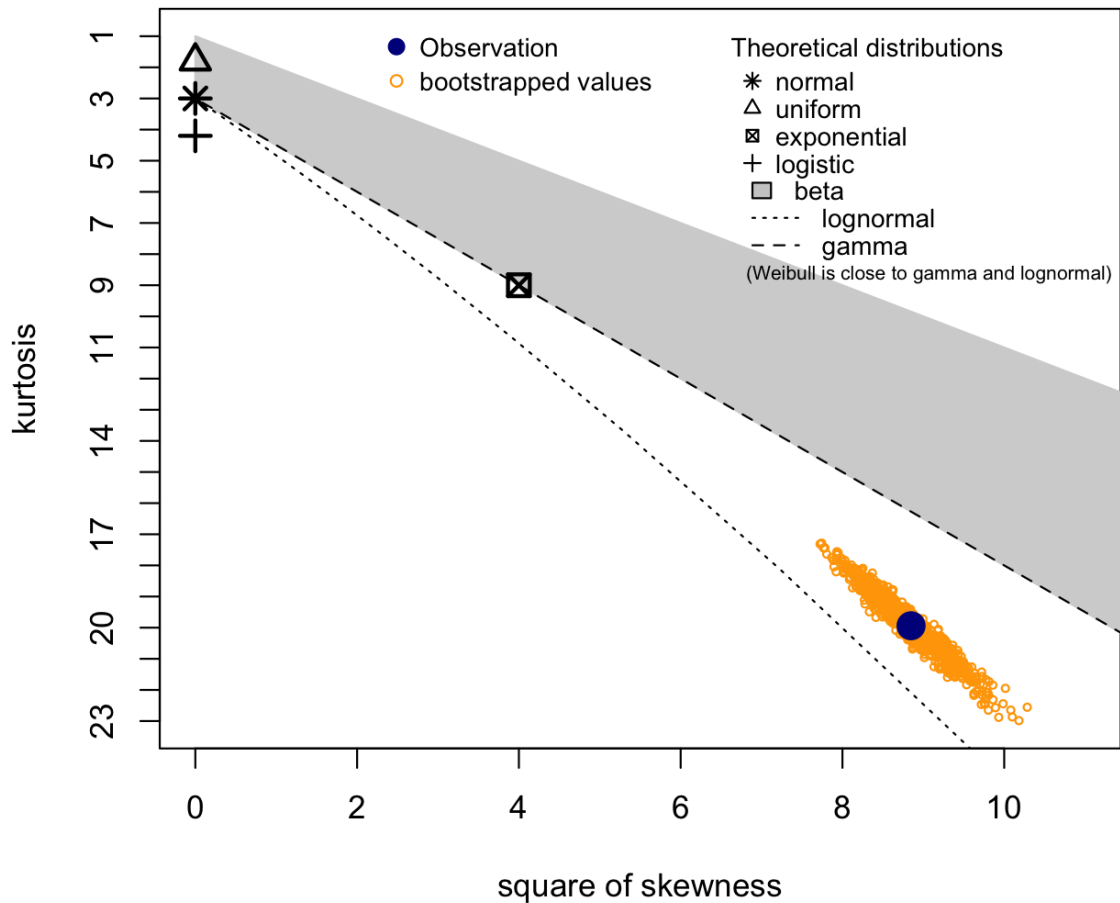
murdoch.edu.au

CRICOS Provider Code 00125J
ABN 61 616 369 313

Appendix II – PPA_{min} coefficients calculated for each shark (P_{min} + 50% value (φ))

Deployment Type	Shark ID	Intercept = 1-coeff2	Squared Value = xsq-coeff2 (b)	50% value (φ)	50% (φ) above intercept = 1-coeff2 (d)
LT	A-1340	0.02694747	13.07575488	0.0035	0.03044747
LT	A-1714	0.02644999	12.23669219	0.0026	0.02904999
LT	A-233	0.02700698	12.48684855	0.0047	0.03170698
LT	A-542	0.02738294	15.48708806	0.0017	0.02908294
LT	A-686	0.02747249	16.54541983	0.0053	0.03277249
LT	A-900	0.02279941	14.48054299	0.003	0.02579941
LT	A-939	0.02655917	9.144302954	0.0051	0.03165917
ST	A-804	0.02360982	21.45624	0.012	0.03560982
ST	A-1831	0.01844379	25.679	0.019	0.03744379
ST	A-1563	0.02389857	11.18404	0.01	0.03389857
ST	A-1442	0.02422764	9.809646	0.012	0.03622764
ST	A-1400	0.02301646	17.97126	0.013	0.03601646
ST	A-542	0.02416407	22.59146	0.0128	0.03696407
ST	A-1753	0.02577663	26.57458	0.015	0.04077663
ST	A-900	0.01367033	24.78541	0.02	0.03367033

Appendix III – Cullen and Fry diagram used to determine the most parsimonious fit for PPA_{min} (response) variable, using the *fitdistrplus* package in R studio. The orange data represents the distribution of PPA_{min} , whilst the proximity to each line represents the best distributional fit for the data.



Appendix IV – AIC and BIC scored used to determine the most parsimonious fit for PPA_{min} (response) variable, using the *fitdistrplus* package in R studio. The distribution chosen has been highlighted in bold.

Distribution	AIC	BIC
Normal	-625646	-625625
Gamma	-709363	-709344
Weibull	-706467	-706447
Log-normal	-701954	-701935

Appendix V – AIC and Δ AIC values for each combination of an additive model combining all variables for the GAMM descent model. Using the *dredge* function from the *MuMin* package (Barton, 2009). The model chosen has been highted in bold.

Model Formula	DF	logLik	AIC	Δ AIC
Depth + Pitch + Tortuosity + Vertical Velocity	11	-2760.092	5542.3	0
Depth + Pitch + Vertical Velocity	9	-2764.672	5547.4	5.12
Depth + Pitch + Hour + Tortuosity + Vertical Velocity	12	-2764.693	5553.5	11.22
Depth + Pitch + Hour + Vertical Velocity	10	-2773.69	5567.5	25.17
Depth + Pitch + Tortuosity	9	-2781.57	5581.2	38.91
Depth + Pitch	7	-2793.386	5600.8	58.51
Depth + Pitch + Hour + Tortuosity	10	-2792.775	5605.7	63.34
Pitch + Tortuosity + Vertical Velocity	9	-2799.439	5617	74.65
Depth + Pitch + Hour	8	-2801.816	5619.7	77.39
Pitch + Hour + Tortuosity + Vertical Velocity	10	-2801.727	5623.6	81.25
Pitch + Vertical Velocity	7	-2807.79	5629.6	87.32
Pitch + Hour + Vertical Velocity	8	-2809.543	5635.2	92.84
Depth + Tortuosity + Vertical Velocity	9	-2832.005	5682.1	139.78
Depth + Vertical Velocity	7	-2835.955	5686	143.65
Pitch + Tortuosity	7	-2836.634	5687.3	145.01
Pitch	5	-2842.698	5695.4	153.11
Depth + Hour	8	-2840.775	5697.6	155.31
Pitch + Hour + Tortuosity	8	-2841.871	5699.8	157.5
Depth + Hour + Tortuosity + Vertical Velocity	10	-2840.61	5701.3	159.02
Pitch + Hour	6	-2846.485	5705	162.7
Vertical Velocity	5	-2872.375	5754.8	212.47
Tortuosity + Vertical Velocity	7	-2871.045	5756.1	213.83
Hour + Vertical Velocity	6	-2875.93	5763.9	221.59
Hour + Tortuosity + Vertical Velocity	8	-2874.722	5765.5	223.2

