WHAT DO NEW PERFORMANCE METRICS, VEDBA AND DYNAMIC YAW, TELL US ABOUT ENERGY-INTENSIVE ACTIVITIES IN WHALE SHARKS?

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

Swansea University
Year of submission: 2022

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Scientific abstract

During oscillatory dives, whale sharks (*Rhincodon typus*) expend varying levels of energy in active ascent and passive descent. They are expected to minimise movement costs by travelling at optimum speed unless having reason to move faster, for example during feeding or evasion of danger. A proxy for power, dynamic body acceleration (DBA) has previously been used to identify whale shark movement patterns but has yet been used to identify occasions where power is elevated above minimum requirements. 59 hours of biologging data from 13 juvenile whale sharks (Ningaloo Reef, Western Australia) including depth, body pitch angle, magnetometry and DBA, was analysed to investigate minimum power requirements for dives and identify events of elevated power. Dynamic yaw (the rate of change of heading), a new proxy for power, was introduced to determine its effectiveness compared to the already-established DBA. The relationship between pitch angle and these two proxies was investigated to determine which had the stronger relationship. Dynamic yaw produced a poor relationship with pitch angle compared to DBA, and thus DBA was selected as the focus proxy for the remainder of the study. DBA was utilised to produce a minimum power trend versus body pitch angle using a convex hull analysis which allowed for the identification of proxy for power utilisation above the minimum (PAM). 16 instances of PAM were identified in 59 hours of data, which could all be considered instances where energy minimisation is not prioritised, such as feeding or avoidance. The PAM method was capable of identifying instances where energy minimisation is not prioritised, and therefore has future implications in investigations of location-specific behaviours in relation to feeding and anthropogenic disturbance.

Lay summary

Animal movement is energetically costly, and animals are expected to minimise the cost of movement unless for example moving at faster speed, allows energy gain from catching prey or is required for survival. Whale sharks make frequent dives to deep water whilst swimming for example feeding or avoiding stressors such as swimmers and boats. Whilst researchers have used a measurement of acceleration to indirectly estimate energy costs and investigate general movement patterns, they have yet to identify the frequency of significantly high-cost behaviour.

Data from 13 whale sharks in Ningaloo Reef, Western Australia which had been collected by tags which recorded data whilst the animals were swimming, including depth, horizontal or vertical swimming, and speed, were used to investigate whether dynamic body acceleration (DBA) and another proposed proxy for energy expenditure, dynamic yaw (the rate of change of heading), which is the rate at which the torso of the animal moves from side to side, can be used to investigate the minimum possible values for a given body angle while diving and then determining the power above minimum (PAM).

I concluded that as dynamic yaw did not share a strong enough relationship with body angle, it would not be used further in this study as other variables had too much of an influence on it. However, DBA had a very strong relationship with body angle during the ascent portion of dives and could be used to calculate the minimum power expected to be used at certain body angles. By creating equations for the relationship between body angle and minimum power, I could examine the spread of PAM data to identify specific points where it was significantly higher than the rest of the data and fell outside of the natural range of power used by each animal.

As the whale sharks were using an unusually high level of energy at these points, we can confidently say that there was likely to be a specific reason, for example swimming faster to catch pray or trying to avoid a loud sound they considered a threat such as a boat engine.

By using this method of finding points of high-power usage in whale shark swimming, future studies can look at where and why these happened. If, for example, by using GPS coordinates, scientists can find an area in which whale sharks are feeding frequently, they can use this information to try and improve conservation of whale sharks, for example encouraging governments to limit fishing and boats in the area to allow them to feed undisturbed.

An underwater image taken of a whale shark with a biologger attached to its dorsal fin.

University statement and declarations

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed .....Abigail Buxton.. (candidate)

Date ....30/02/2022..

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed ....Abigail Buxton... (candidate)

Date ....30/02/2022...

STATEMENT 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed ......Abigail Buxton.. (candidate)

Date ....30/02/2022..

Statement of expenditure

Student name: Abigail Buxton

Student number: 961017

Project title: What do new performance metrics, VeDBA and dynamic yaw, tell us about whale shark allocation of effort to foraging?

Category	**Item**	**Description**	**Cost***
Equipment	HP laptop	Personal laptop was not powerful enough to handle data analysis, thus a new one was required.	£790
Total			£790

* including VAT and delivery where applicable

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

[redacted]

[redacted]

Signature (supervisor)

Signature (student)

Statement of contributions

Contributor role	**Initials of contributors**
Conceptualisation	RW, KR, AB
Data Curation	BN
Formal analysis	AB
Funding acquisition	RW, BN
Investigation	AB
Methodology	RW, KR, AB, JP, BN
Project administration	RW, KR
Resources	RW, KR, MH, BN
Software	MH, RW
Supervision	KR, RW
Validation	N/A
Visualisation	AB
Writing- Original draft preparation	AB
Writing- review and editing	AB, KR, RW

Key:

- Abigail Buxton (AB)
- Dr Kayleigh Rose (KR)
- Professor Rory Wilson (RW)
- Brad Norman (BN)
- Mark Holton (MH)
- Jonathon Potts (JP)

Copy of ethics approval

A copy of my ethics form, details, and approval submitted to the Swansea University ethics committee can be found below

Student Details

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Course:	Biosciences
Project Supervisor:	Dr Kayleigh Rose
Last Updated Date:	23 Jan 2022, 3 p.m.
Last Reviewed Date:	29 Jan 2021, 4:06 p.m.
Reviewed by:	Kayleigh Rose

Projects Ethics Assessment Status

Project Title	Status	Approval Number
What do new performance metrics, VeDBA and Dynamic Yaw, tell us about whale shark allocation of effort to foraging	Completed	SU-Ethics-Student-290121/3705

Project Ethics Assessment

It is mandatory requirement to complete this Project Ethics Assessment before starting any project in the College. Any further assessments can be submitted as and when required. A unique reference number will be generated and sent to you by email for each of the completed Ethics Assessment below.

Approval Number: SU-Ethics-Student-290121/3705

Reference Number: STU_BIOL_161788_290121122559_1

Status: Completed

You will find useful documents at: Ethics Resources

Project Title: What do new performance metrics, VeDBA and Dynamic Yaw, tell us about whale shark allocation of effort to forag

Project Start Date: 01/02/2021

Project Duration: 18 months

Copy of H&S risk assessment

A copy of the health and safety risk assessment for the desk-based study can be found below.

HEALTH & SAFETY
IECHYD A DIOGELWCH

Risk Assessment			
Abigail Buxton			
College/ PSU	College of science	Assessment Date	29/1/21
Location	Swansea	Assessor	Kayleigh Rose
Activity	MRes Project	Review Date (if applicable)	
Associated documents	•	•	

Part 1: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Eye strain	Student	Discomfort to eyes from looking at a screen, Prevented from continuing work	Taking repeated breaks	1	2	2	Limit time infront of computer to 1 hour blocks with 10 minute breaks between each	1	2	2	
Headache	Student	Discomfort, pain, unable to continue work or carry out daily tasks due to looking continuously at a scrren	Drink plenty of fluids	1	4	4	Allow freshair into the room, take breaks stated above	4	1	4	
Back problems and pain	Student	Injury to back and neck due to poor posture and unsuitable equipment, potentially requiring medical attention if severe	Correct posture so sitting corectly	2	3	6	Work sat at a desk or table seated in a comfortable, supportive, padded chair	2	2	4	
Repetitive strain injury	Student	Pain and discomfort to hands after prolonged periods of typing	Taking extended breaks from typing and using mouse and touchpad	2	3	6	Take breaks stated above, reduce the amount of typing done at any one time to minimal	2	2	4	

HEALTH & SAFETY
IECHYD A DIOGELWCH

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
Create schedule for when work should be undertaken so that the required breaks are taken and too much time spent in front of the computer occurs in one day	Student	30/01/2021	
Set up a dedicated workspace near window with all required items to minimise health risks	Student	28/01/2020	Yes
Invest in a good supportive chair to work in	Student	28/01/2021	Yes

Actions	Lead	Target Date	Done Yes/No

Appendix 1. Risk Matrix

		Consequences				
		1 **Insignificant** No injuries/ minimal financial loss	**2** **Minor** First aid treatment/ medium financial loss	**3** **Moderate** Medical treatment/high financial loss	**4** **Major** Hospitalised/ large financial loss	**5** **Catastrophic** Death/ Massive Finanical Loss
Likelihood	**5** **Almost Certain** Often occurs/ once a week	5 Moderate	10 High	15 High	20 Catastrophic	25 Catastrophic
	4 **Likely** Could easily happen/ once a week	4 Moderate	8 Moderate	12 High	16 Catastrophic	20 Catastrophic
	3 **Possible** Could happen/ happen once a year	3 Low	6 Moderate	9 Moderate	12 High	15 High
	2 **Unlikely** Hasn't' yet happened but could happen	2 Low	4 Moderate	6 Moderate	8 High	10 High
	1 **Rare** Concievable but 1/100 year event	1 Low	2 Low	3 Low	4 Moderate	5 Moderate

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Acknowledgements

I would like to thank my supervisors for their continued dedication and support towards my project, for marking numerous drafts and for working around my ever-changing deadlines.

I would also like to thank my family, friends, and significant other Joseph Dowling for always helping me find the right word and providing a near endless stream of coffee and encouragement.

List of tables, figures, and illustrations

Definitions and abbreviations

The below table contains a list of the abbreviations and technical terms used within the text as well as their full term and their meaning.

