Memorandum of understanding

BETWEEN

MURDOCH UNIVERSITY

- and –

UNIVERSITY OF PAPUA

University Registrar's Office
South Street		Tel:	(08) 9360 6614
MURDOCH WA 6150		Fax:	(08) 9360 6847

This Memorandum of Understanding ("MOU") is made between:

MURDOCH UNIVERSITY of South Street, Murdoch, Western Australia, Australia ("Murdoch")

– and –

UNIVERSITY OF PAPUA of Jalan Gunung Salju, Amban, Manokwari Barat, Amban, Manokwari, Kabupaten Manokwari, Papua Barat. 98314 Indonesia (the "Partner")

1. INTRODUCTION

Murdoch and the Collaboration Partner ("Parties") want to collaborate with each other so as to promote the advancement of international understanding, dissemination of learning and strengthening of cultural ties. They have entered into this MOU to create a foundation from which such collaboration may be developed.

2. MUTUAL INTEREST

- This partnership is to support the research activity of a PhD student, Calvin Beala to engage in research within the Raja Ampat / western Papua region through research partnerships with students and professors at UNIPA.
- Students who wish to do research in Indonesia are required to have a local collaborator in order to be granted a research permit for Indonesia.
- Field trips will be planned and interested students will be able to get hands-on experience.

3. NATURE OF COLLABORATION

- The collaboration will potentially involve professors and or students from UNIPA being included in different portions of the research including field trips,
- data analysis and manuscript production. Inspiring further research and building capacity in local students.
- Any students who are interested will be encouraged to look at Murdoch university as an option for further study after graduating from their existing position.
- Murdoch university collaborating directly with UNIPA will highlight the existence of the university, the research currently being conducted and future possibilities which they could be involved in later.

4. DURATION

4.1. Subject to paragraph 4.2, this MOU will commence on the date it is fully executed and will last for three (3) years.

4.2. Either Party may terminate this MOU by giving the other Party 6 months' written notice of termination.

5. NOMINATED REPRESENTATIVES

5.1. The Parties' nominated representatives are:

for **Murdoch**:
Name: Dr Adrian Gleiss
Position: Lecturer, CollegeSHEE
Phone: + 61 8 9360 1667
Email: a.gleiss@murdoch.edu.au

for **University of Papua**
Name: Dr Ricardo F. Tapilatu
Position: Professor
Email: rf.tapilatu@unipa.ac.id
Phone: +62 811 4855 506

5.2. Each Party's nominated representative is responsible for the development and implementation of this MOU, including receiving and acting on proposals for collaborative activities referred to in paragraph 3.1.

6. LEGAL ISSUES

Nothing in this MOU will create a legal relationship between the Parties or be legally binding on them. This MOU is to affirm the intent of the Parties to work together in good faith in an attempt to progress the matters described in this MOU.

EXECUTED as a memorandum of understanding by the Parties:

EXECUTED for and on behalf of
MURDOCH UNIVERSITY by

Name: Professor Lucy Johnston
Position: Pro Vice Chancellor (Research & Innovation)

Date: 11.08.21

EXECUTED for and on behalf of
UNIVERSITY OF PAPUA by

Name: Dr. Meky Sagrim, S.P.,M.Si
Position: Rector

Date:

Technical Agreement

Between

Calvin Steven Beale, Ph.D Candidate, Murdoch University (MU)

and

Professor Ricardo F. Tapilatu, The University of Papua (UNIPA)

The Murdoch University (MU) and the University of Papua (UNIPA), hereafter referred to as 'The Parties';

Referring to the Memorandum of Understanding (MOU) between Murdoch University and the University of Papua, signed on the 19th August 2021;

Considering the principle of equality and mutual benefit between the Parties and recognizing the benefit of cooperation in the area of scientific research;

We, the undersigned, hereby agree to the following:

Article 1 – Objective

The objective of this Technical Agreement is to establish a framework for cooperative activities conducted by the Parties in the fields of scientific research and conservation.

Article 2 – Areas of Cooperation

Cooperation under this Technical Agreement may be undertaken in the following areas:

1. Scientific research focusing on oceanic manta rays (*Mobula birostris*) in Kabupaten Raja Ampat, Indonesia
2. Marine conservation development
3. Community outreach and education initiatives
4. Education, training and capacity building in the field of marine scientific research
5. Such other areas that may be mutually agreed upon by the Parties in writing

Article 3 – Forms of Cooperation

The Parties agree to cooperate as follows:

1. The opportunity of lead authorship of scientific publications based upon or arising from data or observations gathered pursuant to this Technical Agreement will be available to researchers from both Parties. Lead authorship of a paper will be equally matched by the author's intellectual contribution and publication content will be agreed upon by both Parties.

2. Murdoch University will ensure capacity building efforts designed to strengthen the skills and abilities of UNIPA researchers and students are undertaken during the course of the collaborative research project. Such efforts may include (but are not limited to):

   a) Scientific knowledge transfer
   b) Field training for manta ray photo ID data collection

    c) Sharing data collection, field interaction and other protocols related to the collaborative research project
    d) Involvement of UNIPA staff and students in data analysis where applicable
    e) Conducting guest lectures online as part of the Merdeka Belajar program, or during visits to the UNIPA campus, or during field visits where possible.
3. Where appropriate each Party shall invite the other Party to participate in conferences and symposia when presenting results from collaborative research efforts.

4. The Parties will work together to conduct outreach and education initiatives focusing on marine conservation and awareness relating to Oceanic Manta Rays in Raja Ampat communities and for local government officials.

Article 4 – Intellectual Property Rights

The Parties agree to follow intellectual property rights laws, and where there is any doubt, agreement shall be made in writing before any data shall be shared with any external body.

1. Each Party shall protect, within its territory, intellectual property rights of the other Party in accordance with the domestic law in force in their respective countries.

2. The protection of intellectual property generated in the course of the cooperative activities shall be governed by the terms set out in the MOU to which this Technical Agreement refers.

3. Data collected for the purpose of this research shall remain the property of the researchers and made available via online data storage platforms to all parties when available. Publication of this data may only be done so with the written agreement of the primary researchers involved and co-authorship opportunity shall be given to primary researchers upon the publication of any scientific works.