Depth + Tortuosity	7	-2891.13	5796.3	254
Depth	5	-2895.95	5801.9	259.62
Depth + Hour	6	-2898.345	5808.7	266.42
Depth + Hour + Tortuosity	8	-2896.449	5809	266.66
~1	3	-2939.306	5884.6	342.31
Tortuosity	5	-2946.741	5903.5	361.2
Hour + Tortuosity	4	-2953.468	5915	372.64
Hour	6	-2954.504	5921	378.74

Appendix VI - AIC and Δ AIC values for each combination of an additive model combining all variables for the GAMM level travel model. Using the *dredge* function from the *MuMin* package (Barton, 2009). By observing plots of each variable, the variable depth was included, although AIC was increased. The model chosen has been highted in bold.

Model Formula	df	logLik	AICc	delta
Pitch Angle + Time + Tortuosity	8	-41931.96	83879.9	0
Pitch + Time	6	-41978.7	83969.4	89.47
Time + Tortuosity	6	-42014.64	84041.3	161.37
Time	4	-42058.11	84124.2	244.3
Pitch +Tortuosity	7	-42190.88	84395.8	515.85
Pitch	5	-42240.58	84491.2	611.25
Pitch + Time + Tortuosity + Vertical Velocity	10	-42244.63	84509.3	629.34
Tortuosity	5	-42261.24	84532.5	652.57
1~	3	-42308.42	84622.8	742.92
Pitch + Time + Vertical Velocity	8	-42318.48	84653	773.05
Time + Tortuosity + Vertical Velocity	8	-42370.28	84756.6	876.65
Time + Vertical Velocity	6	-42439.77	84891.6	1011.63
Pitch + Tortuosity + Vertical Velocity	9	-42544.75	85107.5	1227.59
Pitch + Vertical Velocity	7	-42624.21	85262.4	1382.49
Tortuosity +Vertical Velocity	7	-42666.37	85346.8	1466.83
Vertical Velocity	5	-42743.9	85497.8	1617.88

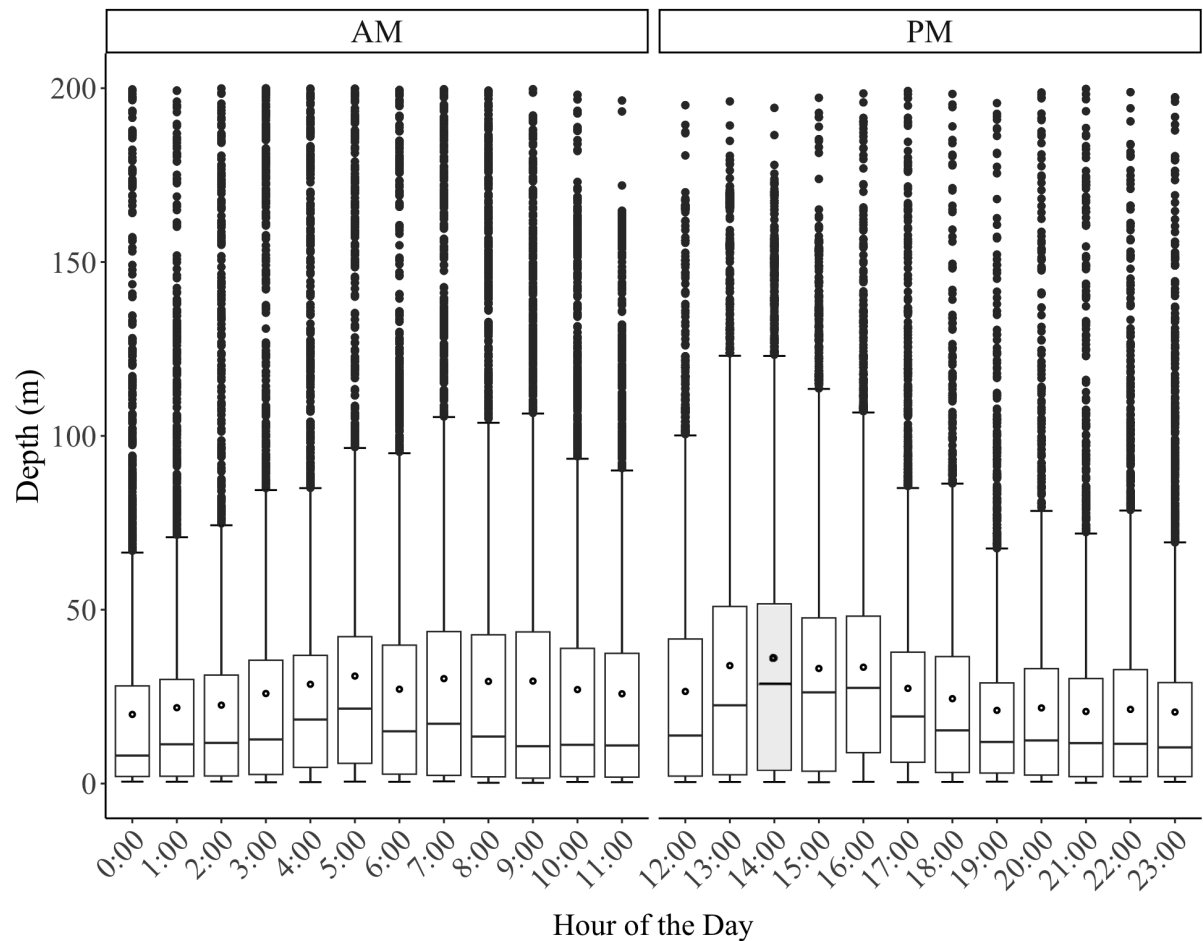
Depth + Pitch + Time + Tortuosity	10	-44299.72	88619.4	4739.53
Depth + Pitch + Time	8	-44381.95	88779.9	4899.99
Depth + Pitch + Time + Tortuosity + Vertical Velocity	12	-44392.59	88809.2	4929.27
Depth + Pitch + Time + Vertical Velocity	10	-44475.11	88970.2	5090.31
Depth + Time + Tortuosity	9	-44600.17	89218.3	5338.43
Depth + Time + Tortuosity	8	-44624.97	89265.9	5386.02
Depth + Pitch	7	-44665.84	89345.7	5465.75
Depth + Time	6	-44698.88	89409.8	5529.84
Depth + Pitch + Tortuosity + Vertical Velocity	11	-44694.58	89411.2	5531.25
Depth + Time + Tortuosity + Vertical Velocity	10	-44733.48	89487	5607.05
Depth + Pitch + Vertical Velocity	9	-44760.28	89538.6	5658.65
Depth + Time + Vertical Velocity	8	-44806.83	89629.7	5749.74
Depth + Tortuosity	7	-44934.75	89883.5	6003.59
Depth	5	-44993.93	89997.9	6117.94
Depth + Tortuosity + Vertical Velocity	9	-45045.56	90109.1	6229.2
Depth + Vertical Velocity	7	-45104.33	90222.7	6342.75