Abbreviation / technical term	**Full term**	**Definition**
ODBA	Overall dynamic body acceleration	Dynamic acceleration around an animal's centre of mass. Measured in three dimensions. Overall sum of DBA (Wilson *et al*., 2006)
DBA	Dynamic body acceleration	Acceleration-based proxy for power
VeDBA	Vectoral dynamic body acceleration	Vectoral sum of DBA
PAM	Power above minimum	VeDBA exhibited-minimum VeDBA required for that movement
Dynamic yaw	Dynamic yaw	Rate of change of heading

Introduction

Animal movements are behaviours that influence fitness in events such as feeding, avoidance, mating and habitat selection (e.g. Brunnschweiler *et al*., 2008; Gallager *et al.,* 2014). Animals are expected to behave to balance energy gained from feeding with energy expended searching for food (Papastamatious *et al*., 2018), and decisions on biological processes such as reproduction are often directly influenced by energy budget (Hammerschlag *et al*., 2018) due to the high energy output required (Scarnecchia *et al*., 2007). Metabolic demands are directly proportional to oxygen consumption rates and foraging requirements (Whitney *et al*., 2016) however some animals have succeeded in minimising energy spent whilst foraging (Sims *et al*., 2006) for example data recorded from tiger sharks (*Galeocerdo cuvier)* showed that when the sharks dived at an angle of between 5^{o} and 14^{o} the energetic cost of transport (energy per unit distance) was minimised and thus foraging efforts were more efficient due to less energy expenditure required to forage (Andrzejaczek *et al*., 2020). Oscillatory dives undertaken whilst swimming allow for negatively buoyant animals such as whale sharks (*Rhincodon typus*) to reduce energy expenditure whilst swimming (Weihls, 1973) as gliding on the descent allows for reduced body movement and energetic output (Andrzejaczek *et al*., 2020) which can then be utilised for high-energy activities such as feeding. Ascent on the other hand requires propulsion and thus a higher energy expenditure than descent (Gleiss *et al.,* 2011b), especially in negatively buoyant animals who do not possess a swim bladder (Iosilevskii and Papastamatiou, 2016). This is due to the requirement to produce dynamic lift to enable them to rise in the water column (Strand *et al*., 2004).

Until recently, quantifying energy expenditure in the field was difficult, with the only available data coming from estimations made in laboratories using calorimetry (Gleiss *et al*., 2011) and the doubly labelled water method which uses isotope measuring of hydrogen and oxygen in water (Speakman 1998), monitoring the oxygen isotope exchange between the isotope in the water and the isotope in respiratory carbon dioxide (Butler *et al*., 2004). Whilst this method has been successful for smaller animals (e.g. Speakman and Król, 2005) and humans (Schoeller, 1999), whale sharks can reach up to 18.8m in length when fully matured (McClain *et al*., 2015) and accommodating this size in a lab based setting is near impossible, thus making recreation of the conditions required for this experiment unfeasible. Additionally, due to issues in the accuracy of measurements, the method cannot produce reliable results pertaining to the energy demands of an animal (Butler *et al*., 2004).

A new proxy for energy expenditure based on acceleration measurements recorded onboard individual animals is now used widely as a proxy for energy expenditure in the field but requires calibration in a laboratory (Wilson *et al.,* 2020). Recently, data from on-board accelerometers has been shown to be a powerful proxy for energy expenditure in free-living animals. One such proxy is dynamic body acceleration (DBA), a metric calculated from accelerometer measurements collected from tags deployed on animals near to the centre of mass (Halsey *et al*., 2008). DBA measures acceleration induced around the trunk of an animal as a result of moving body parts. DBA is calculated as either the sum (Overall Dynamic Body Acceleration, ODBA), or vectorial sum (Vectorial Dynamic Body Acceleration, VeDBA) of acceleration in three axes after subtracting static acceleration (Wilson *et al*., 2020). Regardless of the sum used, DBA correlates with movement related energy expenditure in a wide range of animals moving terrestrially or in water (Wilson *et al*., 2006; Gleiss *et al*., 2011; Fourati *et al*., 2011; Laich *et al*., 2011; O'Mara *et al.,* 2019). ODBA was first used as a proxy for energy expenditure in 2006 in a study of cormorants on a treadmill (Wilson *et al*., 2006) and calibrations have since been done for a wide range of animals including humans (*Homo sapiens*), Magellanic penguins (*Spheniscus magellanicus*) (Halsey *et al*., 2008) and elasmobranchs including the nurse shark (*Ginglymostoma cirratum*) and lemon shark (*Negaprion brevirostris*) (Lear *et al*., 2017).

ODBA and VeDBA (collectively DBA), are both considered sufficient proxies of movement related energy expenditure, with a regression between the two values producing a nearly perfect linear fit (Wilson *et al*., 2020). However, VeDBA accounts for angular inadequacies and orientation issues of tags which ODBA does not (Wilson *et al*., 2020) and thus was chosen for this study.

Magnetometers are a key aspect of biologgers as they can be used to extract heading but are not affected by acceleration and so can be used in conjunction with acceleration date to derive metrics useful for identifying specific behaviours (Williams *et al*., 2017). Magnetometers record data by measuring the intensity of the Earth's magnetic field and calculating the changes in orientation of the tag within this field, with orientation to the north producing maximum values and orientation to the south producing minimum values (Wilson *et al*., 2017).

Dynamic yaw is a newly presented proxy for power (energy expended per unit time). It is quantified by the measurement of magnitude along the magnetometry Y axis which records the frequency at which the heading of the tagged animal changes. It is therefore expected that as the frequency of heading change increases, so does the energy expended. It is hypothesised that using dynamic yaw to approximate energy expenditure in place of DBA will eliminate the issues surrounding low DBA signals for slow moving animals.

In order to examine elevated power levels required for feeding or other urgent behaviours that take priority over minimising energy output, the normal power requirements for swimming must first be considered. Like many other elasmobranchs, whale sharks are negatively buoyant, therefore they are denser than the surrounding sea water and are required to actively swim forward to stop themselves from sinking (Gleiss *et al*., 2011b). Looking at the power requirements (using DBA as a proxy), descending whale shark can evidently swim via gliding, at no expense of power, by using their negative buoyancy to aid in the descent (Gleiss *et al*., 2011b). However, ascending in the water column necessitates power, with steeper climb angles requiring more power (Gleiss *et al.,* 2011b) due to the need to counteract their negative buoyancy. I therefore propose that when DBA is plotted against mean shark body pitch angle for a series of different body pitches, the results will detail how power (specifically a relevant proxy for it such as VeDBA or dynamic yaw) varies with pitch. Graphs of DBA values taken for any given pitch angle during dive ascent will allow determination of the minimum power required to swim at any given pitch angle, with any DBA values above this indicating that the whale shark is working at a level above the minimum to ascend, which could be due to feeding activity or other energy-intensive activities such as avoidance.

Whale sharks generally travel slowly, with swim speeds recorded around 3.9 km/hour (Eckert and Stewart, 2001) with a particularly low tailbeat frequency, with tail beat periods ranging between 5.5±1.1 s during non-feeding swimming and 8.4±1.7 s whilst feeding (Cade *et al*., 2020). As a result, VeDBA is predicted to be less effective as a predictor of power due to the whale sharks' reduced acceleration signals (Hopkins *et al*., 2021). Dynamic yaw is being proposed as a new metric as, despite DBA proving useful for fast-moving terrestrial animals (e.g., O'Mara *et al*., 2019), it produces small signals for slow moving aquatic animals, making analysis difficult (Hopkins *et al*., 2021). Dynamic yaw has some of the same drawbacks as DBA e.g. DBA calibrations for whale sharks also cannot be completed due to lack of laboratory space, and it has previously not been correlated with body pitch angle for use as a proxy for power expenditure. Nevertheless, it still shows initial promise as a proxy for power for large, slow moving marine animals (Wilson *et al*., 2022) and thus will still be utilised in this study to determine whether it presents a better method

Whale shark movements primarily consist of oscillatory dives which take place largely in the epipelagic zone (Brunnschweiler and Sims, 2011). Previous assessments have noted dives at depths of 1300 m (Brunnschweiler *et al*., 2009), however these appear to be uncommon events, as whale sharks spend 96% of daylight hours at <100 m depth (Rowat and Gore, 2007), with up to 60% of this time within the top 10 m of the surface (Gunn *et al*., 1999). These dives are theorised to be driven solely by biological pressures, such as prey distribution, thermoregulation, and navigation (Araujo *et al*., 2020) all of which are factors that heavily influence energy expenditure in animals (Torres *et al*., 2006; Thums *et al*., 2012). However, there is also evidence of crepuscular and diel patterning, as dives have been recorded reaching greater depths during daylight hours than during darkness, and sudden swimming pattern variations are reported to occur at dawn and dusk (Tyminski *et al*., 2015). In addition, more recent studies have noticed that the diving behaviour of whale shark changes when in proximity to tourists and their accompanying vessels, as diving is their most common method of avoidance (Legaspi *et al*., 2020), making it more difficult to understand the biological factors driving diving behaviour. Nonetheless, these types of studies have documented behavioural changes that could lead to an increased expenditure of effort, including more frequent directional changes (Raudino *et al*., 2016) and increased swim speed (Haskell *et al*., 2015) indicating that such behaviours are not sustainable over long periods of time in terms of energy expenditure as they are only performed when placed under stress or other external pressures.