Article 5 – Amendments and Disputes

1. Both the primary researcher and local counterpart are sufficiently fluent in each-others language to discuss openly and freely any amendment or dispute that may arise, and come to an amicable outcome.
2. Amendment to this agreement can only be made after mutual consent achieved by consultation and confirmation in writing from both Parties given at least thirty (30) days in advance.
3. Any disputes arising out of, or in connection with the application and interpretation of this agreement shall be settled amicably by the Parties through consultation and negotiations.

Article 6 – Conditional Clauses

All agreements above are dependent upon:

1. The Parties being granted a collaborative research permit from appropriate Indonesian Government Agencies (Badan Riset dan Inovasi Nasional).
2. The foreign researcher being granted a research visa for Indonesia
3. The current Corona Virus pandemic may have unforeseen consequences for the ability to conduct this research as planned.

Article 7 – Final Provisions

1. This Technical Agreement shall be effective on the date of signature of all parties and will remain in effect for three years unless otherwise amended or terminated in writing by either Parties.
2. Either of the Parties may terminate this Technical Agreement upon six months prior written notification to the other Parties.
3. The termination of this Technical Agreement shall not affect the completion of ongoing activities or programs implemented under this Technical Agreement, unless otherwise decided by the Parties.
4. The implementation of this Technical Agreement shall be concluded between the Parties in specific arrangements on a case by case basis.

We, the following, agree to the terms and conditions outlined in this Technical Agreement.

First Party **Murdoch University**	Second Party **The University of Papua (UNIPA)**
C. Beale	
Calvin Steven Beale, BSc Ph.D Candidate, Harry Butler Institute – College of Science, Health, Engineering and Education, Murdoch University	**Prof. Ir. Ricardo F. Tapilatu, M.App.Sc, Ph.D** Pusat Penelitian Sumberdaya Perairan Pasifik, University of Papua
Date: 15/09/2021	Date: **15/09/2021**

Technical Agreement

Between

Calvin Steven Beale, Ph.D Candidate, Murdoch University (MU)

and

Assoc. Prof. Kadarusman, Politeknik Kelautan dan Perikanan Sorong (Politeknik KP Sorong, KKP)

The Murdoch University (MU) and the Politeknik Kelautan dan Perikanan Sorong, hereafter referred to as ‘The Parties’;

Referring to the conversation between Calvin Beale and Kadarusman PhD, on the 11th October 2021;

Considering the principle of equality and mutual benefit between the Parties and recognizing the benefit of cooperation in the area of scientific research;

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2. Murdoch University will ensure capacity building efforts designed to strengthen the skills and abilities of Politeknik KP Sorong researchers and students are undertaken during the course of the collaborative research project. Such efforts may include (but are not limited to):

    a) Scientific knowledge transfer
    b) Field training for manta ray photo ID data collection

   c) Sharing data collection, field interaction and other protocols related to the collaborative research project
   d) Involvement of Politeknik KP Sorong staffs and students in data analysis where applicable
   e) Conducting guest lectures online as part of the Merdeka Belajar program, or during visits to the Politeknik KP Sorong campus, or during field visits where possible.
3. Where appropriate each Party shall invite the other Party to participate in conferences and symposia when presenting results from collaborative research efforts.

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4. The implementation of this Technical Agreement shall be concluded between the Parties in specific arrangements on a case by case basis.

We, the following, agree to the terms and conditions outlined in this Technical Agreement.

First Party
Murdoch University

C. Beale

Calvin Steven Beale, BSc
Ph.D Candidate, Harry Butler Institute – College of Science, Health, Engineering and Education, Murdoch University

Date: 7 October 2021

Second Party
Politeknik Kelautan dan Perikanan Sorong

Kadarusman, Ph.D
Politeknik Kelautan dan Perikanan Sorong

Date: 7 October 2021

PhD Research Proposal by Calvin Steven Beale

Project Title:

An investigation into the movement ecology of oceanic manta rays (*Mobula birostris*)

Research supervisors:

- Principal and coordinating supervisor - Dr. Adrian Gleiss, Research Leader Marine Megafauna, Harry Butler Institute, Murdoch University
- Murdoch Co-supervisor – Dr. Neil Loneragan
- External Supervisor – Dr. Ricardo F. Tapilatu. University of Papua
- External Supervisor – Dr. Mark Erdmann. University of Auckland
- External Supervisor – Dr. Mark Meekan. Australian Institute of Marine Science

Proposed mode of research:

A combination of analysis of existing data sets and field research deployment of pop-up archival satellite telemetry tags and biologger tags.

Aims and objectives:

My aim is to enhance the understanding of the movement ecology of oceanic manta rays through satellite telemetry and biologger tags.

Project objectives:

1. Identify the function of super-deep dives (>300m) for oceanic manta rays
2. Identify drivers of vertical movement behaviours in oceanic manta rays using pop-up archival tag satellite telemetry data
3. Identify critical areas of use and drivers of horizontal (e.g. migratory) behaviours in oceanic manta rays using pop-up archival tag satellite telemetry.
4. Identify specific behaviours and their functions based on biologger tag data.

Synopsis:

This study will investigate the movement ecology of oceanic manta rays (*Mobula birostris*) in the Birdshead Seascape area of Western Papua, Indonesia. This area is not a National Park in Indonesia, but is home to a series of smaller protected areas spread throughout Raja Ampat and the Birdshead Seascape. Currently, very little is known about short or long-term horizontal movements of oceanic manta rays and even less regarding vertical diving behaviours. Pop-up archival satellite telemetry (PSAT) tags will be used to monitor long-term horizontal movements throughout the region and record vertical diving profiles, highlighting where and when dives occur and the ambient conditions during those dives. The analysis of these data will allow for a better understanding of why these dives happen, relating this to bathymetry and local oceanographic conditions and how these dives relate to the position of mixed and scattering layers. Biologger tags will further inform the energy output requirements of these behaviours and potentially help predict where aggregations of oceanic manta rays may occur.

Expected research contribution:

This research will significantly contribute to the knowledge base surrounding the movement ecology of oceanic manta rays both locally in eastern Indonesia but also be applicable to global populations. While foraging and movement behaviours will vary with location, the methods, prey density thresholds and environmental conditions which trigger those behaviours will likely be the same. To date, very few studies have been published with long-term recorded movement of oceanic manta rays, this study will include the data from 11 previously deployed satellite tags including 5 recovered tags. The amount and detail of the data already recorded will significantly increase the published data available and should inform a lot of future research into the movement ecology of oceanic manta rays. The additional tags to be deployed will further bolster this data set and allow for comparisons between sexes and individual variation amongst a population.