Appendix VII - AIC and Δ AIC values for each combination of an additive model combining all variables for the GAMM ascent model. Using the *dredge* function from the *MuMin* package (Barton, 2009).

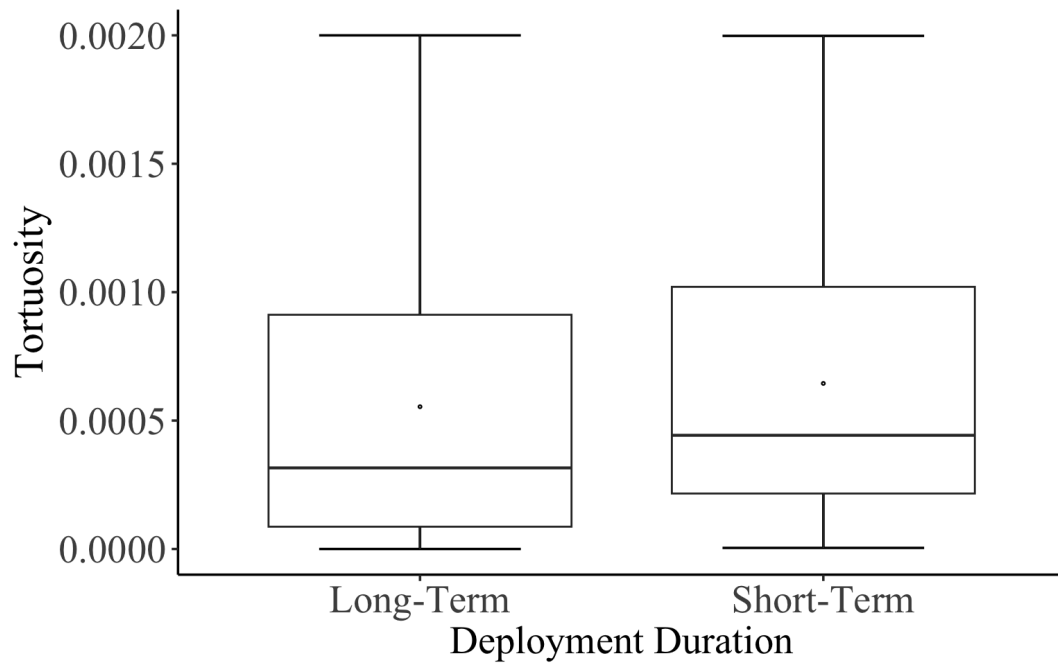
Model Formula	DF	logLik	AIC	Δ AIC
Pitch + Tortuosity + Vertical Velocity	9	-7181.27	14380.6	0
Pitch + Hour + Tortuosity + Vertical Velocity	10	-7183.821	14387.7	7.11
Depth + Pitch + Tortuosity + Vertical Velocity	11	-7186.113	14394.3	13.7
Depth + Pitch + Hour + Tortuosity + Vertical Velocity	12	-7190.687	14405.4	24.85

Hour +Tortuosity + Vertical Velocity	8	-7204.047	14424.1	43.55
Depth + Hour + Tortuosity + Vertical Velocity	10	-7210.365	14440.8	60.19
Pitch + Hour + Vertical Velocity	8	-7215.529	14447.1	66.51
Tortuosity +Vertical Velocity	7	-7220.395	14454.8	74.24
Pitch + Vertical Velocity	7	-7225.475	14465	84.4
Depth + Tortuosity + Vertical Velocity	9	-7226.325	14470.7	90.11
Hour + Vertical Velocity	6	-7230.652	14473.3	92.75
Depth + Pitch + Hour + Vertical Velocity	10	-7234.01	14488	107.48
Depth + Pitch + Vertical Velocity	9	-7241.908	14501.8	121.28
Depth + Hour + Vertical Velocity	8	-7244.205	14504.4	123.86
Vertical Velocity	5	-7256.052	14522.1	141.55
Depth + Vertical Velocity	7	-7270.967	14555.9	175.38
Depth + Pitch + Hour + Tortuosity	10	-7330.31	14680.6	300.08
Pitch + Hour + Tortuosity	8	-7338.244	14692.5	311.94
Depth + Hour + Tortuosity	8	-7338.338	14692.7	312.13
Hour +Tortuosity	6	-7340.856	14693.7	313.16
Depth + Pitch + Tortuosity	9	-7362.072	14742.2	361.6
Pitch + Tortuosity	7	-7376.786	14767.6	387.02
Depth + Hour	6	-7386.116	14784.2	403.68
Hour	4	-7388.282	14784.6	404.01
Depth + Pitch + Hour	8	-7395	14806	425.45
Pitch + Hour	6	-7397.986	14808	427.42
Depth + Tortuosity	7	-7404.994	14824	443.44
Tortuosity	5	-7413.587	14837.2	456.62
Depth + Pitch	7	-7436.406	14886.8	506.26
Pitch	5	-7444.181	14898.4	517.81
Depth	5	-7455.223	14920.5	539.89
~1	3	-7463.019	14932	551.48

Appendix VIII - Box and whiskers of the distribution of depth use per hour of the day, showing each interval by the start of the hour. The y axis has been reduced to 0.05, to better observe the distribution centred around the mean. The box with the deepest depth (14:00) has been shaded.



Appendix IX - Box and whiskers of the tortuosity by deployment group. The y axis has been reduced to 0.002, to better observe the distribution centred around the mean. A Mann-Whitney U test revealed that there was no significant difference in Tortuosity between the two groups based on deployment duration ($W = 72800268$, $p = 0.058$).



15. Statement of Expenditure

Category	Item	Description	Cost*
Fieldwork	Flight	GF10 – London Heathrow to Perth	£1391
Fieldwork	Flight	QF9 - Perth to London Heathrow	
Fieldwork	Flight	QF1600 – Perth to Learmouth	£866.79
Fieldwork	Flight	QF1603 – Learmouth to Perth	

*Including VAT and delivery where applicable

I hereby certify that the above information is true and to the best of my knowledge.