An influence on depth change is the diel migration of zooplankton (Graham, Roberts and Smart, 2006), notably crustacea larvae (Sampaio *et al*., 2018) and krill (Australian Government, 2021). The whale shark is one of only three extant species of filter-feeding shark, the other two species being the basking shark (*Cerophinius maximus*) and the megamouth shark (*Megachasma pelagios*) (Compagno, 1984). Whilst the filter-feeding apparatus of the whale shark has yet to be described in detail, the first and most widely accepted description comes from Gudger (1941a), who described the feeding organ as a large mouth possessing disproportionately small teeth and gill arches, the latter containing sieves with a texture likened to a sponge. Whilst the whale shark does possess teeth, it is the gill arches and sieves which are used most in the feeding process, by taking in large volumes of sea water containing prey items and then pushing the water through the gill arches, allowing the sieves to retain any organisms (Heyman *et al*., 2001). The most common method of obtaining this food is by RAM filter-feeding (Whitehead *et al*., 2020) a technique employed by all three filter-feeding sharks; however, the whale shark has the additional ability to feed via suction feeding (Nelson and

Eckert, 2007). RAM filter-feeding is hypothesised to be a highly energy intensive activity due to the increased drag caused by the large open mouth decreasing the stream-lined nature of the body (Carey and Goldbogen, 2017) and thus instances of RAM filter feeding are likely to only occur when the energetic gain from the food obtained outweighs the energetic cost of feeding. Since feeding by planktivorous sharks requires their mouths to be open, the drag from water resistance will increase (Potvin and Werth, 2017) and are thus required to exert higher level of power (energy per unit time) (Carey and Goldbogen, 2017). As RAM filter-feeders, whale sharks are required to be in a constant state of motion for the process to be effective (Brown and Muir, 1970). It is therefore hypothesised here that studying the power requirements for swimming will reveal feeding events.

Although the diet of whale sharks was originally presumed to be purely planktonic (Gudger, 1941b), organisms including squid, tuna, algae and other medium to large nektonic species have also been found in gut samples from deceased whale sharks (Borrell *et al*., 2011). The wide variety found in the diet is due to the shark's opportunistic feeding habits, with feeding events influenced by prey density (Sampaio *et al*., 2018). Feeding is considered to occur almost exclusively at the ocean's surface or a few metres below as plankton tend to aggregate in these areas (Motta *et al*., 2010). However, there is still a lack of information on the foraging behaviour of whale sharks, so feeding patterns remain poorly understood (Rowat and Brooks, 2012). Despite the lack of foraging information on whale sharks, they have been documented inhabiting areas of high plankton densities for extended periods of time (Hsu *et al*.), meaning that they are likely to expend less energy searching for food if they remain surrounded by high food densities.

This study's aim was to examine the incidence of high-power periods which could be any behaviours during which minimisation of energy expenditure is not prioritised, e.g., feeding (Sims, 1999) or avoidance of unwanted influences such as predators or tourists (Montero-Quintana *et al*., 2020). This was achieved using both VeDBA and dynamic yaw. Dynamic yaw is predicted to be more accurate in calculating the power used within that timeframe as individuals may differ in power usage despite moving the same distance over time. Here, by examining the relationship of DBA versus dive ascent pitch angle, and dynamic yaw versus dive ascent pitch angle, a trend for the minimum possible power for a given pitch angle will be determined, allowing calculation of the power above minimum (PAM) to aid in the identification of high-power periods. It is proposed that certain high-powered activities including feeding and evasion can then be identified in future research using this method.

Methods

The study site

Ningaloo Reef lies off the coast of Western Australia (22º33’45” S 113º48’37” E) (Figure 1). It spans more than 300 km along a narrow section of the Australian continental shelf, and exhibits a steep depth contour which levels out at 200 m less than 20 km offshore (Kobryn *et al*., 2013).

Data collection

Thirteen juvenile whale sharks, measuring between five and nine metres, were tagged using Daily Diaries (Wilson *et al*., 2008; DDMT: Wildbyte Technologies, http://wildbytetechnologies.com/) between June 7th 2020 and May 5th 2021.

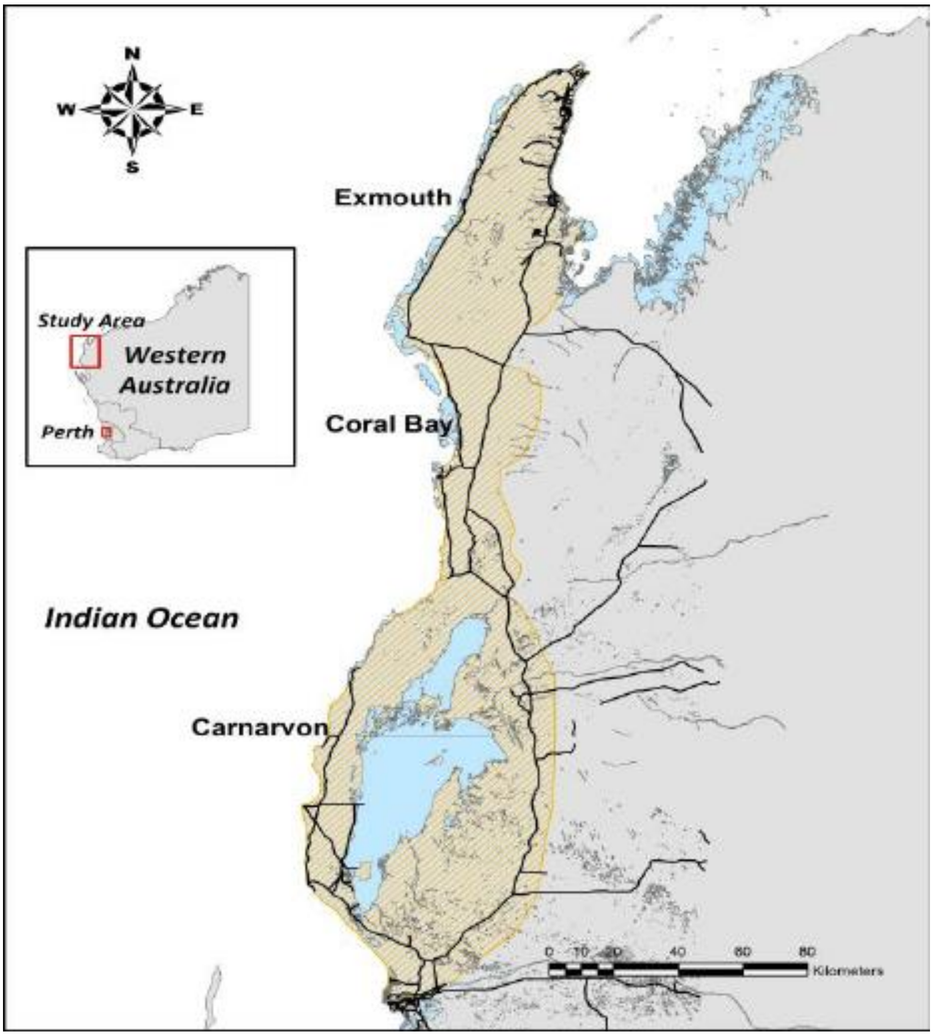

Figure 1. Scale map of Ningaloo Reef, Western Australia (Kahtani et al., 2011)

The tags were deployed on the first dorsal fin of each shark (Figure 2) by Brad Norman and his team by entering the water and swimming alongside each shark. A tag was attached to the dorsal fin using a spring clamp method (for details of equipment and tagging protocol see Gleiss *et al*., 2009). Subsequent to tagging, spotters were deployed on a boat and swimmers in the water to keep track of each shark and ensure the boat followed at a distance of approximately 80 m to ensure the sharks were not disturbed during this process. Once an allotted time had passed (between two hours and six days) the tags were detached from the shark manually by releasing the cotter-pin located inside the tag. The tags recorded tri-axial acceleration, tri-axial magnetic field intensity and pressure (depth) data, each at a frequency of 20 Hz.

Figure 2. Daily Diary tag attached to the first dorsal fin of a juvenile whale shark in Ningaloo Reef, Western Australia. Photo taken by Brad Norman, 2020

Ethics

The Swansea University Ethical Committee approved the ethics for this project on 29th January 2021, allowing the project and subsequent analysis to go ahead. The ethics form for the collection of data used was completed by Brad Norman and approved by the relevant Australian ethics board prior to collection: Murdoch University (Permit No. RW3327/21) and The University of Queensland (Permit No. SBS/085/18/WA/International).

Data analysis

The movement data was analysed using the DD-MT software (Wildbyte Technologies, http://wildbytetechnologies.com/), which plots recorded data against a timeline and allows exportation of selected data (for further information see http://wildbytetechnologies.com/). Due to imperfect attachment of the tags to the sharks, each dataset had to undergo a correction for tag pitch with respect to shark body pitch to ensure that the tag pitch, which represented the animal's body pitch, was 0 º when the shark body pitch was 0 ^{0}. This was done by rotating the pitch values within DD-MT so that, when the shark swam for extended periods at a constant depth, the pitch read 0 ^{0}. This process corrected all recorded pitch values accordingly.

Several parameters were calculated within DD-MT and exported for further analysis. These were:

- Pressure (hbar), converted to depth (m)
- Vertical velocity (m/s)
- Body pitch angle (^{o})
- Smoothed VeDBA (g [see below for definition])
- The rate of change of heading or heading differential (hereafter termed dynamic yaw) (^{o}/s)

VeDBA (Vectoral dynamic body acceleration (Qasam *et al*., 2012)) is a one of two commonly used metrics (Wilson *et al*., 2020) calculated from tri-axial recordings of acceleration (Jeanniard-du-Dot *et al*., 2017) and is calculated as;

$$VeDBA = \sqrt{(A_x - \overline{A_x})^2} + (A_y - \overline{A_y})^2 + (A_z - \overline{A_z})^2$$

where A_n is the measured acceleration in the direction n (based on triaxial recordings), whereby the subscripts for n; x, y and z represent the three orthogonal axes; surge, sway and heave respectively (Wilson *et al*., 2019), and $\overline{A_x}$, $\overline{A_y}$ and $\overline{A_z}$ are the 2-s running means representing the static components of acceleration (Stothart *et al*., 2016).