The addition of biologger tags including camera systems and accelerometer data loggers will provide significant insight into the triggers behind the observed behaviours. Prey density thresholds have yet to be calculated for oceanic manta rays, and as the species is rarely observed in-water when not at cleaning stations, these data will assist in predicting where and when aggregations may occur and how best to protect such aggregations from incidental catch. Video data collected may also increase our understanding of social behaviours and interactions with other individuals and species.

‘Research Project Details’ / Proposed methodology

Data will be collected by use of different sensors physically attached to individuals. Previously, 9 MiniPAT and two MK10 pop-up satellite archival (PSAT) tags made by Wildlife Computers have been deployed on oceanic manta rays. Of these, 7 were deployed on females and 4 on males. Deployment time for 7 of the miniPATs was the full intended 180-day deployment, and the remaining two miniPATs were deployed for 270 days however one released early from the manta after 163 days. The two MK10’s were deployed for 160 days each. Of the miniPATs, five of these (four female and one male) were recovered from the water post-release. Tag recovery allows for complete download of the tag data, giving high-resolution (e.g. 5 second interval) temperature & depth recordings for the entire deployment period. These tags were deployed over the period of September 2013 through February 2017. They were all deployed in southern Raja Ampat at a remote seamount named ‘Magic Mountain’ where there are multiple cleaning stations where oceanic manta rays are frequently encountered.

Pop-up archival tags record data allowing the examination of daily activities including daily geolocation of the individual typically over a 6 to 9-month period. These tags record ambient data on depth, light levels and temperature, allowing the extrapolation of a movement track of the individual through Wildlife Computers bespoke software package ‘GPE3’, which deduces the animal’s daily location. Depth and temperature data, along with light levels is used to investigate diving behaviour during the deployment period. Deployment length is chosen based on a trade-off between the data resolution, available memory and battery life.

I intend to deploy tags at a seamount with cleaning stations in northern Raja Ampat, ‘Blue Magic’. These tags will ensure minimum data requirements are met for investigation of my aims as per Sequeira *et al.*, 2019. At present, data collected is biased to female mantas (7 : 4 tags, 1333 : 679 days deployment). Additional tags will help to fill the gap of data of movement patterns of male oceanic mantas while also having female comparative data to determine if any differences with previously recorded data are due to different conditions between these deployment periods (such El Niño Southern Oscillation events). According to Sequeira’s study, for good estimates of space use, home ranges and to characterise spatiotemporal patterns, while allowing for specific behaviours of individuals to be examined the number of tags necessary is between 10 and 100, with increasing numbers of tags allowing for more robust analysis.

I aim to deploy a minimum of 3 miniPAT tags to females and 8 to males, bringing the total to 20 miniPATs, being within (although at the lowest end) of the bracket set out by Sequeira for both sexes independently, allowing for data to be examined on a per-sex basis for space use, home ranges, and characterising spatiotemporal patterns along with individual specific behaviours. The additional tags will provide sufficient extra data to allow more in-depth analysis, as described by Sequeira. Tags will be deployed for 9-month periods, reducing the need for more animals to be used by having short deployment time, while maximising the amount of satellite transmission time and the chances of physical tag recovery. Tags will be deployed on adult manta rays minimum 3m in disc width as per all previous satellite tags, to ensure consistency of data among adults of the species. Juvenile oceanic manta rays are almost never encountered in the study area.

Biologger tags have not yet been deployed on manta rays in this region. The tags will provide paired data which allow us to see what the animal is doing on recorded video, while having a measure of the effort exerted by the animal during this period. 30 Biologgers will be deployed for periods of 30 hours after which they will automatically release from the animal and float to the surface to be recovered for data download. Deployment periods will vary considerably based on the individual manta ray, results from Stewart et al, 2019 showed manta rays dislodging the tags by breaching on a number of occasions. We aim to use the existing knowledge and recommendations in Stewart's paper to extend retention periods, reducing the number of individuals needed by having longer deployment periods, maximising battery life and efficiency of tagging while not causing any long-term effects on the tagged manta ray. Data from biologger tags will be used to create state-space models predicting the probability of an animal being in a given state or changing state (e.g. high activity: searching for food, feeding or low activity resting) based on a set of measurable oceanographic conditions, allowing us to predict the impact of changing climate conditions on animal behaviours.

Skills audit:

Data analysis will require learning how to various software packages and various other analytical tools. A combination of online tutorials, peer and supervisor training will be used to develop these skills.

Training will be required in the use of biologger tags. This will be achieved via communication with tag manufacturers (Customized Animal Tracking Solutions), and my supervisors who have significant experience in the use of these systems.

Research project communication:

My thesis will be formatted as a series of papers highlighting the data chapters of my study. The first chapter on vertical movement ecology will be completed by June 2022. The second chapter on migratory behaviours by November 2022 and the third chapter reporting biologger tag deployment information by August 2023.

Publication journals will depend on possible collaborations, if collaborations with researchers in other geographical areas can be achieved, higher impact factors journals can be targeted. Target journals include Marine Biology, Frontiers in Marine Science, Marine Ecology Progress Series, Biological Conservation and Diversity and Distributions.

Data Management:

Data will be transmitted via satellite or downloaded directly from miniPATs and then uploaded into Wildlife Computers online cloud storage system where it will be processed using their bespoke GPE3 software and available for download at a later date.

Data from biologger tags will be uploaded into a cloud storage solution such as dropbox or google to ensure backups and accessibility from anywhere.

Data will be available upon request for local collaborator and we hope to expand collaboration to include students from UNIPA, so they can be directly involved in the research.

Budget:

Funding for tags will form the major part of the budget needed for this PhD. This will be broken down into three parts:

1. Pop-up archival satellite tags. A total of 11 tags at $4,000 USD would cost $44,000 USD plus an additional estimated $6,000 USD on ARGOS satellite fees
2. Standard CATS-CAM biologger tags cost 5,900 EUR, not including customisation which will be required. Tags can however be recharged and reused with replacement animal attachment systems. A total of 30 deployments is estimated to cost 30,000 EUR (~$36,000 USD).
3. Additional costs include Indonesian research permit $1000 yearly, field trip accommodations up to $10,000 USD, international flight costs $1200, domestic flight costs $1,200, additional equipment costs $100, and possible COVID related test or quarantine costs. Totalling $13,000 USD

I believe these targets are feasible however in this Covid economic climate uncertainty may limit available funding. In this case, I will be forced to modify my goals to complete my thesis with the dataset already available.