Signature (Supervisor)



Signature (Student)

16. Statement of Contributors

Contributor Role	Persons involved
Conceptualization	AF, RW
Data Curation	BN, SR, JR, JP
Formal Analysis	AF, JR
Funding Acquisition	RW
Investigation	AF
Methodology	AF, RW, JR
Project Administration	RW
Resources	RW, MH
Software	MH
Supervision	RW
Validation	N/A
Visualisation	AF,
Writing	AF, RW
Editing	AF, RW, SR

Key:

- Amy Fisher (AF)
- Professor Rory Wilson (RW)
- Dr Brad Norman (BN)
- Dr Samantha Reynolds (SR)
- Dr Mark Holton (MH)
- Dr James Redcliffe (JR)
- Dr Jonathon Potts (JP)

17. Copy of Ethics Approval

Project Overview - Judicious power use in Whale Sharks (Rhincodon typus); under what conditions do they employ power above minimum?

Project Tree

Judicious power use in Whale Sharks (Rhincodon typus); under what conditions do they employ power above minimum?

1. Research Ethics Application Form

1.1 Amendment Form - 11/03/2024

FormsSubmitted DocumentsTransfersHistory


Forms

Search forms...

Form	Reference	Current Status	Date Modified
1. Research Ethics Application Form	1. Research Ethics Application Form	Approved	19/02/2024
1.1 Amendment Form	1.1 Amendment Form - 11/03/2024	Approved	11/03/2024

18. Copy of H&S and Risk Assessments

Office Risk Assessment

College/ PSU	Biosciences	Assessment Date	24.01.2024
Location	Wallace Visulaisation Suite	Assessor	Proffesor Rory Wilson 
Activity	Sitting at a computer	Review Date (if applicable)	24.01.2024
Associated documents:	• Sitting at a computer (A4 Poster)		

Part 1: Risk Assessment

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/ No
Slips and trips.	Staff and visitors may be injured if they trip over objects or slip on spillages.	<input type="checkbox"/> All areas well lit. <input type="checkbox"/> The flooring is well maintained. <input type="checkbox"/> General good housekeeping is carried out. <input type="checkbox"/> Staff/ students keep work areas clear, e.g. no boxes are left in walkways. <input type="checkbox"/> Trailing leads or cables are moved or protected. <input type="checkbox"/> Staff/ students mop up or report spillages.	No	Amy Fisher	24.01.2024	Yes
Manual handling of	Staff risk injuries or back pain from	<input type="checkbox"/> Trolleys are used to transport heavy items if required.	No	Amy Fisher	24.01.2024	Yes

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
paper, office equipment, etc.	handling heavy/ bulky objects.	<input type="checkbox"/> Heavy items are stored/ accessible at the appropriate height. <input type="checkbox"/> Staff are aware/ trained on how to split heavy loads and make them easier to handle.				
Display screen equipment e.g. computers, laptops.	<p>Staff risk posture problems and pain, discomfort or injuries e.g. to their hands/ arms, from overuse or improper use or from poorly designed workstations or work environments.</p> <p>Headaches or sore eyes can also occur, e.g. if the lighting is poor.</p>	<input type="checkbox"/> All staff have received mandatory DSE training as part of their induction. <input type="checkbox"/> All DSE users self-assess their workstation; issues identified are raised with their line manager/ supervisor and risks are reduced. <input type="checkbox"/> Review assessment upon change to user, equipment or the location of the workstation. <input type="checkbox"/> Work is planned to include regular breaks or change of activity: <ul style="list-style-type: none"> • Employer pays for eye tests for display screen "users". • Employer pays a fixed amount to cover the cost of basic spectacles prescribed for DSE use only; or to contribute to a more expensive pair. 	No	Amy Fisher	24.01.2024	Yes

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
		<input type="checkbox"/> Laptop users trained to carry out own DSE assessment for use away from office. When used at office, laptop should be used with docking station, screen, keyboard and mouse.				
Health of workers in the office environment.	All staff could be affected by factors such as, lack of job control, bullying, not knowing their role, etc.	<input type="checkbox"/> Staff/ students have management/ supervisory help to understand what their duties and responsibilities are. <input type="checkbox"/> Staff/ student can speak confidentially to a manager or supervisor if they are feeling unwell or uneasy about things at work. <input type="checkbox"/> Change is managed and communicated effectively. <input type="checkbox"/> Systems are in place to ensure demands are reasonable. <input type="checkbox"/> Signpost staff to mental health assistance and professional mental health services should they require them (see University Guidance - Health and Wellbeing).	No	Amy Fisher	24.01.2024	Yes
Electrical	Staff could get electrical	<input type="checkbox"/> Staff/ students are trained to spot and	No	Amy Fisher	24.01.2024	Yes

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
	shocks or burns from using faulty electrical equipment Electrical faults can also lead to fires.	report any defective plugs, discoloured sockets or damaged cable/ equipment. <input type="checkbox"/> Defective equipment taken out of use safely and promptly replaced. <input type="checkbox"/> Staff/ students are told not to bring in their own appliances, toasters, fans, etc. Electrical appliances are PAT tested.				
Fire	If trapped, staff could suffer fatal injuries from smoke inhalation/ burns.	<ul style="list-style-type: none"> • A Fire risk assessment has been completed and adequate fire safety measures are in place. • Evacuation plan has been implemented and tested. • Fire alarm tested regularly. • Fire drills carried out at least once a year. <input type="checkbox"/> All staff have received mandatory fire awareness training as part of their induction. <input type="checkbox"/> Regular checks made to ensure escape routes and fire exit doors are not obstructed. <input type="checkbox"/> Combustible materials are stored	No	Amy Fisher	24.01.2024	Yes

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
		safely. <input type="checkbox"/> Waste is removed regularly.				
Work equipment including, photocopier, printers, paper shredders, guillotines, etc.	Staff could get electrical shocks or burns from using faulty electrical equipment. Staff may also suffer injury from moving parts of equipment or unbalanced equipment.	<input type="checkbox"/> All new equipment checked before first use to ensure there are no obvious accessible dangerous moving parts, or siting of the equipment does not cause additional hazards. <input type="checkbox"/> Staff/ students trained in use of equipment where necessary. <input type="checkbox"/> Checks in place to ensure new staff/ students are trained to use equipment. <input type="checkbox"/> Staff encouraged to spot and report any defects. <input type="checkbox"/> Defective equipment is taken out of use safely and promptly replaced.	No	Amy Fisher	24.01.2024	Yes
Cleaning	Staff risk skin irritation or eye damage from direct contact with cleaning chemicals. Vapour from cleaning chemicals	<input type="checkbox"/> Offices are cleaned by trained cleaning staff. If cleaning is carried out by office users: <input type="checkbox"/> Cleaning products marked 'irritant' have been replaced by milder alternatives where available. <input type="checkbox"/> Mops, brushes and protective gloves are provided and	No	Amy Fisher	24.01.2024	Yes

What are the hazards?	Who might be harmed and how	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
	may cause breathing problems.	used, if required. <input type="checkbox"/> Staff are shown how to use cleaning products safely. <input type="checkbox"/> Cleaning materials are stored in a safe location.				