VeDBA was also used to identify tail beats, with each spike in smoothed VeDBA (a running mean over 5 s) identifying the initiation of a single tail beat (where the tail undergoes a whole beat cycle, finishing up where it began).

All the data was smoothed over 1 second to remove noise before being exported as the data was recorded at 20 Hz. This smoothing was intended to remove minute signal changes which would interfere with the overall result.

Dynamic yaw (the rate of change of heading) is the newly proposed metric in this study, and is calculated as:

$$Dynamic\ yaw = \frac{\Delta x\ (^\circ)}{time\ (s)}$$

where 'Δx (°)' is the change in heading of the individual in degrees, taken from the magnetometry Y axis, and 'time (s)' is the timeframe the section of recording is taken over in seconds.

Identification of body pitch versus metrics for power

To be able to plot body pitch *versus* the metric for power (VeDBA or dynamic yaw), sections of data had to meet strict criteria in order to qualify. These criteria were determined by the researcher to ensure that the sections of data were long enough to contain enough information for analysis and were not influenced by changes in behaviour which occur as part of the natural dive process e.g., swim speed increases in the final portion of the descent to prepare to begin the ascent.

These criteria were;

- Span a timeframe of longer than 10.0 s
- Be more than 5 seconds from a turning point in rate of change of depth (i.e., where the shark goes from descending to ascending or *vice versa*)
- Have a mean pressure differential that varied by no more than 0.002 pa for the allocated timespan.

Not all dives analysed met these criteria, however data meeting these requirements was identified and then it was 'bookmarked' using the DD-MT bookmark multisession masterfile tool. The bookmarked data were then exported for further analysis together with the following data;

- Start time
- Duration
- Start pressure (depth)
- End pressure (depth)
- Dynamic yaw
- Mean smoothed VeDBA
- Mean pitch angle
- Vertical velocity
- Magnetometry Y

Magnetometry along the Y axis was a key reading which needed to be extracted as it represents the sway of the animal, i.e., the movement of the trunk from side to side. This movement is the basis for dynamic yaw and would be needed to graph how the rate of change of heading of the sharks changed with differing body angles and depths.

Vertical velocity was included in the extracted data as it's linear relationship with pitch angle would provide a baseline for the expectations of how effort at a given body pitch angle changed with changing levels of energy output.

The exported parameters were loaded into Excel, where the depth change and vertical velocity for each data point was calculated.

The master file containing the extracted data from all the datasets was loaded into R and scatter graphs using ascent data only (because sharks can glide down in the water column without actively swimming [Gleiss *et al*., 2011b]) were plotted for the following relationships:

1. Vertical velocity and mean pitch angle
2. Dynamic yaw and mean pitch angle
3. Mean smoothed VeDBA and mean pitch angle
4. Mean smoothed VeDBA and vertical velocity

R studio (R Core Team, 2021) and specifically the ggplot2 package (Wickham, 2016) were used to construct graphs and calculate line equations. The data from all 13 whale sharks was combined into a single data set and then quadratic equations were then used to calculate regressions between the variables and calculate p values, R^2 values and F statistics to determine the relationship between the data sets.

The initial graphs displaying the above relationships contained data from all 13 whale sharks tagged for the study, however six sharks where then chosen at random to undergo further analysis and comparison. These were chosen using a random number generator to eliminate possibility of researcher bias towards data sets which may have contained more frequent dives to ensure that a wide range of the sharks were analysed further, not just those that appear to have potential for instances of PAM. Due to time constraints, not all individuals were able to be further analysed for instances of PAM, and so six were chosen as it represented half of the data set and allow sufficient analysis.

The mathematician Jonathon Potts (Sheffield University) derived the minimum power lines for each of the six whale sharks for mean smoothed VeDBA against mean pitch angle. To fit each curve, all pitch angles below 0 were removed due to the assumption that whale sharks exert no power when moving down in the water column. Next, a quadratic equation of $VeDBA=a+b*(pitch)^2$ was fitted to the data points and the 95% confidence intervals mapped, with any datapoints falling outside this boundary removed to eliminate outliers potentially caused by noise in the data. A convex hull was drawn by connecting the outermost remaining points on the graphs, then the data points on the underside of the graph, joined by the convex hull were used to generate another quadratic equation $VeDBA=a+b*(pitch)^2$ that provided a minimum power line.

Power above minimum (PAM)

This minimum power equation was used to derive the (proxy for) power above minimum (hereafter PAM) with which the sharks swam by subtracting the minimum power line values from the power proxy values (VeDBA or dynamic yaw). Using this methodology, the majority of datapoints will fall above the minimum power line. However by how much, how often and the causes of it are questions that will be answered by this report.

Points were identified as PAM if they were identified as statistical outliers within the remaining data. Having removed any outliers that are likely to be caused by noise or incorrect data recording, any outliers in the remaining data were taken as instances of high power use.

Results

Animal profiles

Table 1. Details of the whale sharks monitored, including their size (where data was available), length of time tagged, and the number of dives analysed per whale shark.N/A indicates that the data for that particular aspect of the shark was unavailable due to gaps in the metadata. Sharks listed below were used in the initial analysis, and those with ID numbers underlined represent the six used in the further PAM analysis.

Animal ID	*Size (m)*	*Length of time tagged (hrs)*	*Number of dives per shark analysed*
020521	8	5	8
060521	N/A	6	15
080521	9	4.5	10
090521	8.5	5	14
<u>120521</u>	7	4	9

130521	N/A	4	12
250421	6.5	5.5	6
290421	N/A	4	8
240421	8.5	4	11
270421	5	4.5	12
150620	6.5	4	9
110620	7.5	4	13
070620	6.5	4.5	11
Total tagging time		59 hours	

Dive profiles

All of the dives sampled followed a stereotypical 'up down' dive profile (Figure 3a), where the whale shark descended in the water column to a certain depth and then turned sharply and ascended almost immediately. In the instance illustrated in Figure 3a, the shark descended to a max depth of 8.5 m, with the whole dive and ascent taking a total of 9 minutes. The difference in PAM between the ascent and descent portion of the dive can be seen in Figure 3b; the animal is using more power than the minimum expected at the surface, with the PAM staying close to zero during the descent phase and increasing during the ascent. The tailbeat pattern during the decent compared to the ascent can be seen in the magnetometry Y axis signal (Figure 3c); during the descent there is a large drop in tail beat signal, indicating little to no tail movement, with the tail staying mostly central for the majority of the descent, however during the ascent, the tail beats are a lot more uniform and pronounced, indicating active effort is taking place. The vertical velocity (Figure 3d) of the dive shows that during the descent phase the shark descends at a variable speed, with the speed of descent ranging from 0 m/s to –0.14 m/s . When the shark makes the turn at the bottom of the dive and begins to ascend, the vertical velocity rapidly increases to above 0 m/s as the shark swims at varying speeds to ascend in the water column before finally returning to surface swimming with no vertical velocity as at the beginning of the dive.

The body pitch angle during the dive follows the expected pattern (Figure 3e); the body is pitched downwards for the duration of the descent, levelling off as it nears the bottom of the dive and is pitched upwards for the ascent, however does dip back downwards again during one portion of the ascent.