Description	Year cost incurred				Source		
	Year 1	Year 2	Year 3	Year 4	School(s)	Graduate Research School	Other
Administrative costs	-						
Indonesian research permit	-	$1000	$1000	$1000			
Research costs	-						
Replacement spear band	$100						
miniPAT costs	$44000						
ARGOS costs	$6000						
Biologger tag costs		$18000	$18000				
Training costs	-						
Travel costs	-						
International flights	-	$400	$400				
Domestic flights	-	$400	$400				
Field work accommodation	-	$5000	$5000				
Sub-totals	$50,100	$24,800	$24,800	$1000			
TOTAL					$100,700		

Thesis Outline:

Chapter 1 – General Introduction

The aim of this thesis is to understand the movement ecology of oceanic manta rays (*Mobula birostris*). Key questions to address are:

1. What drives site fidelity in this pelagic species?
2. What is their main food source locally? How does this overlap with local reef manta (Mobula alfredi) populations?
3. What foraging behaviours does this species use? What are the energy requirements of these behaviours?
4. What drives differences in diving behaviour through the area and differences between sexes?
5. How is climate change impacting food sources and foraging behaviour of oceanic manta rays?

To explore these questions, I will be researching the population of oceanic manta rays in eastern Indonesia in the area known as the Birdshead Seascape. The population consists of approximately 2000 individuals which show high site fidelity in the region [98]. Research will include analysis of satellite tag telemetry including location, temperature, dive behaviour, mixed layer depths and maximum dive depths. I aim to augment this with accelerometer data and additional novel data. The research program can be divided into stages:

Stage 1. Literature review
Stage 2. Analysis of existing data
Stage 3. Development of data collection plan with new tag advances, deployment and collection of tags.
Stage 4. Analysis and interpretation of data
Stage 5. Write-up and publication of chapter
Stage 6. Writing of thesis introduction and conclusion around these data chapters.

Data Chapters:

Data Chapter one

Research question: What function do super-deep dives (>300m) serve for oceanic manta rays?

Rare super deep dives have been recorded in almost all pelagic predators. Many theories exist for the function of these dives, this chapter will investigate the dive profiles and potential reasons for these super deep dives. This chapter will use existing satellite tag data in collaboration with researchers in Peru and New Zealand to identify the function of super-deep dives.

Data Chapter two

Research question: What are the drivers of vertical movement behaviours in oceanic manta rays?

I will investigate the vertical movement behaviours of oceanic manta rays to determine what conditions impact these behaviours, including: seasonal changes, association with the mixed layer and thermocline, the deep scattering layer, diel patterns of vertical movement and thermal optimum. This will be based on satellite-transmitted summaries from pop-up archival tags and towed satellite tags, as well as high-resolution time series of five recovered satellite tags.

- Analyse diving records of 5 recovered MiniPAT tags. (4 female, 1 male. Total 883 days deployment. Depth, temperature and light level recording time interval of 4 tags is 5 seconds and 1 tag at 15 seconds)
- Analyse satellite transmitted histogram diving records of 5 non-recovered tags: 2x MK10 PAT (both males) and 4 MiniPAT (3 female, 1 male)

- Potentially use cluster analysis to determine different diving patterns throughout deployment periods, including differences between sexes.
- Investigate relationships between diving behaviour and mixed layer, thermocline, deep scattering layer and how these change through the two major seasons in the Birdshead Seascape
- Investigate thermal optimum for oceanic manta rays

Data Chapter three

Research question: What are the drivers of horizontal movements in Oceanic Manta Rays?

I will investigate oceanic manta ray seasonal movements, home ranges, inter-annual variability, association with fronts and productivity hotspots and interactions with fishing activities and marine reserves. This will be based on deployments of pop-up archival tags on oceanic manta rays at key aggregation sites in Raja Ampat.

- Analyse movement tracks of previously deployed tags: 2 mk10 PAT, 9 miniPAT
- Look for correlations with productivity hotspots - Chl-a, SST, upwellings and seasonal changes between monsoons.
- I plan to compare movement tracks with a metric of local fishing activity using boat AIS / tracking systems
- I will also look at usage of marine protected areas by oceanic manta rays and how they might be expanded to increase protection
- I will examine differences in horizontal movements between sexes

Potential differences in movement behaviours might result in different survival rates between the sexes e.g. white sharks [180]. Philopatric behaviours, as shown by reef manta rays, are often sex specific. Female philopatry has also been observed in other marine megafaunas like reef sharks, white sharks, sea turtles, whales, and sea lions [92], [181]–[185].

Data Chapter four

Research question: What behaviours and their functions can be identified from on biologger tag data, and how what can we learn about movement costs from these?

I will investigate the energy saving and foraging efficiency strategies used by oceanic manta rays, highlighting food encounter and feeding techniques vs energy expenditure through the use of diary / biologger tags (potentially CATS tags, Critter-Cam or miniature ADL's from other companies) including accelerometers and gyrometers, tags would be deployed over different monsoon seasons to cover differing SST's found throughout the year.

- Deploy and analyse findings of biologger tags on oceanic manta rays
- Investigate oceanic manta metabolic rate. Compare differences between two main seasons as SST's vary
- Investigate movement efficiency (potential 'sleep' behaviour (low vertical velocity gliding) down to thermocline on some tags). Compare efficiency of different foraging techniques (surface ram-feeding, constant depth filtering, summersault feeding?)
- Investigate predator (or perceived threat) avoidance behaviours from high resolution dive profiles. Potential predator avoidance e.g. fastest movement (28m in 5 seconds = 5.6m/s vertical velocity). Correlate location at times of 'threat', possible anthropogenic cause (tourist / fishing / cargo boats) or predator hotspots?

- Breaching behaviours – some tags appear to breach a lot more than others

Chapter 3 – Conclusion chapter of PhD (thesis by publication)

Summarise the main and significant points and findings in the study from each chapter. Answer the research questions, concisely summarising the results and practical contribution of the study. Highlight any study limitations, and possible future study areas.