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No

Further information can be found on the Health & Safety intranet page:
<https://staff.swansea.ac.uk/healthsafety/>

Off Campus Activities & Fieldwork Risk Assessment (Moderate/ High) - Red Form

This form should be completed for moderate/ high risk fieldwork activities

- For low-risk activities in the United Kingdom (e.g., attending conferences/ business meetings/ museums or other low risk-controlled sites) use the **green form**.
- If the fieldwork is arranged jointly between one or more Faculties/ PSUs, a shared risk assessment and authorisation should be undertaken.
- If travelling as a group undertaking the same activity, only one risk assessment form needs to be completed along with the **Participant Declaration and Information Form**.

g

General Information This section MUST be completed by the Fieldwork Risk Assessor (leader)

Fieldwork Risk Assessor

Name:	Amy Fisher		Please Specify	Staff <input type="checkbox"/> PG Student <input checked="" type="checkbox"/> UG Student <input type="checkbox"/>
Staff/ Student Number:	[REDACTED]			Other <input type="checkbox"/>
Email:	[REDACTED]@swansea.ac.uk		Tel:	[REDACTED]
Faculty/ PSU:	Biosciences		School:	Biology
Risk Assessment Date:	12/03/2024			
Expected Departure Date:	05/05/2024		Expected Return Date:	20/05/2024
Number of persons taking part in this field trip:	Supervisors:	0	Participants:	1

Line Manager/ Supervisor of Fieldwork Risk Assessor

Name:	Rory Wilson	Department:	Biosciences
Email:	[REDACTED]@swansea.ac.uk	Tel:	

Fieldwork Information

Fieldwork/ Research Title:	Data Observation with ECOCEAN
Type of fieldwork: Please include a brief description and goal of the type of work to be performed e.g., collection of samples, observation of animals/ environment, interviews with human subjects, etc.	Observation and assistance of whale shark DD tag deployment and retrieval. Observation and assistance of on boat whale shark. Identification and following for tag deployment and retrieval, as well as GPS data obtainment.
Please provide details of the activities to be undertaken e.g., interviewing, quadrating, snorkelling, diving, rock climbing	<p>In water: Personnel swim with the whale shark at the surface at between 3-5 m using snorkelling equipment. Identification photographs of the shark will be collected (for later analysis) using a small, compact underwater camera. Whilst an additional member of the team attaches a DD tag to the dorsal fin of the shark, safety swimmers indicate the position of the shark and the direction in which it is swimming to the boat</p> <p>On boat: location of whale sharks will be identified by personnel on boat for tag deployment and retrieval and GPS data collection.</p>
Level of Risk of Fieldwork Please see risk categories in guidance document to determine the risk levels. This will determine the level of authorisation.	Moderate <input type="checkbox"/> High <input checked="" type="checkbox"/>

Additional forms included (see [Staff H&S Pages](#) or [PG H&S Pages](#))

Participant Declaration and Information Form (group travel only)	<input type="checkbox"/>
International Travel Risk Assessment Form (where applicable)	<input checked="" type="checkbox"/>

Insurance

Insurance:	Swansea University Cover Staff - Insurance webpage
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Please provide details of insurance cover. See guidance for further information. Email Insurance@Swansea.ac.uk	Students - Insurance webpage
	Additional insurance required: Yes <input checked="" type="checkbox"/> No <input type="checkbox"/> If yes, please give details: Personal travel insurance, policy number: [REDACTED] Covers worldwide travel, medical excess of £10 Million, cancellation £1500 and gadget £1500.

Location & Communication for Fieldwork

Location of Fieldwork(s): (This may be general location and NGR/GPS/what three words coordinates)	Ningaloo Bay, West Australia. Staying at RAC Caravan park Ninaglo, 3 Truscott Cres, Exmouth WA 6707, Australia	
Nearest Town/ City: (Name, distance from site)	Exmouth	
Mobile Phone Coverage https://www.gsma.com/coverage/	Primary Number:	[REDACTED]
	Coverage:	Good <input checked="" type="checkbox"/> Sparse <input type="checkbox"/> None <input type="checkbox"/>
	If none, nearest location with coverage:	
Local contact details (if applicable)	Name:	Samantha Reynolds
	Tel:	[REDACTED]
	Email:	[REDACTED]@uq.net.au
Satellite phone/ device You must know how to contact emergency services via Sat Phone. 999/ 911 typically does not work.	Device Carried:	Yes <input type="checkbox"/> No <input checked="" type="checkbox"/>
	Number:	000
Radio	Radio Carried:	Yes <input checked="" type="checkbox"/> No <input type="checkbox"/>
	Radio Channel:	VHF Channel 16 or 27MHz Channel 88. (boat)

	Who can be contacted using this radio?	'Distress, Safety and Calling' channel
Other: List any other communication devices/ methods that may be used.		
Nearby Facilities: What facilities are available at or near the site: restrooms, water, public phone, shop? If there are no facilities, where are the nearest welfare services/ what provisions will you have in place?	Exmouth is a town of approximately 3000 permanent residents and up to 5000 visitors in the peak tourist season (winter). There is a commercial airport at the Learmonth Airforce Base approximately 35 km from town. There are shops, public restrooms and water facilities,	
Down Time (see guidance for definitions): Are side trips planned or allowed during free time? If yes, please describe the activities. Are there restrictions, specific rules, or expected code of conduct? Have these activities been risk assessed? Is insurance in place for these activities?	There is no specific down time activities scheduled. Free time in the evenings will include data inspection at the accommodation.	

Fieldwork Risk Assessment

This risk assessment relates to the activities you will be carrying out during your fieldwork in the countries you are visiting. See guidance for examples of things to consider in this section.