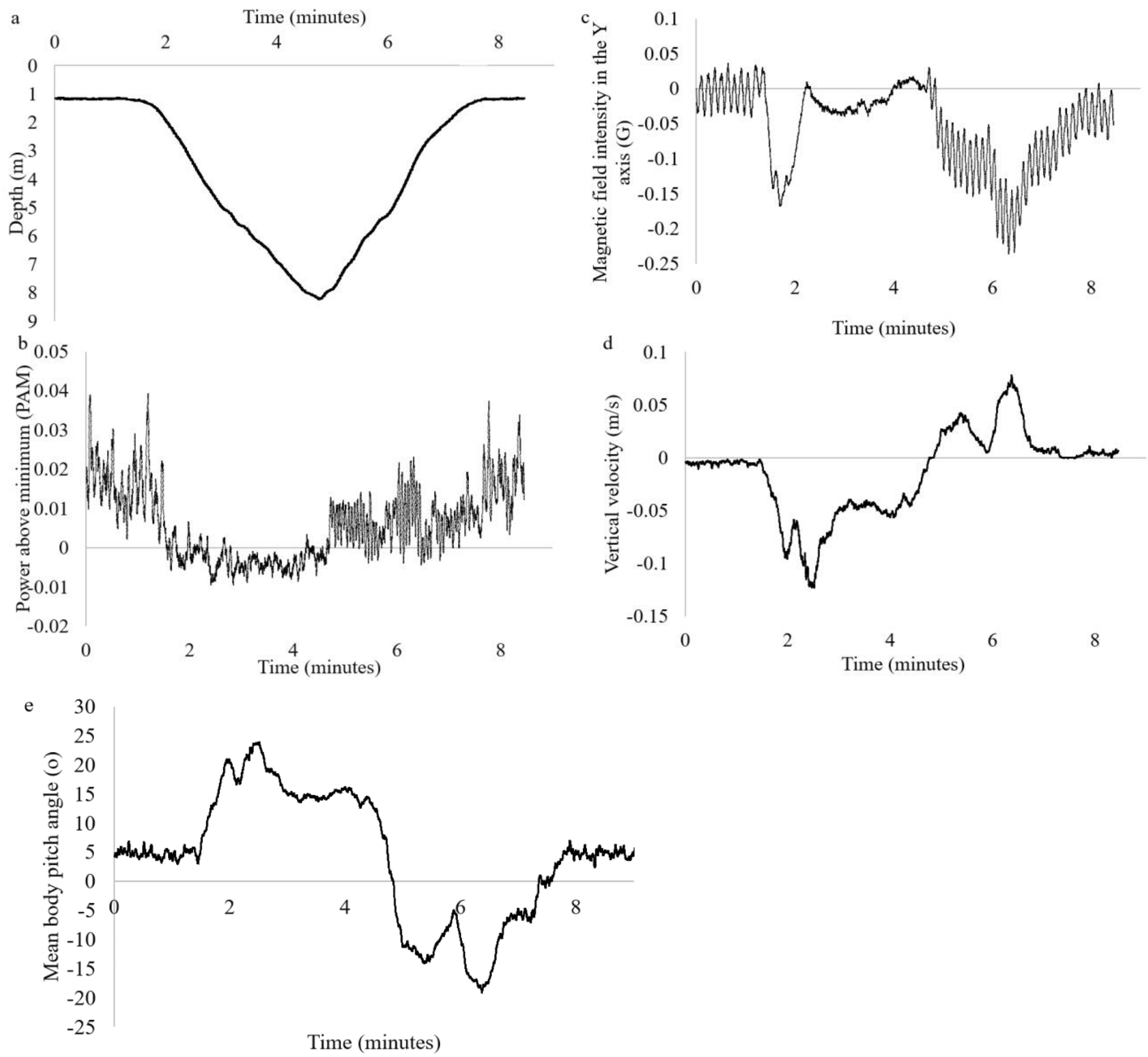

Figure 3. Typical down-and-up dive of a whale shark a) showing depth at each section of the dive; b) the magnetometry depicting tail beats; c) PAM for the duration of the dive; d) the vertical velocity and e) the body pitch angle change

Speed of ascent according to pitch angle

As whale sharks ascended in the water column, vertical velocity increased linearly with increasing pitch angle (Figure 4) ($p < 0.001$, df = 1641, F = 2601, $R^2 = 0.81$). The regression had a strong correlation, indicated by the high R^2. At a mean pitch angle of between 0º and 20º, the data points were close to the regression line, with the exception of a few outliers. However, as the mean pitch angle exceeded 20º, the datapoints spread out more.

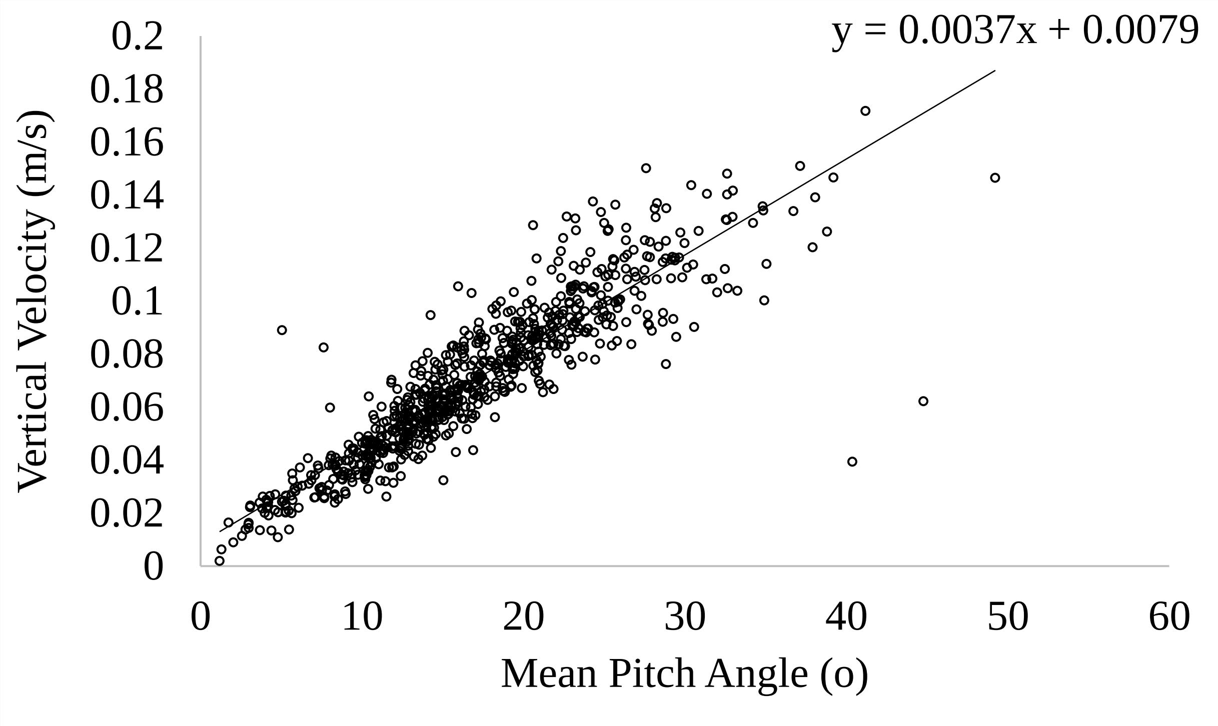

Figure 4. Linear relationship between vertical velocity (m/s) and mean pitch angle (º). The orange line represents the linear line of best fit. The dataset uses ascent data for all sharks amalgamated into one. The high R^2 value indicates a strong correlation between the two parameters.

When mean smoothed VeDBA is graphed against mean pitch angle (Figure 5a [p<0.001, df = 756, F = 433.4, R^2 = 0.6003]) and vertical velocity (Figure 5b- [p<0.001, df = 756, F = 377.8, R^2 = 0.5008]), a quadratic relationship is given for both independent variables; as mean pitch angle and vertical velocity increase from 0, so does mean smoothed VeDBA. The majority of the datapoints fall under 0.05 *g*, indicating weak smoothed VeDBA produced by the animals i.e., their slow movements are producing low signals. There are a few datapoints at the extreme end of smoothed VeDBA closer to the x-axis value limit, with only one datapoint exceeding a smoothed VeDBA of 0.1 *g* in both cases. The quadratic regression does not have a strong correlation, with the R^2 values sitting in a mid-strength regression range, thus giving a wider spread of datapoints across the VeDBA values for each independent variable.

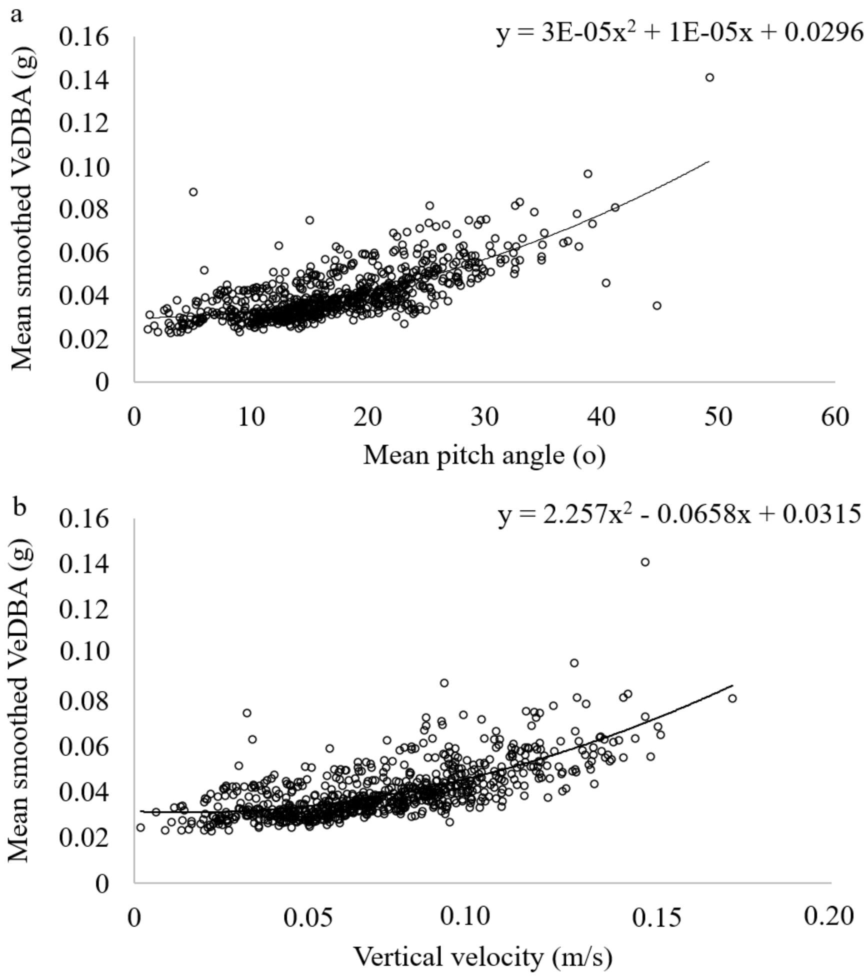

Figure 5. Quadratic relationship between mean smoothed VeDBA (g) and a) mean pitch angle (º) and b) vertical velocity (m/s). The orange lines represent a) VeDBA= a+b(pitch angle)^2 and b) the line of best fit.