End of Research Proposal

Literature Review:

Movement is one of the most basic functions of animal life, yet the causes of movement can be some of the most complex systems on the planet [1]–[3]. Whether a single cell amoeba or a highly intelligent social animal, movement is vital to the survival of the individual and the species [4]–[7]. Broken down into its most basic element, movement means survival, it is the fundamental behaviour by which animals access resources (including conspecifics) or avoid risks [8], [9]. Whether an automated 'fight or flight' response or a decision carefully thought through over a period of time in order to gain the highest level of reward – e.g. food, status or safety – the end game is the same; to survive and ultimately reproduce [10]–[12]. The movement choices of an individual therefore impact individual fitness, gene flow, community structure and species density and distribution [9], [13], [14]. Movement however is not without cost, studies of locomotion of all types reveal a common theme, moving expends energy and time and must therefore have benefits which outweigh the costs in order to be worthwhile [1], [3], [8].

The study of movement ecology has developed many theories including 'optimal foraging' and 'marginal value', among others, which help predict how an animal will behave in a given situation [15], [16]. If we think in terms of fitness, there must be an overall positive outcome to the individual, be this resource aggregation, survival or reproduction [9], there are however many assumptions which are made in such theories which can leave results questionable [17]–[19]. As we are unable to understand the thought processes of an individual, we are limited to making assumptions which later can be disproven or only apply given a certain set of conditions [18], [19]. As a general rule, migratory species which rely on long-distance movements must minimise cost per unit distance (e.g. European Eels [20]), often using intermittent locomotion to lower energy demands [21] (e.g. Arctic Terns & Christmas Island Red Crabs [22], [23]) as fitness gains are generally low or non-existent while migrating (e.g. Leatherback Turtle migrations [24]), while non-migratory species tend to have higher energy cost per unit distance [3], [25].

Costs of movement:

The cost of locomotion per unit distance also varies greatly depending on the medium in which you move. At sea level, air density is 1.2 kgm^{-3}, water density approximately $1000kgm^{-3}$ and soil in the range of 1800 – 2300+ kgm^{-3}. It is not surprising then that the longest recorded migrations are in the least dense medium; the Arctic Tern travels 90,000 km from pole to pole yearly [26], [27]. While the increased density and therefore viscosity and resistance of water increase the energy cost of locomotion, the benefit of not having to support body weight while neutrally buoyant helps minimise the energy costs of locomotion [28] and has facilitated the evolution of the largest animals on earth. The thousand-fold difference between air and water density is a significant barrier which prevents most organisms from living in more than one of these environments as cost of locomotion exceeds the benefits [3], [29]. Those animals which spend significant time in more than one medium typically have evolutionary traits to minimise cost (e.g. webbed feet in Diving Ducks [30]), in other cases animals may save energy by moving from one medium to another temporarily such as dolphins leaping while at high speeds [31], however in highly social animals such as dolphins, leaping is also believed to be a form of both communication and play, and the energy saved may simply be an unintended by-product of these behaviours [32]. The most cost-effective locomotion is typically found when animals are confined to, or specialise in a single medium such as European Eels [20] and Arctic Terns [22], [26].

A secondary yet significant note on costs of locomotion is that a variety of marine species must move in order to breathe. This obligatory ram ventilation makes quantifying movement efficiency more challenging as data on oxygen minimums, thermal considerations and prey density thresholds are often unavailable, however with advances in technology these data are becoming the target of current research in the movement ecology field [33].

Migratory behaviour:

Migrations are driven by an individual's need to maximise overall fitness. Ecological conditions – primarily the seasonality of food availability – are key in whether an animal chooses to migrate rather than being resident [34]. Group migrations, whether in herds, schools or flocks, have additional costs including sophisticated behaviours (communication and leadership), competition for resources and mates and increased risk from infectious disease [35], [36]. The benefits to fitness, in particular, the increased protection from predators for an individual and its offspring must outweigh the costs [37]–[39]. Humans were migratory until as recently as 12,000 years ago when domestication of wild animals and plants began, or arguably the reverse, as certain plants managed to domesticate humans into monoculture farming on large scales [40], [41]. As humans settled, technology rapidly developed and today we can monitor live migrations of almost any animal remotely with satellite technology, both terrestrial and marine (e.g. wildebeest and manta rays [35], [42]).

Anthropogenic Impacts:

Technological advances:

The invent of advanced technologies has allowed the Anthropocene, an era in which humans have hugely accelerated natural extinction rates into what is being termed the Earth's sixth mass extinction event [43], [44]. Technological advanced in farming and fishing and our ever-expanding reach over the earth means that no species is safe from exploitation. Even charismatic megafauna species are not safe from being the target of mankind; rhinoceros, tigers, whales and panda have all been targeted [45], their charisma has often brought unwanted attention as they can be hung on a wall, draped as a rug on the floor or eaten at a wedding party [46]. New tracking technologies allow the geolocation of species [47]–[49] and targeted harvest of every individual in a group, marine species in particular have been targeted in this manner, with so-called motherships allowing catch vessels to stay fishing at sea in remote areas for extended periods [50]. The Anthropocene has increased the costs of movement for almost all species on earth, whether through increased global temperatures, pollution, loss of habitat, ocean acidification, expansion of oxygen dead zones, targeted or incidental catch or otherwise [51]–[53], unfortunately without any long-term baseline data, we struggle to validate models and research outcomes, particularly where different interpretations of baselines can be made (e.g. [54]–[56]).

Fisheries:

Since 1970 the number of fisher folk has more than doubled, and approximately 90% of these are located in Asia [57]. The most prominent threat to cartilaginous fish is overfishing [58]. With so many fishers exploiting the same resources – particularly in relatively low income countries [59] – species which migrate across country (jurisdictional) borders or which are found in remote areas are often ignored due to the difficulties of remote and international / interjurisdictional management [60], [61]. In other cases, a species may be protected in one country but fished to near extirpation while in another countries' exclusive economic zone (e.g. *M. birostris* population extending along the Peruvian and Ecuadorian coastlines. There was a 5-year gap between Ecuador protecting the species and Peru then following suit, however Peruvian fishermen continue to harvest manta rays for their gills [62]–[64]). If fishing pressure continues to increase on mobulid populations as is being witnessed in the Philippines, India, Mexico and Mozambique [65]–[68] it is highly likely there will be more fisheries-induced extirpation events (e.g. Lembeh Strait, Indonesia [69]). Whether migratory or not, the results of exploitation of mobulids are clear, without the implementation of local, national and international management strategies where appropriate, the chances of species survival are very low [70]. Unfortunately, the lack of studies on population dynamics, including abundance and distribution of many elasmobranchs, and in particular *Mobula* rays, has allowed large scale fisheries to operate without restrictions for decades, gradually reducing population viability to the point of potential extirpation [33]. More recently species have been declared endangered due to ever increasing fishing effort yet year on year decreases in landings (e.g. [71], [72]).