What are the hazards?	Who may be harmed? How may they be harmed?	Controls/ Mitigation	By Whom	By When
<p>CLIMATE AND WEATHER CONDITIONS General seasonal weather conditions should be reviewed during work off-campus planning for outdoor activities, Extreme and inclement weather conditions can increase the risk of injury or illness for fieldwork participants. Risk factors to be assessed particularly for outdoor and water based fieldwork include: Season Temperature range and humidity Likelihood of rain and snow Possibility of flood events Possibility</p>	<p>All participants.</p> <p>Increased risk of illness and injury from high UV exposure, such as sun fatigue, sun burn, heat stroke.</p> <p>Increased risk of illness and injury from cold conditions, such as dehydration, numbness, and hypothermia.</p>	<p>Control: CLIMATE AND WEATHER CONDITIONS Check specific weather forecasts obtained four days before embarking on the fieldwork activity. Do not conduct fieldwork activity if forecast weather will place participants at risk of injury or illness.</p> <p>Control: CLIMATE AND WEATHER CONDITIONS Schedule fieldwork activity for a suitable season eg outdoor work at Heron Island outside of cyclone season Reschedule fieldwork activity to another date for which suitable weather conditions are forecast</p> <p>Control: CLIMATE AND WEATHER CONDITIONS Relocate fieldwork activity to another location that for which suitable weather conditions are forecast.</p> <p>Control: CLIMATE AND WEATHER CONDITIONS Use sunscreen, wide brimmed hat, sunglasses, long sleeves and shade for prolonged outdoor work in the sun. Use appropriate wet weather clothing and cover when necessary, including non-slip footwear</p> <p>Control: UQ OHS online Field Safety Training module to be completed by fieldwork participants</p>	Samantha Reynolds	<p>RISK IDENTIFIED ON: 22/03/2018</p> <p>LAST REVIEWED ON: 28/11/2018</p>

of cyclone events and high winds Possibility of electrical storms Likelihood of dry, hot conditions and fire risk Expected UV exposure Ocean and river tides and currents.				
Being bitten or stung by potentially venomous marine organisms. Organisms may include corals, fish, jellyfish, reef invertebrates.	All participants. Risk of venom include, bleeding breathing disorders, organ failure, paralysis and tissue damage	Control: At least two persons competent in first aid on site. Establish First aid procedures Control: First aid for jellyfish stings as per the ANZCOR guidelines, which would be vinegar for the field sites identified Control: PPE – Wear protective swimwear/wetsuit Control: No touching of animals if unsure of its biology and behavior. Do not harass organisms or place hands on places you cannot see (under rocks, etc) Control: Life Jacket to be worn at all times both in water and on boat Control: No lone working in water or on boat. Another person to always be in the water at any time	Samantha Reynolds	RISK IDENTIFIED ON: 22/03/2018 LAST REVIEWED ON: 28/11/2018
Barotrauma of inner or middle ear. Whilst extremely uncommon, a sudden change in middle ear pressure from a forceful valsava manoeuvre can send a shockwave through the cochlea rupturing the round window. This is a serious condition that	All participants. Barotrauma can result in permanent hearing damage,	Control: All snorkellers to be approved by Supervisor and have read Diving policy and manual Control: cease breath-hold diving if there is the slightest resistance to equalising the middle ear Control: Always snorkel with a buddy in case of emergencies/issues and for safety Control: Snorkelers briefed on induction regarding risk of inner or middle ear barotrauma from overly forceful valsava manoeuvre Control: Snorkel dive coordinator ensures that snorkellers under their supervision can equalise the inner/middle ear easily before attempting breath-hold dives.	Samantha Reynolds	RISK IDENTIFIED ON: 22/03/2018 LAST REVIEWED ON: 28/11/2018

requires urgent medical attention		Control: Snorkel dive coordinator ensures that snorkellers are fit and well before undertaking breath-hold diving		
Shark attack	All participants. Risk of major tissue damage, including limb and organ damage, and death.	Control: At least two persons competent in first aid on site. Establish First aid procedures Control: Two quick application tourniquets and a number of large dressing pads will be available Control: Snorkeling not to commence if presence of predatory sharks detected. Always snorkel in pairs and keep a watch for sharks. Control: Life Jacket to be worn at all times both in water and on boat Control: No lone working in water or on boat. Another person to always be in the water at any time	Samantha Reynolds	RISK IDENTIFIED ON: 22/03/2018 LAST REVIEWED ON: 28/11/2018
Entrapment or entanglement. Risk exists where access to the surface is prevented by entrapment or entanglement of snorkeler	All participants. Risk of drowning if entrapment occurs	Control: All snorkelers to be approved by Supervisor and have read Diving policy and manual Control: Snorkelers should avoid entering areas where direct ascent to the surface is obstructed (eg overhangs, caves, swim-throughs) Control: Snorkelers should avoid areas with large amounts of fishing line or entangled fishing nets Control: knife or cutting implement capable of cutting monofilament line easily can be carried by the snorkeler in high risk areas. Control: Consider not tagging animals if they are trailing fishing line over the top of the animal, nets etc Control: Life Jacket to be worn at all times both in water and on boat Control: No lone working in water or on boat. Another person to always be in the water at any time	Samantha Reynolds	RISK IDENTIFIED ON: 22/03/2018 LAST REVIEWED ON: 28/11/2018
Drowning or hypoxia (shallow water) blackout. various things can lead to accidents in the water, such as currents and fatigue, or holding breath (Shallow water	All participants. Drowning poses risk of organ damage especially the brain, causing prolonged	Control: Snorkel in buddy pairs Control: Advice given regarding existing medical conditions that with exercise can increase risk of injury or death Control: First aid and CPR equipment and personnel on site Control: Minimum equipment required - good fins and snorkel. Control: Snorkelers briefed at induction regarding excessive hyperventilation and risk of hypoxic blackout. Snorkel dive coordinator ensures all research	Samantha Reynolds	LAST REVIEWED ON: 28/11/2018 LAST REVIEWED

blackout occurs when oxygen levels in the blood fall below the level required to maintain consciousness.) SCUBA cannot be used because of management permit conditions and is not practical when tagging whale sharks swimming at the surface	cognitive issues, seizures, and potential death.	snorkellers under their supervision are aware of risk of excessive hyperventilation and risk of hypoxic blackout. Control: If weight belts are used, the snorkeller should weight themselves so that they are not excessively negatively buoyant at depth and at least neutrally buoyant at the surface. The weight belt must have a quick release system, and all persons involved in the snorkelling operation familiar with the operation of the quick release. Control: Life Jacket to be worn at all times both in water and on boat Control: No lone working in water or on boat. Another person to always be in the water at any time		ON: 28/11/2018
Non-associated boat traffic - In areas of high boat traffic, additional controls may need be to put in place (see UQ Diving Policy and Procedures Manual 2003 Section 8.15)	All participants. Boat traffic increases risk of collision, which may cause injury such as tissue damage, organ damage and bone fracturing.	Control: All snorkelers to be approved by Supervisor and have read Diving policy and manual Control: Dive Flag (Code 'A') flag clearly displayed in areas of high boat traffic or when in deeper water. Snorkelers should remain within 30 metres of the flag Control: On hearing propeller noise, snorkelers should scan the area for approaching boats or avoid the area/s Control: Life Jacket to be worn at all times both in water and on boat Control: No lone working in water or on boat. Another person to always be in the water at any time	Samantha Reynolds	RISK IDENTIFIED ON: 22/03/2018 LAST REVIEWED ON: 28/11/2018
Propeller injuries from associated boat traffic	All participants. Collision with propeller include	Control: All snorkelers to be approved by Supervisor and have read Diving policy and manual Control: Dive Flag (Code 'A') flag clearly displayed in areas of high boat traffic or when in deeper water. Snorkelers should remain within 30 metres of the flag Control: Associated boat will remain at a distance of 30-50 m from swimmers until pick up, when the vessel will approach to within 10 m of swimmers and	Samantha Reynolds	RISK IDENTIFIED ON: 22/03/2018 LAST REVIEWED