Similar quadratic relationships were found for dynamic yaw versus both mean pitch angle and vertical velocity displayed albeit less extreme; as mean pitch angle and vertical velocity increases, so does dynamic yaw (Figure 6a and 6b). However neither of these curves are not as steep as is found when VeDBA is the dependent variable, indicating a weaker relationship between dynamic yaw and the independent variables. Whilst the relationship between the two independent variables and dynamic yaw are significant, it is a very weak regression (mean pitch angle: $p = 0.006$, $df = 756$, $F = 13.48$, $R^2 = 0.03537$; vertical velocity: $p = 0.002$, $df = 756$, $F = 13.62$, $R^2 = 0.03968$) thus giving a large deviation of datapoints from the regression line. In both instances, there are numerous datapoints which have a noticeably higher dynamic yaw than the majority.

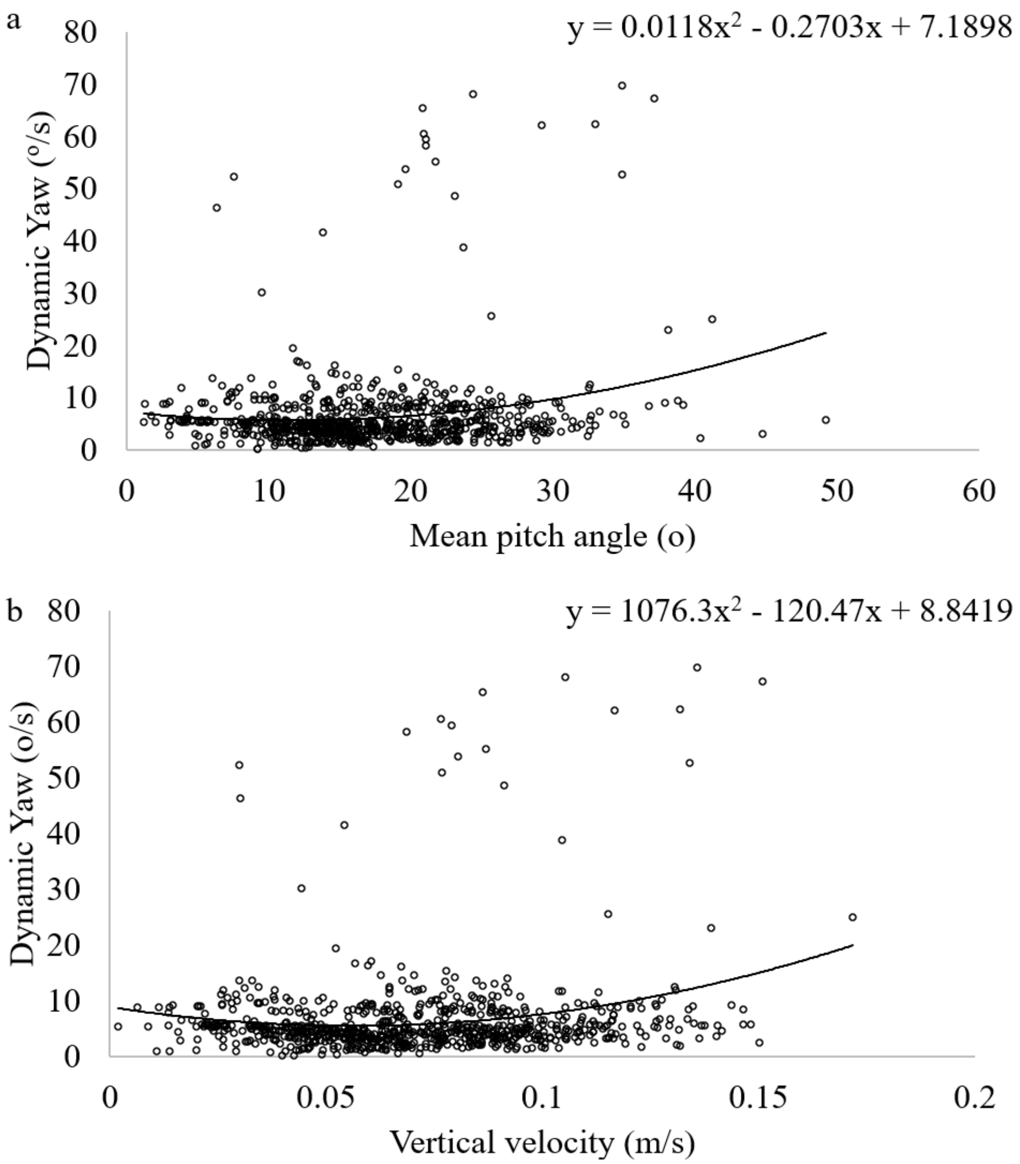

Figure 6. Dynamic yaw correlation with a) pitch angle and b) vertical velocity. All shark datasets have been amalgamated into one to produce this dataset. The orange lines represent the line of best fit for the regression.

Determining the minimum power for a given pitch angle

The sharks selected for the PAM analysis showed appreciable variability in the height of their VeDBA values above the minimum power line (examples shown in Figure 7a-f. For example, one animal had all VeDBA points very close to its own minimum power line (Figure 7d) while others (e.g. Figure 7a and 7c) had VeDBA values that regularly exceeded 0.02 *g* above the minimum power line.

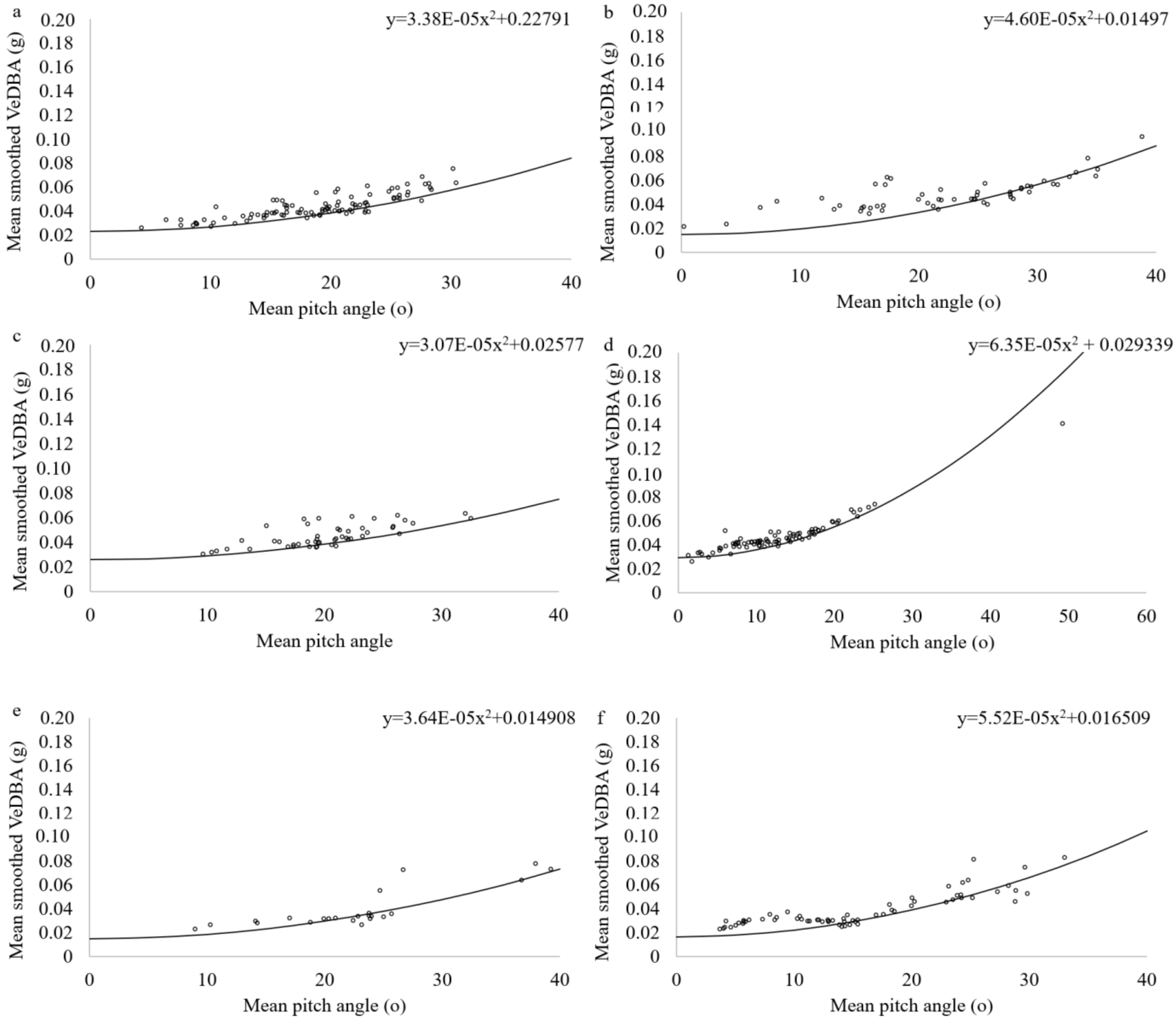

Figure 7. Examples of sharks selected for the PAM analysis with smoothed VeDBA against pitch (blue) with the regression line (orange) for the equation: VeDBA=a+b (pitch angle)^2. Equation values provided by Johnathon Potts (2021).

PAM

As expected, the PAM of all six sharks shows a positive skew in distribution (Figure 8), i.e., they all have more frequent instances of PAM at the lower end of the scale (under 0.01 *g*) with fewer points towards the higher end of the scale (>0.01 *g*) indicating a favour towards lower levels of energy expenditure. All six sharks exhibit levels of PAM greater than 0.01 *g*. All six sharks also exhibited a PAM of above 0.02 *g* on more than one occasion, with two sharks exceeding 0.03 *g* on 3 occasions. The maximum PAM observed was 0.033 *g* and occurred once (Figure 9b)

The spread and pattern of the PAM data can be seen in Figure 8. The minimum PAM for all six sharks was >0.001 g and the highest (excluding the outliers) was 0.029 *g*, leading to a total range of <0.029 *g*. 13 outliers were identified in the data and ranged from 0.019 *g* to >0.003 *g*.