Pollution:

Contamination is a primary stress factor in most marine organisms, whether mobile or not [73]. Cetaceans, sea birds and sea turtles [74]–[77] have all been shown to be under threat from increased in marine pollution, however there have been very few studies on the impact of pollutants on elasmobranch populations, a lot of which are apex predators and potentially under greater threat through bioaccumulation of chemicals [73], [78]. Filter-feeding mobulid rays are under increasing threat from microplastics and feeding hotspots have been shown to overlap with microplastic pollution hotspots [33], [79], [80].

Ocean acidification:

Carbon dioxide pollution threatens marine life in different ways, as CO2 levels increase, oceans become more acidic which has variable impacts on marine species [81]. In fast-swimming non-obligate ram ventilators there is a linear decline between increased swimming speed and blood CO2 levels [82] suggesting impacts may be negligible in these species. Rosa et al, [83] and Melzner [84] however, posit that obligate ram ventilators such as mobulids may be more susceptible to ocean acidification as increased CO2 concentrations in waters create a smaller differential between ambient and blood-carried CO2 levels, impacting swimming abilities as lactic acid will build up faster. Ocean acidification is of further concern due to changes which have been witnessed in feeding behaviours and activities in non-reef dwelling elasmobranchs [83], [85], where elevated CO2 appears to affect the electroreceptor systems which allow for food detection, taking up to four times longer in controlled conditions [83]. When coupled with decreases in zooplankton availability in increased CO2 levels [86]–[88] it is likely these factors will act synergistically increasing the costs of foraging for elasmobranchs.

Ocean warming:

As global ocean temperatures rise, we are witnessing a poleward shift of zooplankton away from the warm equatorial region [89]–[91]. Marine megafauna species are often philopatric to important aggregation sites, such as mating and pupping grounds [92]–[94], reef manta rays have recently been shown to return to nursery areas to give birth [95]–[97]. Shifts in prey distribution may force marine filter-feeders to travel further between foraging grounds and locations important to life history, impacting individual fitness or population viability [98]–[100].

As most elasmobranchs are ectothermic they try to maintain an optimum body temperature to maximise energy consumption. It is believed that thermal regulation in filter feeding species such as oceanic manta rays limits the both the duration and frequency of deeper dives during the daytime, this inhibits many species abilities to forage in the deep scattering layer where prey density is often as its highest. Stewart et al., [101] showed *M. birostris* exhibits strong associations with the thermocline, this is due to the diurnal descent of prey species to avoid predators and their inability to pass through this layer into deeper waters. In other studies, mobulids have been shown to migrate seasonally to cooler waters where prey are predicted to be more abundant [33], [63], [102]–[105]. As sea surface temperatures continue to increase, many marine species will likely reach the upper limit of their thermal range and be forced to change their behaviours to accommodate for this, whether this be a poleward or depth related shift.

Oxygen dead zones:

Increased temperatures, along with increased precipitation and eutrophication, all caused by anthropogenic impacts on the environment are contributing to a decrease in dissolved oxygen content in the oceans [106]–[109]. Current hypoxic zones are likely to expand into shallower water and new zones may form, particularly in coastal environments [107], [110]. This expansion of hypoxic zones is likely to compress the habitable range for species between this raised hypoxic floor and species' upper thermal limit in warmer in surface waters, while at the same time reducing habitat suitability for coastal nurseries (e.g. [106]). For many species, particularly mobulids, upper thermal limits have not been calculated, but simply assumed based on habitat selection through migratory behaviours (e.g. reef manta rays in Komodo [102]), numbers are frequently then cited in later publications as fact rather than assumptions, and may refer to prey species thermal preference rather than upper thermal limits of predators.

Predicted anthropogenic impacts:

The synergistic impact of predicted shifts in prey distribution, lower prey density, increased size of hypoxic zones, microplastic and chemical pollutions, fisheries impacts and thermal constraints will likely lead to further increases in species extinction rates, as we are currently witnessing in what is now being termed the '6th mass extinction event' of our planet [43], [111]. The speed at which environmental change is occurring is significantly faster than any climate change actions we as a species are currently taking and as such there is an ever-increasing threat to many marine megafauna species.

Protected Areas:

Marine protected areas (MPA's) have been implemented to protect fish and coral species around the world with varying degrees of success [112]–[115]. In order to be effective MPA's must cover a large enough area and be actively managed to prevent illegal poaching [115]–[118]. MPA's also have limited usefulness for migratory species or species with large home-ranges such as elasmobranchs [119]–[121]. Further to this, species which may be highly migratory in some areas may have very small home ranges elsewhere due to local oceanographic conditions [122], meaning species-specific management strategies are may not be applicable in multiple locations.

Most existing research and therefore MPA area development has revolved around attempts to evaluate the value of an area to a species based on intensity of use data [9], typically garnered from surveys or tag data, however there is little research focusing on valuing a locations importance to an individual, yet an individual may choose to move between areas based on a perceived fitness value of each area. Being able to score the value of an area will improve our ability to protect areas vital for species survival, not just what we perceive as high-use areas [9]. Conservation strategies must take appropriate local, national and international approaches to be effective for a single population which migrates across country jurisdictional borders [122].

Tracking Movement:

Until the recent development of archival tagging solutions, it was very difficult to determine what species were doing after leaving the surface or shallow waters. Stomach content analysis is commonly used to identify what a species may target while at depth (e.g. whale sharks [123] mobulids [124] and various sharks [125]) however this requires access to dead animals, prompting animal ethics concerns. While advances in technology allow us to view the movement patterns of animals over a period of time, there are difficulties incurred and assumptions which must be made in order for these technologies to work. A large number of tracking studies on marine life use popup archival tags (PATs), and the vast majority of these tags use a combination of light level recordings, known locations, maximum daily depth, sea surface temperature data, bathymetry data and a user input of average animal speed. These data are then processed, often in tag manufacturer bespoke software packages (e.g. Global Position Estimate 3 (GPE3) created by Wildlife Computers) to provide an output of daily location with percentage confidence interval, providing a 'most likely track'. There is a huge potential for error and interpretation bias in the movement of these animal tracks. On top of this, the remote capture of data from these tags presents further challenges regarding the contextualisation of such data; researchers attempt to interpret the how and why an animal moves or uses a location without having adequate information on the interest of that animal in any particular area [9].