	damage to limbs and organs, permanent disfigurement and disability	<p>stop engine before directing swimmers to come aboard. Persons enter and exit the water only with immediate authority from the master</p> <p>Control: Boat operator competent to manoeuvre boat in an emergency Boat operator shuts engine off where there is risk of contact between the propeller and a person.</p> <p>Control: Where boat operator does not have clear line of sight to propellers a second observer capable of alerting the operator to the risk must be present.</p> <p>Control: Life Jacket to be worn at all times both in water and on boat</p> <p>Control: No lone working in water or on boat. Another person to always be in the water at any time</p>		ON: 28/11/2018
Rough or dangerous sea conditions	<p>All participants.</p> <p>Risks include inhalation of water through snorkel leading to drowning, and capsizing of boat.</p>	<p>Control: When sea conditions i.e. size of swell or high winds, current or tides makes it unsafe to get on and off the boat, and snorkel without inhalation of water, research trip will be postponed.</p>	Samantha Reynolds	<p>RISK IDENTIFIED ON: 22/03/2018</p> <p>LAST REVIEWED ON: 28/11/2018</p>
Swimmers may become fatigued after long periods in the water	<p>All participants.</p> <p>Fatigue may increase the risk of inhalation of water through snorkel, leading to drowning. Increased fatigue</p>	<p>Control: Periods in the water will be restricted to a maximum of 10 minutes. Swimmers will be monitored by boat staff and safety swimmer.</p> <p>Control: Life Jacket to be worn at all times both in water and on boat</p> <p>Control: No lone working in water or on boat. Another person to always be in the water at any time</p>	Samantha Reynolds	<p>RISK IDENTIFIED ON: 22/03/2018</p> <p>LAST REVIEWED ON: 28/11/2018</p>

	increases risk from other risks such as attacks or being bitten.			
HAZARDOUS MANUAL TASKS Hazardous manual tasks may be associated with strain or sprain injuries to the back, upper and lower limbs and manual exertion may be required for handling of equipment, materials, patients or animals.	All participants. Back strain includes risk of painful muscle spasms, ruptured disks and permanent muscle damage.	<p>Control: HAZARDOUS MANUAL TASKS Avoid manual exertion that is frequent, strenuous or that involves poor access, unstable or heavy items. Instead of carrying heavy water supplies to the location, arrange for pre-delivery of water containers to worksite or bulk delivery to water tank at site.</p> <p>Control: Use lighter weight equipment and store in readily accessible location. For example use bags made of lightweight fabric, and aluminium rather than steel equipment.</p> <p>Control: Use mechanical assistance to lift, carry and lower equipment, materials, people or animals whenever possible. Example is a vehicle hoist.</p> <p>Control: Use a two person or team" lift and carry" if risk cannot be otherwise lowered by elimination, substitution and engineering. A combination of substitution and engineering controls and two person or team lifting may be appropriate.</p> <p>UQ OHS Online Field Safety Training module to be completed by fieldwork participants</p>	Samantha Reynolds	<p>RISK IDENTIFIED ON: 26/03/2018</p> <p>LAST REVIEWED ON: 28/11/2018</p>

Add additional boxes as required.

First aid requirements

Name	Contact number whilst in the field:	Qualification		First Aid Kit Carried	Specialist equipment carried? <i>If yes, please give details</i>	
		Tick the qualification held	Expiry Date			
Dr Brad Norman		<input type="checkbox"/> Fully Trained – First Aid at Work (3 days) <input checked="" type="checkbox"/> Emergency First Aid (1 day)	March 2025	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No	Onboard the vessel: Emergency Position Indicating Radio Beacon (EPIRB), flares,

		<input type="checkbox"/> Mountain (wilderness) First Aid Trained (2 day) <input type="checkbox"/> Mental Health First Aid <input checked="" type="checkbox"/> Other – <i>please specify</i> First Aid in remote or isolated site and Cardiopulmonary resuscitation				emergency radio, life jackets, fire extinguisher
Dr Samantha Reynolds		<input type="checkbox"/> Fully Trained – First Aid at Work (3 days) <input checked="" type="checkbox"/> Emergency First Aid (1 day) <input type="checkbox"/> Mountain(wilderness) First Aid Trained (2 Day) <input type="checkbox"/> Mental Health First Aid <input checked="" type="checkbox"/> Other – <i>please specify</i> First Aid in remote or isolated site and Cardiopulmonary resuscitation	March 2025	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No	

Add additional boxes as required.

Training and Competency Requirements

List here any specific training or qualifications that need to be achieved as part of this fieldwork. This will have been identified during risk assessment above.

Training	Required for (supervisors /participants/skipper or named individual etc)	Achieved		Training date if applicable
		Yes	No	
RYA sea survival	Participant Amy Fisher.	<input checked="" type="checkbox"/>	<input type="checkbox"/>	22/09/2022
Snorkel Test	All participants must be approved by Brad Norman for snorkelling competency. Snorkelling competency was assessed by Swansea	<input checked="" type="checkbox"/>	<input type="checkbox"/>	10/02/2023

	University, and therefore approved by Brad Norman.			
		<input type="checkbox"/>	<input type="checkbox"/>	
		<input type="checkbox"/>	<input type="checkbox"/>	
		<input type="checkbox"/>	<input type="checkbox"/>	

Add additional boxes as required.

Emergency Planning

<p>Nearest Hospital(s) (to field working site) information: (Include name, distance from site, phone number, address, and postal code).</p>	<p>Exmouth Hospital, WA 6707, 01395 279684,</p>
<p>Emergency evacuation plan for site: Where abstraction may be difficult provide details of your evacuation plan and transportation options to the nearest hospital.</p>	<p><input type="checkbox"/> if not applicable check the box.</p> <p>In case of emergency while at Ningaloo Reef:</p> <ul style="list-style-type: none"> Fieldwork participants and boat staff are trained in first aid. Exmouth hospital has an emergency department and ambulance service. Medical evacuation by air to Perth can be arranged for serious cases <p>Fieldwork participants will contact the nominated Communications Person (Rebecca Cramp) at UQ if any emergency arises.</p>

Fieldwork Contingency Planning

<p>If the fieldwork risk assessor becomes unable to lead the group for any reason e.g., becomes ill. What contingency do you have in place? i.e., will the students be able to continue/return to accommodation etc.?</p>	<p>Other personnel involved in the project would take on the roles of the fieldwork risk assessor to allow the project to continue.</p>
<p>If disruption to your fieldwork/ research has financial implications, what contingency do you have planned?</p>	<p>I have a contingency of £500 as outlined in my travel application, to cover the cost of accommodation, and travel to accommodation.</p>

Equipment List

It is important the equipment list is completed in full. If something happens to the equipment in transit or it is stolen, then there is a record of equipment that can be provided to the University insurers.