These outliers were identified by the equation:

$$Maximum\ value = \ 3QR + (IQR\ \times 1.5)$$

where 3QR = 3rd quartile value and IQR = interquartile range. If values exceeded the maximum value, it was identified as an outlier (Vinutha *et al*., 2018).

Whilst there were negative statistical outliers for shark F, these have been removed from the dataset and will not be considered as feeding events as during this period the shark is using considerably less energy than expected which does not fit the criteria for a feeding or avoidance event.

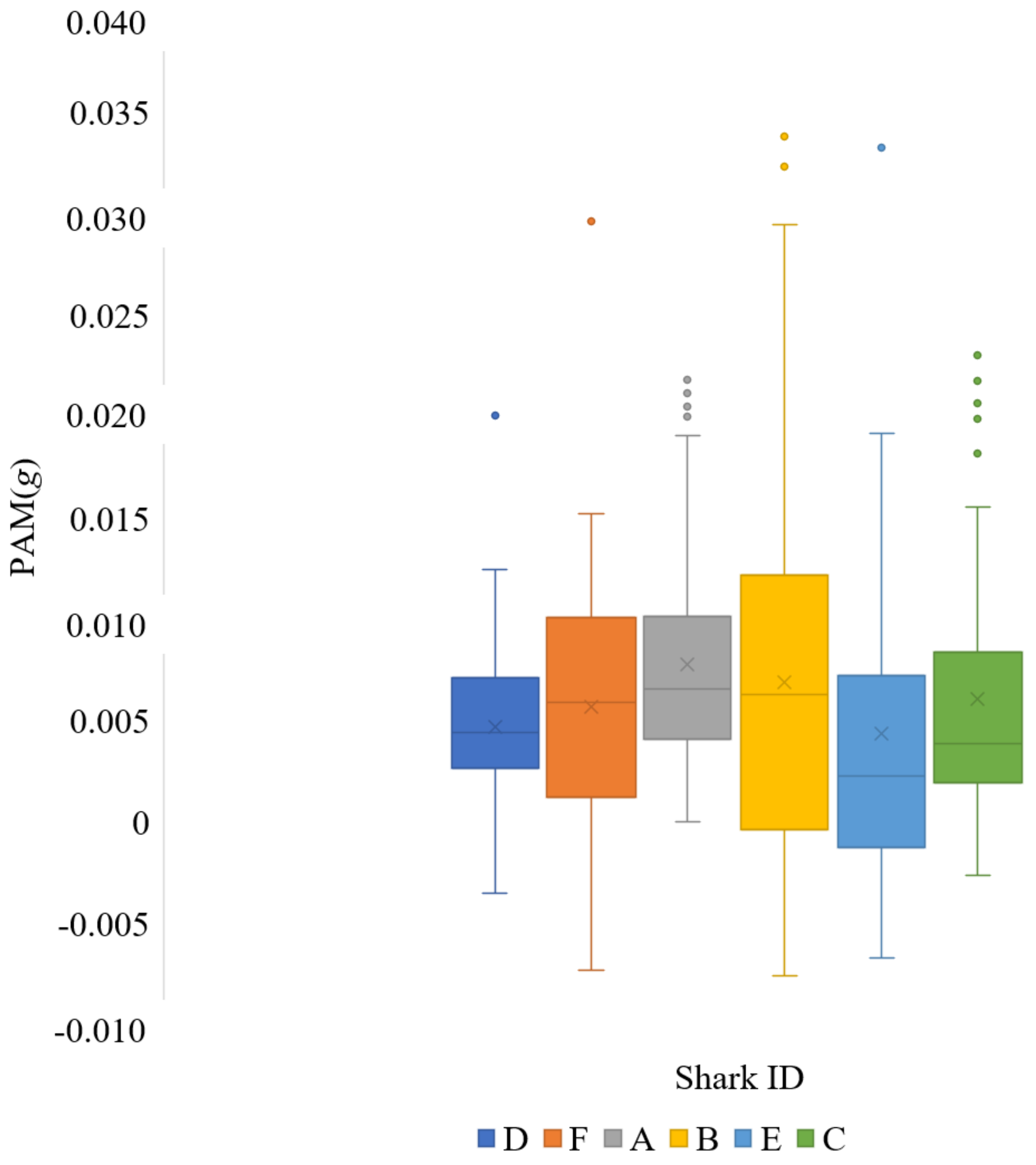

Figure 8. Spread of data for all 6 sharks. Line inside the boxes represents the median value, 'x' the mean and outliers are indicated by circles above and below the main spread of the data. Letters representing shark ID are consistent those in Figure 9. All negative outlier points have been removed due to their inconsequence in the analysis.

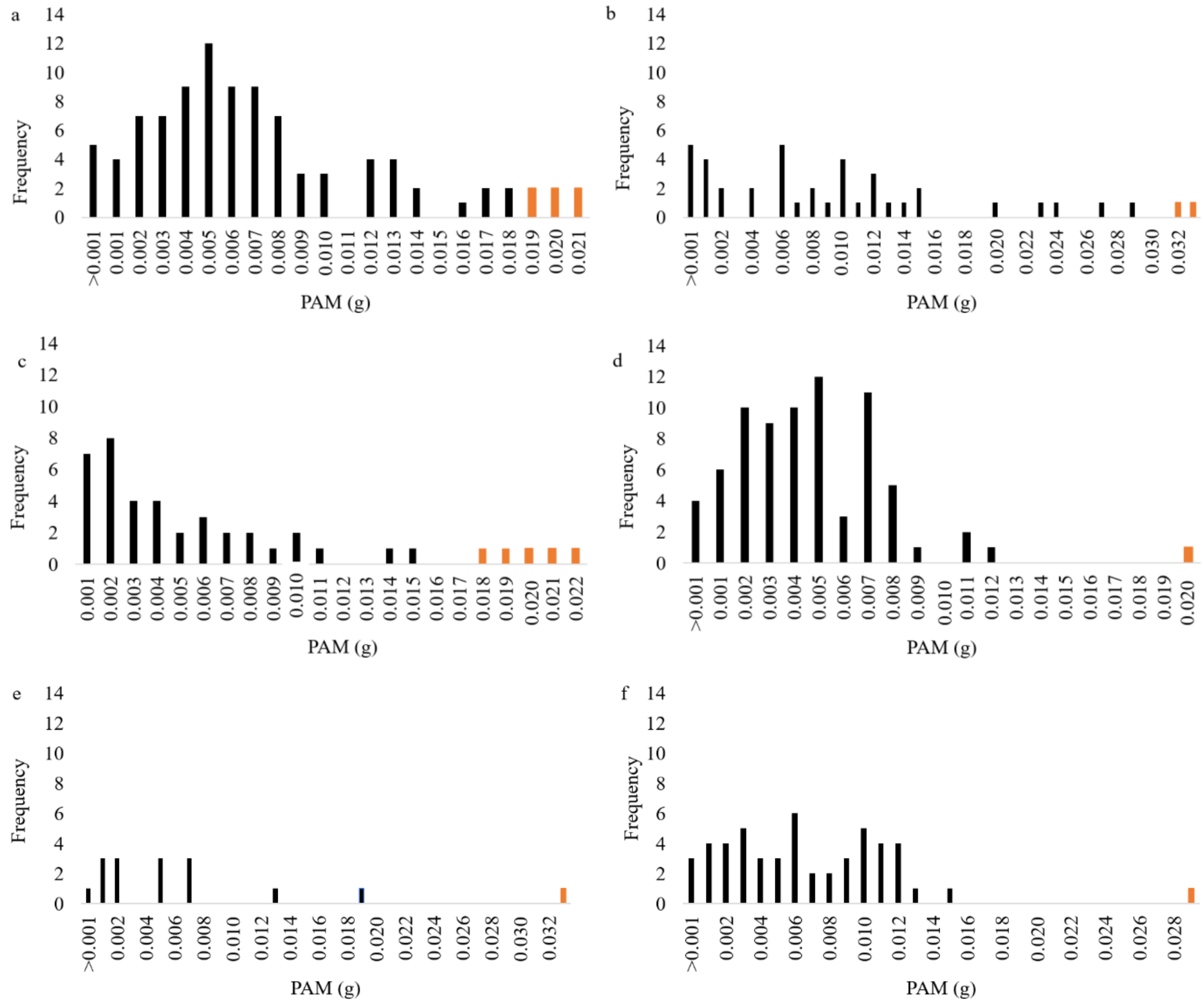

Figure 9. Frequency of PAM values for each shark used for PAM analysis. Values are only representative of those above the minimum power line and represent the value of PAM which the shark is exhibiting at each point. All orange bars represent statistical outliers. In 9A, the orange bar representing a PAM of 0.019 *g* also contains a non-statistical outlier value

Discussion

The principal aim of this study was to determine whether dynamic yaw correlated with body pitch angle more strongly than the correlation between VeDBA and body pitch angle; as the pitch angle increased, so did the energy expended by the whale shark. Against my predictions, dynamic yaw correlated poorly with body pitch angle compared to VeDBA and thus could not be used to identify instances where energy minimisation is not the priority.

However, VeDBA appeared to be a good tool to identify instances where the minimisation of energy was not prioritised, as I identified 16 instances from the six whale sharks, all of which exhibit power above the minimum calculated baseline, and as such can be considered to be a high-powered event such as feeding or avoidance behaviour.