Further to the potential processing and interpretation bias, a number of constraints are present that limit the usefulness of tracking studies. A large number of studies are the first of their kind and involve a single animal, while these studies may be proof of methodology and provide initial movement data, with no previous data to compare with, erroneous data or individual variation can be considered normal [126]. Even for studies where previous data exist, there may be no accurate estimate of animal speed, in these cases, estimates are often used from research on different species, potentially limiting the accuracy of tracks produced (e.g. oceanic mantas [42]). Slow movement speeds can also impact the ability of processing software to produce accurate tracks [127]. Furthermore, accuracy and detail of bathymetry charts are frequently limited, impacting the accuracy to which movement tracks can be drawn. Studies undertaken around the equator also suffer from larger spatial errors in latitude estimated from light-level based data [128], [129]. For these reasons, it is important to have sufficient sample size to be able to answer the questions posed in a study [126].

Vertical migrations in marine life:

A key factor in establishing reasons for horizontal movement is the accompanying vertical movement behaviour. An animal may appear to stay in a very small area of the ocean when looking at geographical position only, but may be migrating vertically throughout the day in search of food, exerting significant movement costs in a 3-dimensional plane. While studies may focus solely on horizontal movement, typically to examine the extent of a population's distribution, these studies often lack detail on the associated diving behaviours needed to explain horizontal movements (e.g. [130], [131]). Vertical movement is vital to the foraging strategies of most elasmobranchs, and in particular filter-feeders. Most zooplankton migrate to colder, deeper waters at dawn and return to warmer shallow waters at dusk, this diel vertical migration behaviour is believed to represent predator avoidance through avoiding higher light levels associated with visual predators and the rising sun [132]–[137] it is also witnessed around the full moon and higher lunar illumination [64], [138], [139]. Zooplankton predators must therefore make a cost-benefit analysis whether to adapt feeding techniques to target other prey species during daylight hours, wait until prey returns to shallow waters or follow the prey to depth, likely through the thermocline to the deep scattering layer, where temperatures can be up to 20 ^{o}C lower than surface waters.

Andrzejaczek et al., [140] list vertical movement concerns which must be optimised in gill-breathing animals of the epipelagic: food encounter rates, energy expenditure, predator avoidance and searching for mates. Maximising each of these concerns should ensure high individual fitness but species are confined by their physical limitations such as thermal range and oxygen minimums which can impede preferred behaviours. Zooplankton feeding obligate ram ventilators in particular have energy expenditure concerns as they must maintain a minimum velocity yet prey species are no longer available at the same prey density.

Four major types of vertical movements were highlighted after a review of 120 studies targeting sharks, rays, tunas, sunfishes and billfishes: swimming at a relatively constant depth, single dives, oscillatory swimming and diel vertical movements [140]. Their analysis also revealed a minimum tag deployment of approximately 100 days is required to document ‘very deep dives’ with longer tag deployments providing greater opportunity to record changes in vertical movements over larger temporal or spatial scales (e.g. seasonal diving changes in movement of blue sharks [141]). While they separate dives into these four major types, they note the great variability that occurs within movement of gill-breathing fishes and how high-resolution data sets show multiple vertical movement behaviours can be used within a single dive as an animal reacts to changes in the ambient environment [140].

Issues with movement data:

Many theories exist within movement ecology to help explain observed behaviours, each with a unique set of benefits and disadvantages based on assumptions which must be made. Determining the drivers of movement is a multi-faceted problem in the marine environment as visual confirmation is typically not possible. Recent advances in tracking solutions are helping to reduce common problems incurred in studies (namely author bias, observer influence and partial observability) [9]. Relatively few hypothesis-driven studies have been undertaken, the general trend in literature is still ‘discovery’ papers lacking analytical approaches, however as the body of work on horizontal and vertical behaviours of elasmobranchs grows, it is likely so will the number of analytical studies [142].

Many satellite telemetry studies attempt to derive and explain intensity of use metrics using correlations with remotely sensed data such as satellite derived sea surface temperature and chlorophyll-a (Chl-a) concentrations. These remotely sensed data are limited by the large spatial scale on which they are recorded (typically 40-50 km [143] but potentially down to 3km [144]) and local variations caused by bathymetry or other oceanographic variables are averaged out of consideration [145]. For example, studies on zooplankton feeders highlight lag-times or little correlation between Chl-a concentrations and animal movement, suggesting zooplankton prey concentrations are not closely related to Chl-a (e.g. oceanic manta rays [98]) as such, paired data collection involving plankton tows can help explain observed behaviours (e.g. correlation of feeding and prey density [146]), however, this is not possible over large spatial and temporal scales. Alternatively, network theory may be more useful than intensity of use for certain species as centrality measures can identify important areas even if animals do not spend a disproportionate amount of time there. Vital corridors between locations may have low intensity of use but without them an animal may be prevented from accessing a resource in a specific area [147].

When creating conservation and management objectives it is vital that the data used accurately represent actual use patterns of the animal. Paired data studies reduce the level of uncertainty in such movement ecology studies, studies should be designed to collect data from additional, or multiple sensor tags to support findings. These include biologger tags collecting accelerometry or magnetometer data, acoustic tags, animal borne video, physiological monitoring and environmental monitoring [9]. Physiological biologger tags or animal-mounted cameras provide huge insight into observed movement behaviours, yet often assumptions must still be made regarding why it happened when it did [148]. We must take into account a variety of unknown variables such as interspecific and intraspecific competition or a risk of predation which may not be determinable even from paired data.

Regional differences within a species:

It is important that we treat each population of a species as a separate entity as they are under completely different oceanographic conditions. Management decisions based upon research conducted in another area may have minimal benefits to the species in another area and the research accuracy must also be taken into account. For example, Andrzejaczek [64] report data and observations from three popup archival tags deployed simultaneously in coastal Ecuador waters where oceanic manta rays are hunted while at the surface. The data show a median tag depth of 5m +- x, and considerable time spent in surface waters. However, Burgess [63] shows significant variation in C and N isotopes and high prevalence of mesopelagic zooplankton in the diet of the same population. Coupled with the very short-term deployments of the three reported tags and an apparent transition to deeper diving immediately after moving off the continental shelf suggests that data collected may be seasonally or location biased and not representative of long temporal scale behaviours. In comparison, median tag depth from five archival tags (with cumulative 883 days' deployment) on oceanic manta rays around western Papua, is significantly deeper at 60 +-m (Beale, C. unpublished) and the majority of their time is spent in non-coastal waters along the edge of an ocean trench.