Use this list to specify items of clothing/footwear, include also, sun creams, water bottles, mobile phones. Specify items of equipment that will be taken by fieldwork organiser such as life jackets first aid kits, GPS equipment, sample pots etc. Include items of communication equipment such as mobile phones, satellite phones, etc.

Item	Provided by participant	Provided by the University	Sourced locally
Wetsuit	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Snorkel	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Fins	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Life Jacket	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>
GPS	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>
Mobile Phone	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sunscreen	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Rash Vest	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Small Underwater camera	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>
Speed Tag	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>

Add additional boxes as required.

Brief Itinerary

Date	Depart from	Depart time	Destination	Arrival time	Destination address or coordinates if applicable	Mode of travel and company name and flight no if applicable.	Activities and other information
5 th May, 2024	London, UK	11:55AM		11:40AM 6 th May	Perth, Australia	Flight	
			Great Eastern Motor lodge. 81 Great Eastern Highway, 6103 Perth,		Perth	Layover. Taxi to and from airport	
7 th May, 2024	Perth	5:10AM		7:10AM	Learmouth, Australia	Flight	
			RAC Caravan park Ninagloo, 3 Truscott Cres, Exmouth WA 6707, Australia		Exmouth	Location	
18 th May, 2024	Learmouth	3:15PM		5:05PM	Perth	Flight	

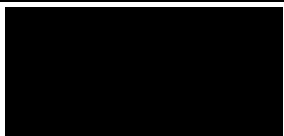
Date	Depart from	Depart time	Destination	Arrival time	Destination address or coordinates if applicable	Mode of travel and company name and flight no if applicable.	Activities and other information
			Great Eastern Motor lodge. 81 Great Eastern Highway, 6103 Perth,		Perth	Layover, Taxi to and from airport	
19th May, 2024	Perth, Australia	6:60PM		5:05AM 20 th May	London, Heathrow	Flight	

Fieldwork Declarations

Field Risk Assessor(s):

When signing this document, as the Field team leader you are confirming you:

- Have personally, considered and understand the nature of the risks and the potential impact(s) and have considered steps to reduce and mitigate the risks associated with the fieldwork.
- Have completed a suitable and sufficient fieldwork risk assessment.
- Are fit to undertake the activity/ fieldwork, are not participating against medical advice and reasonable adjustments have been agreed where required.
- All information and responses given are true and accurate to the best of my knowledge and belief.
- If group leader, will ensure the information is shared with all participants, and will ensure the participant declaration and information form, and health declarations (where appropriate) are completed prior to travel.
- All information and responses given are true and accurate to the best of my knowledge and belief.

Name:	Signature:	Faculty	Date:
Amy Fisher		Biosciences	20/05/2024

Once completed please send to the appropriate Faculty/ PSU teams for approval.

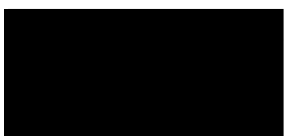
Fieldwork Authorisation

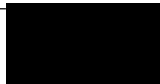
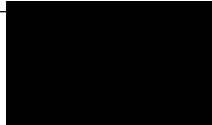
If the Fieldwork involves more than one Faculty/ PSU. Authorisation is required for all Faculty/ PSU's involved.

Approver

By signing this document, I am confirming I have read the fieldwork risk assessment and I am satisfied that the proposed reasonable precautions are in place for the activity.

Approval Moderate Risk:

Line Manager/ Supervisor	Name:	Rory Wilson
	Signature:	
	Faculty/PSU:	Science and Engineering, Biosciences
	Date:	20-3-24
	Name:	Luca Borger

Head of department /Programme Director		
	Signature:	
	Faculty/PSU:	FSE
	Date:	26/04/2024
High Risk:		
Head of School/ Director of PSU OR Head of L&T/ Research	Name:	Kevin Rees
	Signature:	
	Faculty/PSU:	FSE - School of Biosciences, Geography and Physics
	Date:	25-04-2024

Appendix 1 - Accommodation Safety

Field Course Leader Accommodation Safety Checklist

If it has not been possible to verify the safety standards of accommodation through an approved travel agent, completing this form using the Fieldwork guidance document is one method you can use to help establish whether acceptable standards are in place.

Please complete the table below, *if required*, to confirm that an assessment has been completed:

☐ This is not required

	Checked	Comments
Fire Safety	<input checked="" type="checkbox"/>	
Security	<input checked="" type="checkbox"/>	
Building Safety Issues	<input checked="" type="checkbox"/>	
Local Environment	<input checked="" type="checkbox"/>	

- ☒ I have completed the review and consider that the accommodation is safe to use.
- ☒ I have considered and noted relevant points to include in the fire brief to fieldworkers on arrival.
- ☐ **This accommodation must be assessed on arrival.**

Appendix 2: Accident reporting **only to be used if online form is inaccessible.*

It is important that all accidents are investigated and, as soon as possible, a factual report, including any statements taken, should be forwarded to the University Safety Office. Whilst adverse events are usually reported online, it would be useful in some cases to have printed versions of the adverse event form to be completed when access to the university systems may not be possible or practicable. This procedure is important because serious accidents may have to be reported to the appropriate authorities.

All members of staff accompanying a fieldtrip must be aware of the emergency arrangements and the means of contacting the emergency services. It is also useful to be able to take photographs of the accident/incident and location(s) where appropriate and you can do so without compromising the health and safety of those involved.

The completed details of this form should be emailed to healthandsafety@swansea.ac.uk as soon as reasonably practicable. If this is not possible, please phone your University Contact and provide the details over the phone.

What is being reported?			
Date:		Time:	
Brief Details (What, where, when, who and emergency measures taken):			
Details of Injury (Person):			
What first aid was administered:			
Damage (Equipment/ Property/ Habitat):			
Witnesses (Name, Occupation and Tel No):			
Who was involved in the adverse event?			
Full Name:			
Age and DOB:			
Occupation/Course of study (if student):			
Job Title:			
University Faculty / PSU or Employer:			
Email:			
Tel:			
Full Name:			
Status:			
SU Staff/ Student number:			
Visitor:			
Other (specify):			
Has the adverse event resulted in an absence from fieldwork?		Yes <input type="checkbox"/> No <input type="checkbox"/>	
If yes, for how long?			
Reported by:			
Name:			
Job Title:			
Tel:		Email:	
Date			



Travel Prepare

CERTIFICATE OF COMPLETION

This is to certify that

Amy Fisher

successfully completed the following course

Basic Travel Security Awareness

on

drum-cussac.com

info@drum-cussac.com

+44 (0)1202 802060