As dynamic yaw was not a suitable proxy for power in whale sharks due to its poor regression fit with dive pitch angle and vertical velocity, smoothed VeDBA can be used to approximate the expected minimum power for individual animals and then to calculate PAM to highlight energy-intensive activities. The method of identifying an assumed minimum power for individuals as opposed to the group as a whole allows a more in-depth analysis of instances of high energy expenditure as it considers the natural variation of each individuals swimming speeds which may result from changes in external temperature and body mass (Graham *et al*., 1990) and body length (Graham *et al*., 1990). The method also has promising future applications in other species, specifically slow-moving species where VeDBA signals are weak and thus harder to analyse as it is easier to differentiate instances of high-power use using PAM for a given pitch angle than VeDBA alone.

As whale sharks ascend in the water column, they exert a range of power dependent on other variables (Figure 6a and 6b). When examined in relation to mean body pitch angle (Figure 6a), whale sharks dynamic yaw increased as body angle increased, with the trend being at its highest when body pitch angle equalled 50º which confirms that a steeper angle of ascent requires a higher energy expenditure. There are several datapoints that do not fit the trend, for example a shark exhibited a body pitch angle of between 20^{o} and 40^{o}, and yet exhibited a dynamic yaw greater than 60^{o} /s. These points to not conform with the expected trend between body pitch angle and dynamic yaw and the reason for them is unknown however could be the result of a feeding or avoidance event due to the individual exerting more power than necessary to ascent at the given pitch angle. This increased dynamic yaw could also be compensation for drag caused by the open-mouthed feeding style of whale sharks (Meyers *et al*., 2020) which requires increased energy to continue moving in the water column whilst feeding.

During the ascent phase, whale sharks must actively power up to reach their desired depth meaning that they are expending more energy. Elasmobranchs, including whale sharks, lack a swim bladder (Withers *et al*., 1994), the primary function of which is to aid in maintaining neutral buoyancy (Price and Mager, 2020). Consequently, whale sharks must rely on power produced by tail beats and body movement to move upwards through the water column. This increase in effort can be observed in the elevated levels of mean smoothed VeDBA as the whale sharks ascend, with a higher mean smoothed VeDBA being exhibited for steeper body pitch ascent angles (Figure 5a and 5b).

The regression for mean smoothed VeDBA against mean body pitch angle and vertical velocity is stronger than that of dynamic yaw against the two variables, indicating that it is a more reliable proxy for power as data points follow the trend in a stronger pattern. Therefore, despite the low signals VeDBA produced for slow-moving animals, it can still be considered the best proxy for power to use when identifying energy-intensive activities. Furthermore, by using VeDBA to calculate PAM for a given body pitch angle and identify specific behavioural events, it presents a promising method that can be used to accurately identify high powered events for slow-moving animals, as well as provide a more comprehensive understanding of the smaller biological changes and activities exhibited by whale sharks. Gliding down in the water in an effective way of preserving energy as the animal is utilising its ability to move without expending more energy than necessary (Naemi *et al*., 2010; Adachi *et al*., 2014), thus conserving it for activities such as feeding where there is a demand for higher energetic costs. However, there may be instances where sharks need to increase speed of descent and use active tailbeats, which this method will be able to identify.

There were several instances in this dataset where possible feeding events occurred (Figures 8 and 9a-e). Any event which is identified as an outlier can be considered a feeding or avoidance event as the individuals are using noticeably more power than what can be accepted within the general range of natural power use variation. All the outliers lie above the PAM value of 0.019 *g*, indicating a possible threshold for datapoints passing from general spread to feeding events, however as one of the sharks (Figure 9b) has general spread data points above this value, this cannot be confirmed.

There is a potential third cause for the instances of PAM; gill clearing or ‘coughing’. Observations of gill clearing have been made whilst the shark is pitched upwards in the water column (Motta *et al*, 2010) and is widely accepted to be the mechanism for clearing the gill rakers of any leftover or unwanted food (Taylor, 2006). This process is undertaken by closing the gill slits and forcing remaining matter from the gills to the mouth where it is then ingested (Nelson and Eckert, 2007). This could be a cause of increased energy expenditure as the shark must work harder to account for the increased drag caused by the opening of the mouth whilst swimming forward.

There is the potential to combine this data with tailbeat frequency analysis in future studies to further identify the causes of instances of PAM, as well as provide a method of preliminary identification of such instances. When teleost fish are swimming at increased speeds, often their tailbeat frequency and amplitude are increased (McHenry *et al*., 2005), with similar changes in tailbeat characteristics being observed in sharks (Graham *et al*., 1990), thus providing a visual characteristic that can be used to identify potential PAM instances visually from the raw data.

This data presented focuses primarily on daytime feeding, and whilst no variation in swimming mechanisms and power expenditure between behaviours is expected to occur diurnally versus nocturnally, night-time feeding analysis would be required to better understand proxies for power in the overall case of feeding events. Also, the lack of underwater observation means that whilst the outlying datapoints can be proposed to be feeding events, no definitive cause for these increases in PAM can be given, however it is highly likely that these are indeed feeding events.

The initial analysis presented here can make a case for the use of smoothed VeDBA to calculate the PAM values of a specific event or identify instances of feeding or avoidance. Further analysis of larger numbers of individuals would aid in confirming whether outliers in the spread of PAM per individual can be suggested as feeding events however the initial study exhibits the ability of PAM to aid in identification of biological processes without the need for visible evidence of these behaviours.

Furthermore, the method presented here can be combined with additional sensors and biologgers such as dead-reckoning and ground-truthing data during instances of high PAM for individual sharks to explain more complex behaviours such as circling whilst feeing and patterns of movement and feeding on large-scale migrations. Moreover, video recording technology can be used alongside these additional sensors to identify any external factors that may affect whale shark behaviour that cannot be picked up with biologgers, such as the presence of boats and other large marine fauna. Deep-sea GPS tags such as the mark-report satellite tag (mrPAT) have been deployed on Greenland sharks (*Somniosus microcephalus*) to track deep-sea movement patterns (Hussey *et al*., 2018) and have the potential to be used on whale sharks to track the co-ordinates of deep-water dives.

By combining all of these factors in future studies, there is a potential opportunity to learn more about key behaviours of not just whale sharks but large, slow-moving marine fauna as a whole.

Despite the lack of definitive identification of what is causing these high-powered instances, knowing when and generally why they occur is a key element in understanding whale shark energy expenditure and biology as a whole and can aid in implementing actions to help protect them, either by identifying key feeding grounds or by introducing new codes of conduct for interactions with co-tourists.

Limitations

There were several limitations that may have impacted the outcome of the study. The first is the lack of visual data to go along with the tracking data. Whilst it was possible to identify instances of PAM from the tracking data, it is impossible to say with any certainty what those events are. To be able to definitively determine which events are feeding and which are avoidance, visual data would also need to be collected in collaboration with numerical data.

An additional limitation is the number of animals available to tag. Seventeen animals were tagged in total during the data collection; however four data files were unusable due to large sections of missing data or the tags not recording past deployment. Time constraints also meant that not all individuals tagged could be used in the further PAM analysis. It is therefore more difficult to identify whether the same threshold applies for all instances of PAM, however this could be a focus point for a future study

Furthermore, whilst all steps were taken to avoid anthropogenic stressors towards the animals during data collection, it is impossible to know whether the presence of the research vessel and the watchers in the water caused any level of stress to the study animals, which could have caused a change in behaviour from their natural states to include faster swim speeds. Ideally, longer term tags would have been deployed.

Future implementations

Whilst the identified instances of PAM cannot be definitively assigned to a specific activity, when combined with other recording devices such as underwater cameras and GPS in future studies it will allow for accurate identification of activities such as feeding and avoidance which can be used to implement restrictions around activities in key feeding areas and guidelines around the tourism related to whale sharks to ensure minimisation of avoidance responses from the animals.

A comprehensive understanding of whale shark energy expenditure can help the drive to protect them in the wild. Knowing when and why they exhibit instances of high-power usage can aid in the understanding of their overall biology and reproductive patters and can help in protecting specific areas of their environment where they have been identified feeding and using PAM has preliminarily proven to be an effective way of identifying these key biological instances.

This method lays the groundwork for future studies focusing on whale shark behaviours. By combining this method of determining potential feeding events with GPS tracking and dead-reckoning, it can identify areas of biological importance in terms of key feeding grounds, specific aggregation sites and potentially even breeding sites. Furthermore, by identifying these key sites using the PAM method, it could have effects on protection measures for whale sharks moving forward, such as areas which are seasonally off-limits to tourists and implementing protected marine areas to preserve essential feeding grounds and by extension, the species as a whole.

Conclusions

This research aimed to discover whether dynamic yaw was a more effective proxy for power than DBA, and whether it was possible to utilise a proxy for power to identify instances where energy minimisation was not the priority. Whilst dynamic yaw proved to be an ineffective proxy due to its poor relationship with body pitch angle, DBA was successfully utilised to identify instances of PAM. Whilst it has not been possible to directly identify the causes behind the instances of PAM, the method and results show that it is possible to identify instances of increased energy expenditure, thus laying the groundwork for future studies to look more in-depth at the cause of these instances. This study represents notable information regarding the measurable changes in whale shark behaviour, as well as proposing reasons behind the changes. As a difficult to study animal, the ability to identify instances of abnormal behaviour in whale sharks is vital to understanding how external stressors impact their lives, both in the short and long term. This data has the potential to influence protective measures put in place to safe-guard whale shark populations against decline caused by anthropogenic stressors, as well as aid in identifying sites of key biological processes such as breeding, which is currently unknown.

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