Thermal considerations & temperature preferences:

Zooplankton feeding ectotherms must maximise diving efficiency in cold waters, often performing a series of fast vertical dives to depth where they target high prey-density patches in deep waters (e.g. whale sharks [149], reef manta rays [150], Chilean devil ray [151], oceanic manta rays [101]), before rapidly returning to the warmer surface waters to rewarm the body [152]. In order to investigate vertical migrations within a species, it is necessary first to establish central or baseline depths [153], variations around this can then be used to classify different patterns of vertical migration [140], [153] and create a definition of a dive for an individual. These baseline depths however may vary dependant on spatial and temporal scales within and across populations of the same species. The use of mesoscale eddies by blue sharks [154] highlights how individuals will opportunistically use local oceanographic features to their advantage to maximise individual fitness.

While ectotherms are restricted by thermal regulation, the thermal boundaries of many species have yet to be investigated or in some cases have simply been assumed by lack of presence. Dewar [102] for example assumes that as no reef manta rays were observed above 29 ^{o}C in her study that 30 ^{o}C must be the thermal limit for the species. She does not take into account that this may be the thermal limit for target prey which shift in correspondence to Indo-Pacific monsoon seasons and prevailing currents, and thus the mantas may simply have followed their food source. This possible thermal limit has since been cited in various publications without question [67], [155], [156] yet reef manta rays are regularly seen feeding in 30 ^{o}C water in Raja Ampat, Indonesia (personal observations).

Nakamura [157] provides contrast to the theory of thermal regulation, whereby body mass was the controlling factor of body temperature, regardless of whether the species was endothermic or ectothermic. Whale sharks in the study showed stability of body temperature whereby muscle temperature changed substantially slower than ambient water temperature. Potentially the large body mass of certain mobulids such as the Chilean devil ray and oceanic manta ray may facilitate the records of dives to bathypelagic depths and longer periods in cold waters as body temperature may be more stable [151].

Aggregations of Mobulids:

The general consensus within mobulid researchers is that mobulid rays aggregate to target seasonal increases in productivity and will move considerable distances if necessary, to reach productivity hotspots [33], [104], [105], [156], [158]–[160]. These seasonal changes are frequently related to seasonal changes in monsoons. In some areas this requires large scale horizontal movements to take advantage of specific oceanographic conditions such as increased phytoplankton productivity leading to increased zooplankton prey abundance [98], [159], [161], which can be further concentrated by interactions between monsoonal winds and ocean currents (e.g. Maldives [104]). While in other areas, where oceanographic conditions naturally provide two seasonal distributions of high plankton abundance within close proximity to one another, much smaller migrations are witnessed (e.g. *M. alfredi* in Komodo National Park [102]). Elsewhere, New Zealand experiences seasonal observations of oceanic manta rays in the austral summer [103] after which they have been recorded to migrate 2500 km to Fiji (Erdmann, M. personal communications). Burgess [63] and Beale [98] both show significant aggregation of oceanic manta rays during ENSO events which alter physical processes and biological production in their study areas, likely driving an increase in zooplankton food availability.

In order for feeding aggregations of mobulids to occur, a critical prey density threshold must be met [33], this is calculated as the point when energetic costs of feeding are balanced or outweighed by energy gained, as is seen in many filter-feeding marine life (e.g. basking shark [162], whale shark [163], reef manta ray [164]) but this value has not yet been calculated for many species of mobulids including oceanic manta rays. The difficulty in doing so stems from their apparent targeting of mobile zooplankton prey with unreliable occurrence in shallow waters, along with the logistical challenges of sampling.

Extraordinary deep dives:

Andrzejaczek [140] revealed that while vertical movements to over 500 m are rare, they are found in almost all of the 41 species in their study. Swordfish and whale sharks were both recorded diving to over 1900 m and potentially deeper but records were constrained by tag design. Thorrold [151] has recorded Chilean devil ray dives to 1900 m, Bonfil [165] recorded white sharks diving to 980 m and oceanic manta rays have been recorded to 1200 m (Beale, C. unpublished data). These rare extraordinary deep dives appear a to be a common theme yet there is still no accepted explanation for their occurrence. Various possible reasons exist including: predator avoidance, thermoregulation, navigation, removal of parasitic organisms and prey detection and acquisition however none of these theories have yet been widely accepted among the scientific community. All of the above are valid reasons for individuals to undertake deep dives, but the profile of the dive is likely to be different depending on the initiating cause.

Many species of elasmobranchs have shown highly directional movement while in the open ocean, it is theorised that they may be using the earth's magnetic field directly or indirectly sensing it through the electro-sensory system [166] to maintain navigational headings along particular lines (e.g. whale sharks [167], scalloped hammerheads [168], leopard sharks & round stingray [169] and blue sharks [141]). When considering the distances involved, the geomagnetic field of the earth is likely the only continuously available source of directional information and while the particular methodology the animals use may be different [170], the alternatives such as water temperature, currents, and scents [171], [172] are highly variable within the water column and therefore more likely to be limited to shorter-distance navigation. One potential alternative for longer distance navigation is using ambient noise through the electro-sensory system [170], [173], [174]. Various species of shark have been attracted to acoustic signals transmitted underwater [175]–[177] and could potentially navigate using directional hearing [178] to locate distant reefs which have distinct sound signatures [179].

Navigational dives appear the most likely reason where individuals may use vertical gradients in magnetic and electric fields to orient before resuming shallow dive behaviours. Various elasmobranchs including Scalloped hammerheads [168] and oceanic manta rays [140] are thought to use these magnetic fields given off by seamounts or the sea floor to navigate large distances between areas. While this theory carries weight, not all extraordinary deep dives precede large scale navigations and studies should be designed to further test this hypothesis. Nakamura [157] indicates that individuals with larger body mass have an increased ability to withstand the temperatures experienced during these dives, therefore they are potentially more likely to undertake these dives and then navigate larger distances in open water.

Dive behaviours of oceanic manta rays are still relatively unknown, while there have now been dozens of archival satellite tags deployed on manta rays, few have been on oceanic mantas and very few have been recovered post-deployment, providing high-resolution (3-5s) time interval data. Even with this high-resolution data, without paired data we cannot easily ascertain why the animal moves in the way it does and we remain limited in our understanding of the forces driving the recorded behaviours. Given the increased costs of certain movement behaviours, assumptions must be made to explain choices, particularly regarding prey density, as we attempt to explain behaviours with literature from other species.

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